Chapter 18

The American Herpetofauna and the Interchange

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1. Introduction

Amphibians and reptiles are treated together in this chapter because, overall, they have similar and complementary zoogeographic patterns with respect to the faunal interchange of the Americas. We are each interested in amphibian and reptilian zoogeography, but because we are not systematic specialists in both groups, we have written this Chapter together. The basic amphibian data are discussed by Heyer and the reptile data by Vanzolini.

This chapter depends heavily on distribution patterns and their interpretations. Therefore, it is important at the outset to present our viewpoint on the importance of modern distributional patterns indicating the geographic origin and/or past distributions of groups. We are extremely cautious in interpreting the data in this way. An example illustrates the

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need for caution. The coral snake genus *Micrurus* barely enters the United States in North America, which would seem to indicate that *Micrurus* is a recent invader of the southern United States. However, Tertiary climates in North America were milder and Tertiary *Micrurus* fossils are known from Nebraska. Thus, rather than having a pattern of recent invasion in North America, *Micrurus* most likely demonstrates a pattern of retraction and impoverishment.

A final note on procedure is that we examine details and provide documentation, according to our judgment, only as appropriate.

2. Definition of the Faunal Assemblages

We follow, with minor adjustments, Savage's (1982) concept of faunal assemblages in the Americas. These, as most major faunal units, occupy distinctive land masses.

The North American Faunal Assemblage inhabits continental Canada, United States, and the Mexican Plateau region to the Isthmus of Tehuantepec. Zoogeographically, the herpetofauna of the Mexican lowlands on either side of the plateau is a mixture of both the North and Central American herpetofaunas. Because of this, we ignore for our purposes the Mexican lowland fauna north of the Isthmus of Tehuantepec.

The Central American Faunal Assemblage inhabits the region from southeast of the Isthmus of Tehuantepec to northwestern South America, including the Isthmus of Panama and the Chocoan region of western Colombia and northwestern Ecuador. The herpetofaunas of lower Central America and the superhumid trans-Andean forests of Columbia and Ecuador are so similar (Savage, 1982) that for our purpose they are part of the same faunal assemblage. The zoogeographic consequences will be touched upon later but are not particularly interesting relative to the interchange. The South American Faunal Assemblage inhabits the southern continental land mass east and south of eastern Panama, excluding the Chocoan regions of Colombia and northwestern Ecuador.

The West Indies herpetofauna is not an integral part of our discussion and is included only when it participated in an exchange between North and South America.

3. Nature of the American Herpetofauna

Although the familial limits of American amphibians and reptiles are still being delineated, most families have been systematically stable for several years. For comparability, we follow Savage's (1982) recognition of family units.

There are three families of caecilians in the Americas. Two of these occur in South America; one family occurs in Central and South America.

Six of the seven families of American salamanders occur only in North America; one family occurs in North, Central, and South America.

Two of the 14 families of American frogs occur only in North America. One family of frogs is restricted to Central America and four occur only in South America. Two families occur in both Central and South America, and five frog families occur in North, Central, and South America.

The Family Crocodylidae occurs in North, Central, and South America.

Eight families of turtles occur in the Americas, three of which are found in North, Central, and South America. One family occurs in North and South America. The remaining families occur in only one area: one family each in North America and Central America, and two families in South America.

Three of the twelve families of lizards and amphisbaenians of our study occur only in North America. One family is restricted to Central America. One family occurs in North

and Central America, one in Central and South America. Six families occur in North, Central, and South America.

Six of the ten families of snakes occur in North, Central, and South America. One family each is found only in Central and South America, while two families occur in both Central and South America.

As Savage (1982) points out, the herpetofauna of Central America is characterized by a high degree of endemicity at the species, species-group, and generic levels. This endemic Central American fauna was ultimately derived from both North and South American stocks, with a much stronger South American influence. We do not repeat Savage's (1982) analysis of the origin of current zoogeographic complexities of the Central American fauna, but rather refer the interested reader to his work.

Our interest is to examine those portions of the American herpetofauna that are shared between North and South America and evaluate what role the Pliocene land bridge had, if any, in their dispersals from one continent to another.

