

THE ISTHMIAN LINK AND THE EVOLUTION OF NEOTROPICAL MAMMALS¹

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ABSTRACT: The mammal fauna of the New World Tropics is comprised of four major historical source units. The most ancient of these units (the South American) is composed of marsupials, xenarthan edentates, condylarths, protonotungulates, and some bats whose ancestors were in South America by Early Tertiary and evolved, diversified and in many instances became extinct, *in situ*. A second unit (the Young Southern) is comprised of primates, cavimorph rodents, manatees, some bats and sigmadontine mice, whose ancestors arrived from North America by waif overwater dispersal at various times from Paleocene to Pliocene. No strong evidence for an intercontinental connection between North and South America in Cretaceous or Early Tertiary can be adduced from the available mammal evidence.

During later times (Eocene-Miocene), a series of more modern mammal stocks evolved in Middle America (the North Tropical unit) which invaded South America when the Isthmian Link connection between the two continents was established in Early Pliocene. A final unit (the North American) are stocks only recently moving southward through the Middle American tropics into northern South America. Following establishment of the Isthmian Link 24 southern families of mammals have moved northward into Central America, 12 of these reach temperate North America; 19 northern families entered South America, 15 of these reach temperate areas of the continent. Today both southern and northern faunas have been significantly modified by these increments but the exchange has been balanced without a disproportionate effect in either direction. Tropical Middle America is essentially a complex transitional zone between northern and southern elements and is not now, nor was at anytime in Cenozoic a significant evolutionary center for mammals. The present mammal fauna of the West Indies is derived almost in its entirety from northern South America.

INTRODUCTION

The origins and history of the land mammals of tropical America have long been a source of extreme interest to biogeographers and students of

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evolution (Darlington, 1957). The general accepted classic story of long Tertiary isolation of South America from any land connection to the north, with a Quaternary invasion of southern groups moving northward (16 out of 26 families) and northern groups moving southward (16 out of 25 families) across an emergent land bridge established in Early Pleistocene has been developed by Simpson (1950) extended by Patterson and Pascual (1963, 1968), and accepted through repetition until it has permeated textbooks and even popular accounts (Barnett, 1960).

Recently Hershkovitz (1966, 1968) challenged this interpretation based on evaluation of the distribution of living mammals (Hershkovitz, 1958). He concluded that mammals crossed the water barriers between Nuclear Central America and South America throughout the Tertiary, in both directions, so that present patterns are not the result of dramatic major invasions in the Early Pleistocene.

The critical geographic region involved in the faunal exchanges is the lower Central American Isthmian Link that extends today as a narrow connection between Nicaragua and northwest Colombia. The geologic and ecologic history of this link provides the key to unraveling the apparent inconsistencies and differences in interpretation of mammalian distributional evidence. The geographic and ecologic relations of the Middle American region including the Isthmian Link are summarized (Wauchope and West, 1964) and evaluated with regard to vertebrate distributions (Stuart, 1964, 1966). The terminology for major geographic and ecologic patterns in this paper follows their usage:

North America—the continental mass from the Isthmus of Tehuantepec in southern Mexico, northward;

Central America—the land south and east of the Isthmus of Tehuantepec to the border between Panama and Colombia;

South America—the continent south of the border between Colombia and Panama;

Mesoamerica—Mexico and Central America;

Middle America—Mexico and Central America;

Nuclear Central America—the northern portion of Central America that has been land positive and continuously connected to North America throughout Cenozoic; essentially from the present day Isthmus of Tehuantepec to and including northern Nicaragua, but with its seaward margins variously modified at different times;

Isthmian Link—the unstable area of present day Nicaragua, Costa Rica and Panama that was covered by marine waters during much of Cenozoic;

Tropical North America—the portions of North and Central America under tropical climatic regimens; currently restricted on the north to the coastal and southern areas of Mexico but earlier in Cenozoic including the southern portions of what is the United States; the tropical limits have now been gradually forced southward by the cooling trend of Late Cenozoic;

Upper Central America—Mexico south of the Isthmus of Tehuantepec to the Honduras-Nicaragua border;

Lower Central America—Nicaragua, Costa Rica and Panama.

The present paper is an attempt to review the ideas and evidence advanced to explain current neotropical mammalian distribution, particularly in the light of the almost diametrically opposed views of the outstanding authorities on Latin American fossil mammals (Simpson, Patterson and Pascual) and a leading student of living forms (HersHKovitz). This paper developed out of my interests in the biogeography of tropical America. Although not a specialist in mammalogy, I thought that my recent experience in analyzing the history of the Central America herpetofauna (Savage, 1966) might bring a new point of view to the problem, especially because of my familiarity with, and study of, the influence of Isthmian Link history and ecology on vertebrate distributions. Hopefully, it will at least delineate the basic points at issue between the classic and HersHKovitz' interpretations.

ACKNOWLEDGMENTS

My interest in the problem was initiated by reading the recent papers by HersHKovitz (1966, 1969) and Patterson and Pascual (1968) in the pages of the *Quarterly Review of Biology*. These authors presented lucid and well-documented statements of their opposed theories of the origin and history of mammals in the New World tropics. The paper by Patterson and Pascual and the outstanding illustrations of extinct southern mammals brought the fossil record to life in my imagination. HersHKovitz likewise made the recent situation alive and engrossing through his text and figures of modern forms that reveal his own enthusiastic appreciation of, and intimacy with tropical New World mammals. Both papers contain beautiful coverage of many problems not related to the present discussion and should be read in entirety by those wishing a fuller understanding of the life of present and past mammals of Middle and South America. Although I disagree strongly with these authors on many points of biogeographic interpretation, I deeply appreciate the stimulation provided by them, and the evidence presented in their papers which provided substantial data for my analysis. Simpson's (1969) recent paper agrees with the Patterson and Pascual view in most particulars and is essentially an updating of Simpson's (1950) more popular account. Although not appearing until 1969, the paper clearly was written prior to the accounts of HersHKovitz (1969) and Patterson and Pascual (1968) and much delayed in publication. Reference is made to this latest Simpson paper only where his views conflict with Patterson and Pascual or his own earlier statements.

Several colleagues of diverse background have critically reviewed drafts of the manuscript and offered constructive advice. Although I have not always followed their suggestions I have profited from the ideas they provided and acknowledge the help with thanks to: John S. Garth and Edwin M. Perkins,

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REVIEW OF HYPOTHESES

Simpson (1950, 1969) and Patterson and Pascual (1963, 1968) present the generally accepted view of mammalian history in the American tropics, based ultimately on the original data in Simpson (1940), together with less extensive but recent finds. According to this view three major historical units (strata) are present in South America:

I. *South American Oldtimers*; derived from Cretaceous-Paleocene ancestors and evolving in isolation in South America after the intercontinental land connection floundered in Late Paleocene.

II. *Old Island Hoppers* (Waifs); derived from Middle American ancestors that crossed the water barrier into South America in post-Paleocene times and differentiated in isolation in South America.

III. *Northern Newcomers*; derived from Early Pleistocene invaders that crossed the land bridge into South America after its reconnection or connection to Middle America.

Mammals of units I and II also invaded Middle America (after the establishment of the intercontinental connection) and some (opossums,

TABLE 1

SOUTH AMERICAN MAMMAL GROUPS BY HISTORICAL UNITS OF SIMPSON

I SOUTH AMERICAN OLDTIMERS	II WAIF DESCENDENTS	III NORTHERN NEWCOMERS	
Marsupials	Primates	Insectivores	Perissodactyls
didelphoids	marmosets	shrews	*horses
caenolestoids	monkeys	Lagomorphs	tapirs
*borhyaenoids	Caviomorph rodents	rabbits	Artiodactyls
Edentates	porcupines	Rodents	peccaries
armadillos	cavies	squirrels	camels
*glyptodonts	capybara	mice	deer
*ground sloths	aguti	Carnivores	
tree sloths	paca	dogs	
anteaters	chinchilla	bears	
*Condylarths	vizcacha	raccoons	
*Litopterns	hutia	weasels	
*Notoungulates	tucotuco	and others	
*Astrapotheres	spiny rats	cats	
*Pyrotheres	Carnivores	Proboscidioids	
	procyonids	*mastodons	
	(coati, kinkajou, olingo)		

*groups now extinct in the New World

armadillos and porcupines) have extended their range into extratropical North America. The principal groups associated in these units are summarized (Table 1).

The essential features of Simpson's theory of New World tropical mammal origins are as follows:

1. The Isthmian Link connected Middle and South America for a considerable period in Paleocene; the link was flooded by seas between present day northern Nicaragua to western Colombia from Eocene through Late Pliocene; the link was re-established in Early Pleistocene (3 million years ago).

2. North America and Nuclear Central America were connected throughout the Cenozoic.

3. The ancestors of South American Oldtimers (I) invaded the continent in Paleocene across the link and were isolated and evolved independently from Middle America relatives from Eocene to Pleistocene.

4. The ancestral Old Island Hoppers (II) crossed into South America over the Panamanian Marine Portal in Eocene-Oligocene and underwent differential evolution in isolation there.

5. The ancestors of both stocks became extinct north of the portal.

6. Upon re-establishment of the Isthmian Link in Pleistocene a host of Northern Newcomers (III) invaded South America from Central America.

7. At the same time descendant forms of units I and II invaded Central America from the south.

8. Northern Newcomers generally were derived from tropical stocks already in Central America at the time of Isthmian Link re-emergence; a series of allied holarctic groups remained in more northern temperate areas and have recently invaded Middle America but fail to reach South America.

9. The invasion from north to south was the most effective.

10. The invasions in both directions were massive and dramatic and are often cited as the best example of major faunal interchange.

Patterson and Pascual (1968) substantiated this theory, except they believed that no Cretaceous or early Tertiary land connection existed; Stratum I groups are ancient overwater immigrants into South America in their opinion.

Herskovitz (1969) proposed a more elaborate scheme involving seven strata of mammals in tropical America. Essentially, he recognized only two principal units as contributing to the mammal fauna of South America. These two units are discussed below with the strata described by Herskovitz indicated by Roman numerals and small letter subscripts as in his discussion.

A. *SOUTH AMERICANS*—derivatives of groups isolated from Early Eocene to Pliocene in South America,

- II groups derived from ancestors isolated by submergence of the Isthmian Link in Late Paleocene and groups derived from overwater waifs from Middle America in mid-Tertiary

- III groups derived from stratum II as overwater south to north waifs to Middle America in mid-Tertiary
- IV groups derived from stratum II as post-Miocene overland invaders of Middle America
- Vb groups derived from stratum III as overland invaders of South America in Pliocene onwards.

B. *NORTHERNERS*—North American groups that developed in Middle America after its separation from South America,

- Ib groups that developed in Central America during its separation from South America and Late Tertiary to Recent invaders from the north
- Va derivatives of stratum Ib that have invaded South America since reconnection of the Isthmian Link.