4.   The Amphibians of the Interchange

There are five amphibian families that occur in both North and South America that we examine: the salamander family Plethodontidae and the frog families Bufonidae, Hylidae, Leptodactylidae, and Microhylidae.

4.1.   Family Plethodontidae

The ancestors of the tropical plethodontids occurred in North America (Wake and Lynch, 1976 and references cited therein). The radiations of salamanders from the North American ancestral stock occurred along and dispersed down the upland areas of Central and northern South America (Wake and Lynch, 1976). Two genera occur at present in continental South America: *Bolitoglossa* and *Oedipina*. *Oedipina* has a typically Central American distribution, is found only in the Chocoan region of South America, and is of no further interest here. The genus *Bolitoglossa* has a rather broad distribution in Central and South America and is represented by a moderate species radiation in South America. The South American *Bolitoglossa* were derived from a Central American radiation and did not derive directly from North American plethodontids (Wake and Lynch, 1976).

South American *Bolitoglossa* have often been used as an example of a group entering South America after the Pliocene land bridge was formed (e.g., Brame and Wake, 1963). The reasons for this conclusion were the virtual certainty that the bolitoglossine salamanders radiated in Central America from a stock ultimately derived from North America and that the South American radiation was much smaller, hence reasoned to be younger, than the Central American radiation. Brame and Wake (1963), although postulating the land bridge route to South America, suggested that multiple invasions were involved within the genus *Bolitoglossa*.

Since the benchmark work of Brame and Wake (1963) on South American salamander systematics, it has become clear that the South American radiation is more diverse than previously thought and that its full extent is still not determined. The following lines of evidence suggest, but are not conclusive, that *Bolitoglossa* entered South America, from Central America, prior to the formation of the land bridge. There are two species groups of *Bolitoglossa* endemic to South America and two more that have a major representation in South America with a minor representation in Central America (Wake and Lynch, 1976). The distinctiveness of these lineages suggests they developed in South America and species

group differentiation probably would evolve over a longer time period than that available since the completion of the land bridge. Two salamander species, a *Bolitoglossa* and an *Oedipina*, occur on Isla Gorgona (Wake and Lynch, 1976), a near-oceanic island 56 km from the west coast of Colombia. Both species also occur on the mainland and the same species of *Bolitoglossa* occurs on Isla de Colon, Panama. Plethodontid salamanders also occur on the Channel Islands off the coast of California (e.g., Brame and Murray, 1968). Plethodontid salamanders thus are capable of island hopping and may have entered South America via this dispersal means prior to the formation of the land bridge. Finally, preliminary estimates of genetic relationships among Central and South American *Bolitoglossa* are most consistent with many South American lineages and even some recent species existing in South America prior to the establishment of the Pliocene land bridge (Hanken and Wake, 1982). Although the data are not conclusive, the weight of the present evidence favors *Bolitoglossa* entering and radiating within South America prior to the formation of the Isthmian Link.

4.2. Family Bufonidae

The bufonids are widespread throughout most of the world except for the Australia–Papua New Guinea area (*Bufo marinus* now occurs in Australia by introduction). While the relationships between the New and Old World bufonids are not known with certainty, the New World bufonids represent a single lineage, originating in South America (Blair, 1972; Maxson, 1984). The genus *Bufo* is the only bufonid lineage to penetrate North America. There are several distinct species groups of *Bufo* in North America, suggesting that *Bufo* arrived in North America long prior to the establishment of the Isthmian Link. The North American *Bufo* species groups were derived from the Central American, rather than South American, species groups of *Bufo* (Maxson, 1984). Microcomplement fixation data of albumin suggest that: (1) *Bufo* arrived in Central America from South America in the early Oligocene and underwent a modest radiation, and (2) lineages from the Central American radiation differentiated in North America in the middle to late Oligocene.

4.3. Family Hylidae

Frog systematists are currently debating whether the tree frogs of the Americas and those of Australia and Papua New Guinea belong to the same family. The pattern for the New World hylids is clear and parallels that of the bufonids. The New World hylids originated in South America and reached Central America long prior to the Isthmian Link connection, where they underwent a large radiation. The North American (–Holarctic) hylids, represented today by four genera, consist of a monophyletic grouping that has its closest relationships with lineages of the Central American hylid radiation and the separation of the North and Central American lineages dates to Eocene–Oligocene times (interpreted from data presented in Maxson and Wilson, 1975).