Herskovitz' stratum Ia appears to be a composite of ancestors for both South Americans and Northerners. He recognized that no living or fossil assemblage corresponds to this stratum. For this reason I have not considered it further here. The composite nature of stratum Ib is also a conceptual difficulty since no mammal genera endemic to Middle America appear to be ancient relicts from early Tertiary. The compositions of the Herskovitz units are indicated in the accompanying summary (Table 2).

TABLE 2

TROPICAL AMERICAN MAMMALS BY HISTORICAL UNITS OF HERSHKOVITZ

SOUTH AMERICANS

A. BASIC STOCKS

1. Descendents of Groups Isolated in South America
(part of Stratum II)
 - Marsupials
 - Edentates
 - Condylarths
 - Litopterns
 - Astrapotheres
 - Pyrotheres
2. Descendents of Overwater Waifs from Central America
(part of Stratum II)
 - Primates
 - Rodents
 - Squirrels (*Sciurillus*, *Sciurus* 3 spp.)
 - Sigmodontine mice
 - Caviomorphs
 - Lagomorphs
 - Tapeti (*Sylvilagus brasiliensis*)
 - Carnivores
 - endemic dogs (*Speothos*, *Chrysocyon*, *Lycalopex*, *Atelocynus*, *Dusicyon*)
 - Procyonids
 - endemic mustelids (*Lyncodon*, *Galictis*, *Eira*, *Pteronura*, *Mustela africana*)
 - endemic cats (*Felis colocolo*, *F. geoffroyi*, *F. guingna*, *F. jacobita*)

Perissodactyls

tapirs (*Tapirus pinchague*, *T. terrestris*)

Artiodactyls

peccary (*Tayassu*)

llamas and vicunas

endemic deer (*Mazama*, *Blastocerus*, *Blastoceros*, *Pudi*, *Hippocamelus*)

B. IMMIGRANTS TO MIDDLE AMERICA

3. Descendents of Overwater Waifs from South America to Central America: derived from 1 and 2 (Stratum III)

Genera and species with distribution centered on Central America including representatives of:

extinct edentates

Primates

Sigmodontine mice

some Caviomorphs

4. Overland invaders of Central America from South America: derived from 1 and 2 (Stratum IV)

Species common to lower Central America and northern South America, including as examples:

Central American edentates

tapeti

Some sigmodontine mice (13 sp.)

capybara

aguti

paca

crab-eating raccoon

brocket

C. REPATRIATES FROM CENTRAL AMERICA

5. Overland Invaders of South America: derived from 3 (Stratum Vb)

Species common to lower Central America and northern South America, including as examples:

bare-faced tamarin

black howler monkey

NORTHERNERS

6. Endemic Middle America Descendents of Northern Invaders (part of Stratum Ib)

a squirrel (*Syntheosciurus*)gophers (*Orthogeomys*, *Heterogeomys*, *Macrogeomys*)heteromyids (*Liomys*)peromyscine mice (*Scotinomys*)neotomine mice (*Nelsonia*, *Xenomys*, *Otodylomys*)

7. Invaders of Central America from the North, not reaching South America (part of Stratum Ib)

flying squirrel (*Glaucomys*)peromyscine mice (*Baiomys*, *Neotomodon*, *Peromyscus*)neotomine mice (*Neotoma*)voles (*Microtus*)coyote (*Canis latrans*)weasel (*Mustela frenata*)

8. Overland Invaders of South America (Stratum Va)

a shrew (*Cryptotis*)
a rabbit (*Sylvilagus floridanus*)
some squirrels
heteromyids (*Heteromys*)
peromyscine mice (*Reithrodontomys*)
neotomine mice (*Tylomys*)
gray fox (*Urocyon*)
spectacled bear (*Tremarctos*)
river otter (*Lutra*)
hog-nosed skunk (*Conepatus*)
cats (*Smilodon* and *Felis concolor*, *F. onca*, *F. pardalis*, *F. wiedi*, *F. tigrina*,
F. yagouaroundi)
mastodon*
a tapir (*Tapirus bairdi*)
horse (*Equus*)*
peccary (*Peccari*)
deer (*Odocoileus*)

The basic features of Hershkovitz' ideas on the origins of tropical American mammals (units and mammal groups are indicated in Table 2) are:

1. The Isthmian Link existed as a connection between Middle and South America in Paleocene; the link was submerged from Early Eocene through Miocene; the intercontinental connection was permanently re-established in Early Pliocene (12 million years ago).

2. North America and Nuclear Central America were connected throughout Cenozoic.

3. The ancestors of unit 1 were isolated in South America and evolved independently from Paleocene through Miocene.

4. The ancestors of unit 2 invaded South America from Central America overwater (across the Panamanian Portal) from Eocene onwards and each group as it arrived underwent independent evolution in South America.

5. Derivatives of units 1 and 2 re-invaded Middle America from Eocene to Pliocene overwater and became differentiated in Central America (unit 3).

6. Upon re-establishment of the Isthmian Link in Early Pliocene a great many mammals of northern affinities invaded South America (unit 8).

7. At the same time a large number of southern taxa invaded Central America (unit 4).

8. The Central American mammal fauna at the time of Pliocene reconnection was composed of a mixture of descendants of South American overwater waifs (unit 3) and northern groups endemic or adapted to tropical situations (units 6 and 8).

9. The general direction of invasion before and after the restoration of the Isthmian Link was primarily from south to north.

10. The faunal interchange between Central and South America quickened upon re-emergence of the bridge but overwater exchange from Eocene to Pliocene, a period of 30 million years, is principally responsible for present distribution patterns, rather than the land connection.

The essential differences between the theories developed by Simpson (S) and Hershkovitz (H) center around the following critical points:

A. Time of reconnection of Central and South America: Early Pleistocene (S), Early Pliocene (H).

B. Effectiveness of Panamanian Marine Portal as a barrier to mammal dispersal: extremely effective (S); of little significance (H).

C. Amount of independent faunal differentiation in Middle and South America during Eocene to Pliocene: extreme isolation and differentiation (S); substantial overwater faunal interchange (H).

D. Effect of reconnection of Isthmian Link: dramatic invasions with rapid postinvasion evolutionary radiation by northern groups in South America (S); minimal effects, principally through invasion of Central America by southern forms (H).

All other differences of interpretation by these authors center on these four key areas of controversy. Resolution of these points is the object of this paper as a basis for a revised view of the history of New World tropical mammals.

Keast (1969:133-134) has previously attempted to reconcile the opposing views of Patterson and Pascal (1968) and Hershkovitz (1969) with limited success, since he did not re-evaluate the situation or data in detail. He concluded that 1) the intercontinental land connection was established in Pliocene; 2) some groups including cricetids, otters and squirrels, reached South America from the north by overwater transport prior to Pliocene; 3) few if any large mammal stocks reached South America from the north by overwater transport; 4) many distinctive South American genera originated there; and 5) many groups including the cricetids attained their current diversity in South America.

THE HISTORY OF THE ISTHMIAN LINK REGION

Crucial to any attempt to place the conflicting views of Simpson and Hershkovitz in perspective is the necessity of a clear picture of the geologic history of Central and northern South America. I have previously reviewed the history of the link as it related to herpetofaunal distribution (Savage, 1966) based in large part on the ideas of Lloyd (1963) and Vinson and Brineman (1963). Since that time a revolution in geologic thought has occurred with the emergence of continental drift theory and the new tectonics (Dietz and Holden, 1970) as unifying themes in palaeogeography. Recent detailed studies of the areas of present and possible past intercontinental connections between North and South America from the view of new tectonic evidence (Freeland and Dietz, 1971; Malfait and Dinkelman, 1972) clarify significantly the palaeogeography of the region and seem much more congruent with the mammal evidence than my earlier (1966) interpretation. Where differences are apparent, I have relied heavily on the views of Freeland and Dietz (1971) and Malfait and Dinkelman (1972), together with

the work of Molnar and Sykes (1969) in developing the following section. I follow Hibbard, et al. (1965) in placing the lower limit of the Pleistocene as at the beginning of post-Pliocene Blancan times (Nebraskan onward), about 3 m.y. BP. This corresponds to the beginning of the Villafranchian of Europe and the Uquian in South America.

The significant structural units involved in the region are:

1. Nuclear Central America—including most of what is now southern Mexico, Guatemala, El Salvador, British Honduras, Honduras and extreme northern Nicaragua.

2. Guiana Shield—the major land mass of northern South America.

3. The Isthmian Link—the region from southern Nicaragua to northwestern Colombia, including Costa Rica and Panama.

4. The North Andean area and its western slope—continuous with the Guiana Shield through Cenozoic and uplift into the Andes during the latter part of the era.

There seems no question (Freeland and Dietz, 1971; Falfait and Dinkelman, 1972) that a substantial marine seaway existed between North America, including Nuclear Central America, and South America throughout the Cretaceous and until the Pliocene, between what is now northern Nicaragua and North Andean Colombia. The entire interoceanic connection may be called the Panamanian Portal. As the Isthmian Link became emergent in Late Tertiary, three main straits continued to connect the two seas: a) the Nicaragua Trough through southern Nicaragua, b) the Panama Trough east of the Talamanca-Chiriqui axis across central Panama, c) the Bolivar Trough running generally north to south across extreme northwestern Colombia.

In my herpetofaunal analysis of this area I accepted the views of Lloyd (1963), Simpson (1940, 1950) and others that North and South America were connected by land in the general region of the Isthmian Link during Paleocene (Nygren, 1950). Freeland and Dietz (1971) conclusively demonstrated that the last continuous broad contact between North and South America in the region under discussion, prior to the present one, was in mid-Jurassic (about 150 m.y. BP). Haffer (1970), Maldonado-Koerdell (1964), and Malfait and Dinkelman (1972) showed that the region from what is now Nicaragua to northern South America formed a broad seaway from Early Cretaceous to late Eocene, when a series of volcanic islands developed along the eastern margin of the Middle American Trench as the forerunners of the uplift that culminated in a land connection in earliest Pliocene. Because of sea-floor spreading the Panamanian Portal was about 400 km across in Middle Cretaceous and increased to a maximum of 1000 km in breadth in Early Tertiary.

Some of the biological evidence speaks strongly for a Paleocene-Eocene intercontinental land connection, Brame and Wake (1963), Olsson (1932), Parodiz (1969) and Savage (1966). If such a land connection existed in the Early Tertiary, the new tectonics and continental drift theory suggest that it

lay much further to the east than the present isthmus, somewhere in the proto-Antillean region. The evidence of Freeland and Dietz (1971) hints at a possible early land connection through the Nicaraguan Rise and proto-Antillean area (Jamaica-Porto Rico-Lesser Antilles), but Malfait and Dinkelman (1972) give this possibility little support.