4.4. Family Leptodactylidae

There are two major unresolved (in terms of consensual acceptance by systematists) systematic problems in the leptodactylids. The first is, as with the hylids, whether the New World and Australian leptodactylids form a monophyletic group. This does not concern us, as it is clear that the New World leptodactylids originated in the ancient *Noth-*

ofagus forests of South America (Lynch, 1971; Heyer, 1975). The second problem is the unwieldy nature of the genus *Eleutherodactylus*, currently with over 500 species. At present, it is unclear whether the North American genera *Syrrophus* and *Tomodactylus* are most clearly related to Central American or South American lineages of *Eleutherodactylus*. There have been leptodactylid radiations in both Central America and the West Indies; the source stocks of those radiations ultimately came from South America. The extensiveness of those two radiations suggests ancient distributional events involving South and Central America and the West Indies. The leptodactylid fauna of North America is not extensive and derives from both the Central American (this is a supposition, not a conclusion based on data) and West Indian leptodactylid radiations. The *Eleutherodactylus* species occurring in Florida arrived there from the West Indies. There are four other genera of leptodactylids in North America, three of them endemic (*Hylactophryne, Syrrophus, Tomodactylus*). The species of the nonendemic genus, *Leptodactylus*, are clearly derived from the Central American leptodactylid radiation. It is likely that *Hylactophryne, Syrrophus*, and *Tomodactylus* are derived from one or more lineages of Central American, not South American, *Eleutherodactylus*. The North American leptodactylid radiation occurs primarily along the fringes of the Mexican plateau. Only members of *Hylactophryne, Syrrophus*, and *Leptodactylus* barely enter Texas and the southwest United States. The presence of a modest but well-defined leptodactylid radiation in southern North America suggests that the leptodactylids arrived well prior to the formation of the Isthmian Link but that the radiation has not extended northward as with the hylids and bufonids.

4.5.   Family Microhylidae

Microhylids occur throughout most of the world, with the greatest diversities in the tropics and subtropics. The greatest New World generic diversity occurs in South America, suggesting that land mass as the place of original radiation for the New World microhylids. Only one genus of microhylids, *Gastrophryne*, occurs in North America, with a Central American genus, *Hypopachus*, barely entering the Mexican Plateau of North America. *Gastrophryne* is most closely related to *Hypopachus* (Nelson and Guttman, 1973), so the North American microhylids derive from a Central American microhylid radiation and do not derive directly from the South American microhylids. There are no data with which to infer when microhylids reached North America, but our best guess is that this event took place well before the formation of the Isthmian Link.

4.6.   Family Ranidae

The family Ranidae is represented by only one genus in the New World, *Rana*. The other genera occur in Africa and Asia. Although the species groups relationships of *Rana* are currently being refined, the following statements best describe our current understanding of the dispersal of *Rana* in the New World. *Rana* entered the New World in North America, where the greatest New World species and species group diversity occurs today. There is a modest radiation in Central America, derived from the North American radiation. One species only entered South America, *Rana palmipes*. This species, a member of the Central American radiation, occurs from Mexico throughout Central America and northern South America including Amazonia and the northern Atlantic forest region of Brasil. Although there are no corroborative data other than distribution pattern, *R. palmipes* is an excellent candidate for entering South America sometime after the completion of the Isthmian Link.

Out of all of the islands throughout the Caribbean region, *R. palmipes* is known from only two, the continental islands of Guanaja (Islas de la Bahia, Honduras) and Trinidad (MacLean et al., 1977; Schwartz and Thomas, 1975). As *R. palmipes* occurs only on two islands that were connected at times with the mainland, the species probably reached these islands when they were connected with the mainland. Thus, *R. palmipes* entered South America, at the latest, prior to the last time that Trinidad became separated from South America.

5. The Reptiles of the Interchange

5.1. Crocodylia

Two groups (families or subfamilies) of crocodilians exist in the New World and are found on the three land masses.