The best available interpretations indicate that North and South America have been separated by a broad marine barrier connecting the East Pacific and Caribbean across the Panamanian region for all of the Cretaceous and the Early and Middle Cenozoic. In the Paleocene and Eocene the water gap was approximately 1000 kilometers in extent. Later in the epoch a series of volcanic islands developed to the southwest of the seaway (Fig. 1). From this time until Late Miocene (a span of around 25 million years) the marine barrier to overland intercontinental faunal exchange was relatively constant. Toward the middle of Miocene volcanic ridges and islands became more fully developed in the link region. Increasing and rapid uplift along the axis of present day lower Central America led to reduction of the seaway into three principal straits, the Nicaragua, Panama, and Bolivar Troughs. These portals closed along the Isthmian Link axis from northwest to southeast by the end of Miocene. The data of Whitmore and Stewart (1965) suggest that by Middle Miocene only the Bolivar Trough remained a marine barrier to overland dispersal. This latter area was uplifted and the connection completed in earliest Pliocene. It has persisted until today as a continuous intercontinental land connection.

No evidence supports the concept (Darlington, 1957:575) that Central America was an island or island chain separated from North America during any part of Cenozoic. Durham, Arellano and Peck (1952) laid the myth of a Cenozoic Tehuantepec seaway to rest years ago, although it continues to be invoked by biogeographers unfamiliar with the paleontological record. No question exists that Nuclear Central America has been land positive throughout Cenozoic and has been continuously connected with North America during that time.

Some confusion also persists regarding the role of the Bolivar Trough as a marine barrier to intercontinental exchange. Brame and Wake (1963: 65) presented an excellent summary of the data and ideas of Olsson (1932, 1942, 1956), Nygren (1950), and Durham and Allison (1960) relating to the Trough. These authors unequivocally regarded the Bolivar Trough area as uplifted and land positive from Late Cretaceous to Eocene. From Eocene to Late Miocene the trough was a marine seaway. According to Nygren (1950) the trough was bordered on the west by a land positive area that was submerged as the Andes and Bolivar Trough were uplifted during Miocene. This western borderland was never connected to Nuclear Central America and is not mentioned by other authors. Connections between the borderland across the Bolivar Trough to North Andean South America as mentioned by Nygren for several periods in Tertiary could not provide intercontinental migration

routes as suggested by Hershkovitz (1966:739, 745), since the principal Panamanian Portal was an open seaway throughout this time (Lloyd, 1963; Malfait and Dinkelman, 1972). Such connections, if they existed, did not effect mammal distribution between Nuclear Central America and South America.

Hershkovitz (1969:13) also implies that the Bolivar Trough was the principal marine barrier to overland distribution during Cenozoic and as such (1966:730, 732) was no major obstacle to faunal interchange. Again it must be emphasized that the Panamanian Portal formed an extensive seaway across all of lower Central America from early Cretaceous to at least Early Miocene. The Bolivar Trough was apparently the most persistent element of this seaway and finally closed in Late Miocene. To equate the relatively narrow Bolivar Trough with the Panamanian Portal as Hershkovitz has done ignores the vast marine barrier to land dispersal that restricted faunal exchanges between Central and South America during most of Tertiary. Patterson and Pascual (1968) also weaken their arguments by seeming to equate the Panamanian Portal with the Bolivar Trough.

HISTORICAL MAMMALIAN FAUNAL COMPONENTS

The fossil record

Patterson and Pascual (1968) and Simpson (1969) presented an excellent review of the mammal fossil record for Central and South America. The evidence is clear and uncompromising that South America had a long independent history as an island separated from North America influences until late in Cenozoic. The essential information from paleontology is:

1. Paleocene through Pliocene: predominance of marsupials, edentates, and the condylarths, litopterns, notoungulates, astrapotheres, pyrotheres, xenungulates and trigonostylopoids (the latter two only until Eocene).
2. Early Oligocene: appearance and increasing diversity throughout the rest of Cenozoic of caviomorph rodents.
3. Early Oligocene: appearance and increasing diversity of primates throughout rest of era.
4. Middle Pliocene: appearance of procyonids.
5. Late Pliocene: first appearance of North American groups.
6. Pleistocene: expansion of northern groups into South America.
7. Middle American Tertiary: sites with tropical North American groups.
8. Later Pliocene of Central and North America: first evidence of South American forms in fauna.

Recent distribution

Hershkovitz (1958, 1969) presented a thoughtful and lucid summary of recent distribution patterns. The essence of his ideas is summarized (Table 2) and key points mentioned below:

1. The Neotropical fauna occurs from southern Mexico to extreme South America.
2. The Nearctic fauna is North American in distribution.
3. Early Tertiary Middle America was a center for mammal evolution and the early forms spread into South America.
4. Closure of the Panamanian Portal must have been Miocene-Pliocene.
5. The Panamanian Portal was not a major barrier to faunal exchange.
6. Distributional data do not support the idea of a major invasion of southerners northward or northerners southward in Pleistocene; most mammals had already reached the limits of their present distributions before Pleistocene.

The faunal components

A review of all available fossil and recent data convinced me that a re-interpretation of the components was required. This process led me to re-examine the units that comprise the recent tropical American mammal fauna, with respect to the Isthmian Link. It is clear that four major faunal units are involved, which do not correspond to those previously proposed:

I. SOUTHERNERS (Southern Element)

A. South American Complex—groups descended from ancestors isolated in South America in the Cretaceous; undergoing diversification from Early Tertiary onward.