South American alligatorines, although of ultimate North American origin (Sill, 1968), underwent a Tertiary radiation in the south and, at the time of interchange, occupied Central America as far north as Chiapas (*Caiman crocodilus chiapasius*). North American *Alligator* failed to spread to the south.

As to the crocodilines, two species from a Central American stock (Sill, 1968; Steel, 1973) are now distributed in northernmost South America.

5.2. Testudines

Eight families of land and fresh-water turtles occur in the New World. Five have mutually exclusive distributions: the Trionychidae are North American; the Dermatemydidae are Central American; the Pelomedusidae and Chelidae are South American; the Testudinidae, recent and fossil, are represented by distinct old lineages in North and South America (Williams, 1950; Auffenberg, 1971, 1974).

It should be noted that at least one trionychid made a landfall in South America during the middle Pliocene but did not become established (Wood and Patterson, 1973). It should also be noted that the South American subgenus *Chelonoidis* (genus of some authors) has been capable of colonizing the oceanic Galapagos archipelago and the West Indies (Williams, 1950), but has not been recorded from Central America.

Among the four other families, the Chelydridae of North America (Estes, 1970) entered the Chocó.

The Kinosternidae comprise four genera. The family dates with certainty to the Eocene in North America (Hutchison and Bramble, 1981). *Claudius* and *Staurotypus* are Central American. *Sternotherus* is widely distributed in North America, being recorded from the Lower Pliocene (Holman, 1975). *Kinosternon*, the most relevant genus in the present context, occupies the three land masses. It is present in North America, mostly at lower latitudes, one species (*flavescens*) reaching the Midwest and another (*subrubrum*), Long Island, narrowly along the coast. The fossil record goes no farther back than the upper Pliocene (Gehlbach, 1965). Given the excellent quality of the North American Tertiary record, we consider this date quite meaningful. In Central America the genus is highly diversified; it is plausible to consider this the area of origin of the taxon. The distribution in South America follows a familiar pattern. Two species (*dunni* and *spurrelli*) are Chocoan—doubts about the status of the former (Pritchard, 1979) are not relevant to the present

argument. The two other species range from Vera Cruz to the Chocó (*leucostomus*) and from Sonora to northern Argentina (*scorpioides*). Thus the latter can be said to have invaded South America from Central America.

The distribution of *K. scorpioides*, while not well worked out, is extremely interesting. It is one of the extreme generalists in the continent: as *Iguana iguana* (Trajano and Ghir-inguello, 1978), it is equally at home in the Amazonian rain forest and in the semi-arid caatingas of northeastern Brasil (Vanzolini *et al.*, 1980). This broad ecological valence and lack of major differentiation (only weak subspecies have been described) speak for the recency of the colonization.

The New World Emydidae are basically a North American group, but a clearly Central American element can be discerned. *Rhinoclemmys* does not occur in North America but is diversified in Central America, where it certainly originated within the time scope of the present argument. The taxonomy of the South American forms is far from satisfactory; there is no comprehensive review, and the subspecies concept has been applied with little if any consistency. However, it is safe to say that the usual Chocoan forms are present (*areolata*, *nasuta*) and that a complex of forms, or local populations, under the name *punc-tularia*, occupies northern South America to the limits of the Amazonian forest.

Most interesting among the emydids is the genus *Pseudemys*, specifically the *scripta* series (Williams, 1956). This is a complex of unevenly differentiated forms occurring from southern Virginia in the United States to northeastern Argentina. The distribution is con-tinuous from the northern limit to Venezuela, where the form *callirostris* is found. There is then an enormous gap—some 5000 km—to the area of the next recorded population, *P. dorbigni* (southernmost Brasil, Uruguay, Argentina). This pattern can be very simply in-terpreted as one of extensive immigration, followed by extinction, one outlier being spared. Among probable causes of extinction would be competition with the successful aquatic pleurodires of the families Pelomedusidae in Amazonia and Chelidae south of it. This would agree with Moll and Legler's (1971, p. 93) conclusion that *P. scripta* has not under-gone extensive adaptation to the tropical environment to which it is a newcomer. This is made still more attractive by the fact that *dorbigni* is sympatric with two species of the chelid *Phrynops*, but at the very edge of the distribution of the latter genus, 30 + degrees of latitude South, where *dorbigni*'s northern temperate inheritance would favor survival. However, there is another disjunct population of the *scripta* series in the Middle North of Brasil (Antenor Leitão de Carvalho, personal communication); until its circumstances are better known, sweeping ecological statements are best avoided. ·

As to the time of entry, contrary to what Moll and Legler (1971) believe, the pattern of rapid invasion followed by extinction is so similar to that of many mammal groups (e.g., horses, elephants, bears, camels, etc.), that a same time schedule seems probable.