B. Young Southern Complex—descendants of groups derived from Middle American ancestors in Tertiary by overwater invasion of South America; undergoing diversification from Eocene to present.

II. NORTHERNERS (Northern Element)

C. North Tropical Complex—groups of northern affinities associated with tropical situations, present in Central America in Late Tertiary; many invading South America after reconnection of Isthmian Link.

D. North American Complex—recent invaders of Central and South America from temperate North America.

The composition of these units is summarized (Table 3).

HISTORY OF THE MAMMAL FAUNA

Original colonization

Of the major groups significant to our understanding of tropical American mammalian history, only the marsupials, condylarths and insectivores are known from Mesozoic fossils. In North America at the beginning of Paleocene, marsupials and insectivores are plentiful in the record together with primates, condylarths and other ungulates. By Late Paleocene, creodonts, pantodonts, uinatheres, tillodonts, and a primitive rodent are known. Most of the families represented are now extinct. Late Paleocene fossils in South

TABLE 3
MAMMALIAN FAUNAL COMPONENTS

SOUTH AMERICAN	YOUNG SOUTHERN	NORTH TROPICAL	NORTH AMERICAN
Marsupials:	Bats:	1. Into South America	1. Into South America
Didelphidae	Natalidae	Bats (Molossidae)	a shrew (<i>Cryptotis</i>)
** Borhyaenidae	Furipteridae	a squirrel (<i>Sciurillus</i>)	man (<i>Homo</i>)
** Necrolestidae	Thyropteridae	tropical dogs (<i>Dusicyon</i> , <i>Chrysocyon</i> , <i>Atelocynus</i> , <i>Speothos</i> , <i>Lycalopex</i>)	rabbits
** Polydolopidae	Primates:		Bats (<i>Vesperilionidae</i>)
Caenolestidae	Callithricidae (marmosets)		squirrels
** Argyrolagidae	Cebidae (monkeys)	Spectacled bear (<i>Tremarctos</i>)	heteromyids (<i>Heteromys</i>)
Xenarthran Edentates:			peromyscine mice (<i>Aporodon</i>)
Dasypodidae (armadillos)	Caviomorph Rodents:	procyonids (* <i>Cyonasua</i> , <i>Nasua</i> , <i>Potos</i> , <i>Bassaricyon</i>)	a neotomine mouse (<i>Tylomys</i>)
** Palaeopeltidae	Octodontidae		gray Fox (<i>Urocyon</i>)
** Glyptodontidae (glyptodonts)	Abrocomidae		racoons (<i>Procyon</i>)
** Megalonychidae (ground sloths)	Echimyidae (spiny-rats)	mustelids (<i>Lyncodon</i> , <i>Galictis</i> , <i>Eira</i> , <i>Pteronura</i>)	weasels (<i>Mustela</i>)
** Megatheriidae (ground sloths)	Chinchillidae (chinchilla, vizcachas)	cats (** <i>Smilodon</i> , some <i>Felis</i>)	otter (<i>Lutra</i>)
	Dasyproctidae (aguti)	** mastodons	skunk (<i>Conepatus</i>)
	Cuniculidae (paca)	(Gomphotheriidae)	cats (several <i>Felis</i>)
	Caviidae (cavies)	** horses (Equidae)	deer (<i>Odocoileus</i>)
Bradypodidae (tree sloths)	Dinomysidae (pacarana)		
** Mylodontidae (mylodonts)	Hydrochoeridae (capybara)		2. In Central America
			a bat (<i>Corynorhinus</i>)

**Entelopsidae	Erethizontidae (porcupines)	tapirs (Tapiridae)	flying squirrel (<i>Glaucomys</i>)
Myrmecophagidae (ant-eaters)	Sigmondontine Mice (Cricetidae):	deer <i>Mazama</i> , <i>Pudu</i> , <i>Hippocamelus</i> , <i>Blastocerus</i> , <i>Blastoceros</i>	peromyscine mice (<i>Baiomys</i> , <i>Reithrodontomys</i> , <i>Peromyscus</i>)
**Condylarths	approximately 40 genera	camels (<i>Lama</i> , <i>Vicugna</i>)	neotomine mice (<i>Neotoma</i>)
**Liptoterns	Manatee		voles (<i>Microtus</i>)
**Notoungulates			coyote (<i>Canis</i>)
**Astrapotheres		2. Endemic to Central America	cacomistle (<i>Bassariscus</i>)
**Pyrotheres		a bat (<i>Idionycteris</i>)	skunks (<i>Mephitis</i> , <i>Spilogale</i>)
**Xenungulates		a squirrel (<i>Syntheosciurus</i>)	**mastodon (Mammutidae)
**Trigonostylopoids		gophers (<i>Orthogeomys</i> , <i>Heterogeomys</i> , <i>Macrogeomys</i>)	**mammoth (Elephantidae)
Bats:		a heteromyid (<i>Liomys</i>)	**rhinoceros (Rhinocerotidae)
Emballonuridae		a peromyscine mouse (<i>Scotinomys</i>)	**Protoceratidae
Noctilionidae		a neotomine mouse (<i>Ototylomys</i>)	**oreodonts (Merycoidodontidae)
Desmodidae			*bison (Bovidae)
Phyllostomatidae			

*extinct in area

**extinct in New World

America include marsupials, edentates, condylarths, litopterns and most of the other endemic ungulate lines.