5.3.   Sauria and Amphisbaenia

Among the twelve families of lizards and amphisbaenians that occur in the New World, three (Helodermatidae, Dibamidae, and Anniellidae) are North American; the Xantusiidae are essentially North American but extend in Central America down to Panamá; the Xe-nosauridae are purely Central American. The Gymnophthalmidae (a subfamily of Teiidae according to most authors) are Central and South American. Thus we shall be concerned with the Gekkonidae, Iguanidae, Teiidae, Scincidae, Anguidae, and Amphisbaenidae that occur on the three land masses.

The geckos are represented by three groups. The eublepharines are North American, with one genus, *Coleonyx*, reaching Panamá. The sphaerodactylines have a complex dis-tribution in Central and South America but do not occur in North America except as introduced species. Among the gekkonines the only genus common to the three land masses

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is *Phyllodactylus* (Dixon, 1964; Dixon and Huey, 1970). I believe (Vanzolini, 1968) that this genus, otherwise occurring in the Old World and specifically on the east coast of Africa, is not primarily involved in the Tertiary interchange, but has been rafted across the Pacific more than once, by different oceanic currents. This might also be the case of *Lepidodactylus lugubris*, which has been found several times on the west coast of the Americas, although human agency is very possibly responsible.

The Iguanidae are a complex and much differentiated family. Paull et al. (1976) present a dendrogram, based on osteology and karyotypes, that affords a convenient basis for discussion. Only two lineages are shared among the three land masses, the iguanines and the anolines. The former, a very old and distinctive lineage, has no genera common to North and South America; the South American *Iguana* is widely distributed in Central America.

The anolines are a South American group that shows a rich radiation in Central America and has used the West Indies to reach North America; *Anolis carolinensis* is derived from Antillean stock (Williams, 1969). I do not feel competent enough at present to deal with such a complicated group as the anolines and do not treat them further.

One North American lineage, the sceloporines, has spread into Central America south to Panamá but failed to enter even the Chocó. Given the striking morphological and ecological resemblances between the sceloporines and the South American tropidurines, one is led to think about the role of competitive exclusion in the shaping of this distributional pattern.

The basiliscine lineage is a Central American group that colonized the Chocó, entered Venezuela, but has failed to spread south.

The Scincidae are represented in South America by a single genus, *Mabuya*. According to Greer (1970), this is in a different subfamily than the North American *Eumeces* (which occurs in Central America) and *Neoseps*. It is in the same subfamily, Lygosominae, as *Scincella*, that occurs in North and Central America, but its closest relationships (intrageneric) are with African and Asiatic species, which are good sailors. In fact, the Atlantic archipelago of Fernando de Noronha has a *Mabuya* of apparently African relationships (Travassos, 1948).

The fossil history of the Teiidae indicates close relationships between North and South America in late Cretaceous and Paleocene times, with very modern-looking forms present in the late Cretaceous Lance Formation of North America (Estes, 1983). However, the Recent picture is very different. Only one genus is shared by the three land masses, namely *Cnemidophorus*. In spite of Savage's (1966) opinion, this is probably a South American group. The only recognized difference between *Cnemidophorus* and *Ameiva* is the presence (*Amevia*) or absence (*Cnemidophorus*) of a lingual sheath. This character has never been analyzed beyond the simple statement of presence or absence and, without any deeper inquiry into its taxonomic significance, the two nominal genera are better treated as a unit. Their combined distribution reaches deep into the open formations of South America and speaks for a southern origin. Both *Ameiva* and *Cnemidophorus* (sensu auctorum) are distributed over Central America, where they have speciated (Vanzolini and Valencia, 1965). *Cnemidophorus* has entered deeply into North America, where it shows a consistent pattern of parthenogenesis by hybridization.

North and South American anguids belong to different subfamilies (considered as families by some), the anguines and diploglossines, respectively. Both groups occur together in Central America, where the anguines have two endemic genera.

Finally, there are two purely North American genera of amphisbaenids, and five South American ones, without overlap or interpenetration. Central America is practically devoid of amphisbaenians, only one widespread South American species (*A. fuliginosa*) entering Panamá.

5.4. Serpentes

Ten families of snakes occur in the New World; one of them, the Aniliidae, does not need to concern us here, as it has been limited to South America during all of the Tertiary. The Loxocemidae, by many included in the boids, are Central American.

Anomalepidids and typhlopids are widespread in South and Central America and absent from North America. The former are probably a southern group, while nothing can be said of the Recent forms of the latter. Leptotyphlopids occur in the three land masses, but lack of taxonomic information does not permit a discussion of their movements in geological time.

North and South American booids are related only at the family level and have not undergone interchange. There is a definite Central American group, of which two genera (*Trachyboa* and *Ungaliophis*) have entered the Chocó. In addition to *Boa*, *Corallus* and *Epicrates* are clearly South American, and also are distributed in Central America, the former extending to Sonora. The Tropidophiidae, also a part of the boid complex, are South American and have reached the West Indies but not Central America.

It is not easy to discuss the large, complex, and little understood family Colubridae, especially in what concerns the relationships between South and Central America. However, it is possible to analyze the nine genera that are common to North and South America. One first pattern is presented by *Lampropeltis* and *Masticophis*. These are clearly North American genera, present in the fossil record before the time of interchange (Holman, 1979). They are not a component of the South American Faunal Assemblage as we define it, being found only in the northwestern corner of South America adjacent to Panamá. An apparent second pattern is that of genera of presumed Central American origin that have spread in both directions. These are *Coniophanes*, *Leptodeira*, *Drymobius* and *Oxybelis*; the first two named are assigned to Central America by Cadle (1984), based on molecular arguments. *Coniophanes* and *Drymobius* have relatively restricted distributions in South America, but the other genera are very successful and widespread. On the contrary, their extension into North America is in all cases limited. To this group possibly belongs the large genus *Rhadinaea* (Myers, 1974, p. 225, seq.).

The genus *Drymarchon*, monotypic, is a colubrine related to *Coluber* and so of putative North American origin. Its distribution, however, is not very clear. In North America there are two forms, *D. corais erebennus* and *D. c. couperi*. The latter, occurring in the southeastern United States, is disjunct from the rest of the species. *Drymarchon c. erebennus* occurs in Texas and northeastern Mexico and is continuous with the Central American populations. The species extends deeply into South America. Thus the systematic information does not fit well the distribution pattern.

Finally, *Tantilla* is abundant and well differentiated on the three land masses; its distribution pattern offers no apparent clues. Savage (1966) placed it in the Central American unit, without specific discussion. If this is true, the distribution may be considered of the *Coniophanes*, etc., type, with better success in North America.

There are two micrurid (to most authors elapid) genera: *Micruroides*, restricted to North America, and *Micrurus*, abundant and differentiated in Central and South America, much less so in North America. Savage (1966) considered the genus as "widespread tropical." Holman (1977) described and figured Miocene vertebrae from Nebraska that he felt unable to distinguish from either *Micrurus* or *Micruroides*. This supports Savage's assignment in the sense that, whatever its origin, the genus acquired its distribution before the time of interchange.

Among the crotalines, there is one genus (*Crotalus*) that, on the basis of distribution and fossil record (Holman, 1979), undoubtedly arose in North America. It is widespread and very successful in South America. Such diversification as has been found (Hoge and

Romano-Hoge, 1981) seems to have been determined by Quaternary climatic events. Its success in open formations (to which it is restricted) is remarkable in the face of the large number of equally successful *Bothrops* species in the open formations south of the Amazon.

The other northern viperid, *Agkistrodon*, occurs in Central America as far south as Costa Rica. *Bothrops* and *Lachesis* failed to enter North America, and there is no taxonomic basis for assigning either a South or a Central American origin to them.