It seemed to Simpson (1950) that the Early Paleocene mammal fauna of South America could best be considered an unbalanced assemblage of groups derived from stocks present in the Cretaceous of North America or from these stocks after they reached South America. Patterson and Pascual (1968) accept this view and argue for a definite relation between the South American fauna and that of North America since marsupials, edentates (the North American fossils are now known to be of a different stock, allied to pangolins; Emry, 1970), condylarths and other evolving ungulates are represented on both continents. McKenna (1969) accepts a northern origin for these groups and implies that they immigrated to South America in Cretaceous. He is influenced in part by the close relationship of Paleocene North American (Arctocyonidae) and South American (Didolodontidae) condylarths, and the similarity and probable origin of the most primitive member of this stock (*Protungulatum*, Cretaceous of North America) from northern insectivores. The recently described *Perutherium* (Thaler in Grambast, Mattauer, and Thaler, 1967), a somewhat advanced condylarth from the Cretaceous of Peru, confuses this issue. Nevertheless as suggested by Hoffstetter (1970 a, b), Reig (1968), and Fooden (1972), the North and South American Paleocene faunas may correspond to different stages of evolutionary development from Mesozoic world mammal faunas, with the South American stocks representing lines probably isolated on the continent by the fragmentation of Gondwanaland in Early Cretaceous. The Paleocene South American mammal fauna was a relict endemic fauna of metatherians (marsupials) and other primitive eutherians. The usual view has held (Simpson, 1950, 1969; Patterson and Pascual, 1963, 1968), that the peculiar and distinctive basic Paleocene mammal fauna was derived from North American ancestors respectively by overland or over-water invasion of the southern continent. The more recent view, based on continental drift theory and Cretaceous mammals, emphasizes that the Late Cretaceous and basic Tertiary mammal fauna of South America was principally an *in situ* development from a series of primitive Gondwanaland stocks (Fooden, 1972). McKenna (1973) seems to favor the northern origin hypothesis but implied that some of the similarities between Paleocene North and South America might be due to earlier connections or filter bridges that allowed limited faunal exchanges between South America — Africa — Eurasia — North America in Cretaceous.

Patterson and Pascual (1963, 1968) concur with Simpson (1950, 1969) that the basic lines of South American mammals (marsupials, edentates, and ungulates) arrived on the continent from the north in Late Cretaceous to Early Paleocene. They, however, propose that the composition of the fauna strongly argues for overwater invasion from Central America. Darlington (1957:592) expressed a similar view. The arguments for this position are essentially as follows:

- a. the Tertiary mammal faunas of South America are unbalanced as compared to contemporary continental faunas of the northern hemisphere
- b. only four overwater landfalls are required to establish the ancient mammal lines, marsupials, edentates, condylarths and notoungulates, since the remaining ungulate lines can be derived *in situ* from condylarth ancestors,
- c. the absence of insectivores, creodonts, multituberculates and prosimians from South American records, while abundant to the north, indicates lack of a land bridge.

I (1966) have elsewhere argued vigorously for a Paleocene land connection between Central and South America as essential for explaining the present distribution of amphibians and reptiles. Unlike the mammals these groups show evidence of a long-term independent evolution of major stocks in Central America from lines allied to South American units. The level of divergence led me to postulate an Early Tertiary separation of a Middle American Element and a South American Element derived from a formerly wide-ranging New World Tropical fauna that became fragmented and isolated in two centers (tropical North America and South America) by the separation of the two continents by a water barrier in Paleocene. The relationships and degree of difference between these two stocks are very real.

Of 31 families representing seven of the eight major stocks of living amphibians and reptiles in South America, 21 are wholly or in part (distinct subfamilies) of South America origin and development. Eight are New World tropical endemic families, all of South American origin. All of these stocks go back in time to Early Tertiary and many to Cretaceous. To establish these families in South America by overwater invasion would require a minimum of 13 landfalls, all in Late Cretaceous or Paleocene. Recently, Parodiz (1969), demonstrated that fossil South American freshwater mollusks, from virtually the same localities as the mammal fossils, indicate a Paleocene land-bridge; mid-Tertiary samples indicate isolation and differentiation between North and South America. Simpson (1969:895) re-affirmed his position that a Paleocene land-bridge connected North and South America. These differences in faunal relations cannot be explained in terms of a non-existent Paleocene land-bridge across the Panamanian region. They suggest some kind of Early Tertiary interchange between the North and South American continents, possibly across a filter-bridge or by island hopping through the proto-Antillean region. I cannot explore here the possible reasons for the apparent differences in mammal versus herpetofaunal and invertebrate data. Suffice it to say that the mammal fossil record and present distributions do not support or require the concept of a pre-Pliocene Tertiary land-bridge between North and South America.

Actually it seems possible that neither a land connection nor overwater invasions from the north were involved in establishing the ancient mammal lines, marsupials, edentates, condylarths and notoungulates in South America in Cretaceous and Paleocene. Some at least may be part of, or descended

from groups established on the southern continent prior to the Paleocene as derivatives of the west Gondwanaland mammal fauna (Fooden, 1972).

I have included four bat families as early South American faunal components. Unquestioned bats are known from the Eocene, but the order doubtlessly appeared earlier in Paleocene. Presumed ancestral groups of the modern families are well represented in Eocene in North America. Among the more primitive basal insectivorous stocks are the tropicopolitan family Emballonuriade, with 10 New World genera, all endemic; 7 of these also occur in Central America. The Noctilionidae (1 genus, 2 species) may be closely allied. The family Phyllostomatidae is a New World tropical endemic with 50 genera, only a few of which occur in temperate North America. Probably derived from phyllostomatids are the true vampires, family Desmodidae (3 genera), another New World tropical endemic. In my opinion, these four groups were derived from Early Tertiary ancestors in South America and underwent radiation and familial differentiation there.