6. Zoogeographic Conclusions

6.1. Interchange Was Via Central American Radiations, Not Directly between North and South American Herpetofaunas

No amphibian or reptile species, with one possible exception, that had its origin in North America has entered South America, and *vice versa*. The possible exception is the snake *Drymarchon corais*. Even this exception is suspect, as it is as likely that the species arose in Central America as in North or South America. In all but two trivial cases, the species that penetrated previously unoccupied land masses were Central American endemics, part of the extensive Central American herpetofaunal radiations. The two exceptions are the dispersals of *Anolis* and *Eleutherodactylus* into Florida from West Indian, rather than Central American, radiations. The interchange of amphibians and reptiles between North and South America has been through Central America, where local radiations have combined to act as a filter to the exchange.

6.2. Most Interchange Far Predated Formation of the Isthmian Link

There is growing evidence that much interchange took place at least at the time of the Cretaceous–Tertiary transition (Bonaparte, 1984). Although there are few fossil herpetological data available to document that most interchange took place before the formation of the Pliocene land bridge, we think the known cases of the trionychid turtle and coral snake represent a general pattern and are not exceptional.

For most of the herpetofauna, we must rely of interpretations of Recent distribution patterns. The *Pseudemys* example is extremely important here as a caution. Clearly, *Pseudemys* had a broad distribution in South America that now shows a pattern of retraction. How many other species may have had widespread distributions in South America (or North America), later to retract but without leaving fossils or isolated populations by which we would know of the former widespread distribution? With this caution, we believe the following represents the minimal situation.

There are only five examples of herpetofaunal distributional changes between North and South American stocks that took place owing to the formation of the Isthmian Link:

1. The extension of the Central American lowland fauna into the Chocoan region of northwestern South America, and *vice versa*. This exchange was extensive in terms of numbers of species, but rather trivial in terms of the focus of this chapter.
2. *Rana palmipes* entered South America from Central America. This is the only amphibian apart from those of (1).
3. The *Pseudemys scripta* series entered South America from Central America. The invasion took place long enough ago for differentiation, at the species level, in South America. However, the data are most consistent with the *Pseudemys scripta* series using the Pliocene bridge to enter South America.

4. *Crotalus durissus* entered South America from Central America.
5. *Drymarchon corais* likely used the Isthmian Link to disperse from one land mass to the other.

All other amphibians and reptiles most likely dispersed from one America to the other, if at all, well prior to the Pliocene land bridge connection. Aside from the Chocó–Central American lowland faunas, the Pliocene land bridge did not open floodgates of wholesale dispersals; only four species of amphibians and reptiles trickled through.

6.3. The Interchanges Were Asymmetrical

One way of analyzing the effects of the interchanges is to ask, "What would the faunas of North and South America be if they had never interchanged faunas?" The amphibian data are most appropriate to answer this question. If no amphibians that had their New World origin in South America had reached North America, the amphibian fauna of North America would be quite different. One component that would not differ is the salamander fauna. The frog fauna would consist solely of representatives of the families Ascaphidae, Pelobatidae, and Ranidae. There would be no members of the families Bufonidae, Hylidae, Leptodactylidae, or Microhylidae. The absence of members of these families would be dramatically noticeable throughout North America. Conversely, the absence of North American-derived amphibians would not be much noticed in South America. The caecilian fauna of South America would be unchanged. The extremely rich and diverse frog fauna of South America would differ by only a single species. The largest difference would be the absence of salamanders in the South American fauna, but exclusive of the Chocó region, there are only about 15–16 described species of South American salamanders, only one of which has a widespread distribution outside of the montane regions of northern South America.

The greatest effect of the herpetological interchange was pre-Isthmian Link, and, as shown by the amphibian data, strongly asymmetrical, with the fauna originating in South America much more strongly represented in the present North American fauna than the converse. The opposite is only true for those forms that dispersed via the land bridge: with the exception of the problematical *Drymarchon corais*, there has been not an interchange, but a one way dispersal. *Rana*, *Pseudemys*, and *Crotalus*, of ultimate North American origin, travelled the land bridge to penetrate South America.

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