Later overwater invaders of South America

The immediate ancestors of modern marsupials, edentates, ungulates, and bats evolved in South America from Cretaceous onward to at least Pliocene in essential isolation. All authors agree that several additional groups were added to the core mammal fauna by overwater transport presumably in Eocene-Oligocene, and underwent radiation in isolation in South America. These groups are an ancestor of the platyrrhine primates (Callithricidae and Cebidae) and the caviomorph rodents. Both appear as fossils in Early Oligocene in southern South America. Neither is known prior to these times elsewhere, but potential ancestral stocks of both groups occur in Late Paleocene and Eocene of North America. Whatever the ancestors, they became extinct north of the Panamanian Portal. Simpson (1950), Hershkovitz (1966, 1969) and Patterson and Pascual (1968), further agree that procyonid carnivores giving rise to *Cyonasua* and *Chapalmalania* of middle to Late Pliocene in west central Argentina were also pre-Pliocene overwater invaders from Central America. Hershkovitz (1966, 1969), in direct contradiction to the position of the paleontologists, proposed additional pre-Pliocene overwater transport into South America of the ancestors of mice of the sigmodontine group of the Cricetidae and a heterogeneous mixture of other mammals including some squirrels, a rabbit, several dogs, most mustelids, many cats, tapirs, peccaries, camels and many deer (see Table 2, Unit 3).

The rationale used by the several authors to explain these later invasions is essentially as follows: Simpson (1950, 1969) and Patterson and Pascual (1968) thought that the Isthmian Link was re-established in Early Pleistocene, thus any differentiated group represented in the South American fossil record prior to that time must have been a descendant of overwater waifs that invaded the continent prior to the emergence of the land bridge. Hershkovitz (1966, 1969) on the other hand believed that the Panamanian Portal was essentially

ineffective as a barrier to mammal distribution and that many groups (23 families) crossed it into South America prior to establishment of a land connection. To the possible overwater waifs already mentioned may be added the specialized bat families Natalidae (long-legged bats, 1 species), Furipteridae (smoky bats, 2 genera, 2 species) and Thyropteridae (disk-winged bats, 1 genus, 2 species), all apparently derived from insectivorous ancestors after isolation in tropical South America; and the manatee (Sirenia, Manatidae) with fossil genera from Late Miocene and Early Pliocene and a single living genus, all in South America.

Evaluation of the probability of fortuitous overwater invasions from north to south is closely tied to the history of the Isthmian Link. The following key points are reiterated from my description of its history above:

1. From Cretaceous into Miocene a major seaway extended across lower Central America and separated the Nuclear region from nearest South America by 400-1000 kilometers of water.

2. The closure of the seaway was progressive from north to south through Miocene.

3. By Early Pliocene the final water gap, the Bolivar Trough, was uplifted to complete the link and provide an overland route between North and South America.

Simpson (1950) and Patterson and Pascual (1968) take issue with the latter interpretation. They argue that the closure was in Early Pleistocene on the basis of mammal fossil data. Although the dating of the connection becomes a real issue for discussion later in this paper, for present purposes whether the bridge was completed in Early Pliocene or Early Pleistocene does not affect evaluation of overwater transport for most of the groups. The stocks (Young Southern Complex) that appear to have reached South America by waif overwater dispersal, after the initial establishment of mammals on the continent and prior to a later Cenozoic land connection, are considered below.

Primates.—Platyrrhine primates (usually placed in two families) are known today only from the New World tropics; fossils appear only in South America, the first in Early Oligocene, and on Jamaica. All living genera occur in South America, six range into Central America, two into tropical Mexico. One extinct marmoset (Oligocene) and several cebids (Oligocene-Miocene) are known from pre-Pleistocene deposits. These data support the view that the ancestor of the platyrrhines arrived in South America prior to mid-Tertiary. Although I have accepted the opinion of others that the ancestors of New World marmosets and monkeys reached South America by overwater transport in post-Paleocene times, it is with reservations. Basic prosimian lines occur in North America in Cretaceous and lemurs and tarsiers are relatively well known in Eocene. It is not out of the realm of possibility that an early tropical proto-platyrrhine may have crossed from Nuclear Central America or Africa to the South American continent in Cretaceous or Early

Tertiary. Nothing in the fossil record favors these alternatives and the morphology of African versus South American primates (fossil and living) seems to preclude any close relationship.

Caviomorph Rodents.—The first records of this important group are in the Early Oligocene of Argentina. An Eocene time of arrival is suggested because of the diversity of groups already present by upper Oligocene (6 families). Today 43 genera occur in tropical America, in 10 families; 6 genera, all common to South America, range into Central America and one (*Erethizon*) occurs far north into Canada. Three families are found in the West Indies, two (Capromyidae, with 6 genera, 3 living; Heptaxodontidae, with 7 genera, all extinct) are endemic, one (Echimyidae with 5 extinct insular genera, 4 of which are endemic) has a wide range in mainland tropical America. Rodents first appear in the fossil record in Late North American Paleocene and possible ancestors (Paramyidae) to the caviomorphs are of that age and area. A probable mid to Late Eocene overwater arrival of caviomorph ancestors from the north seems likely. Lavocat (1969) has argued that the caviomorph rodents of South America and the hystricomorph line of Africa are from a common origin. In this view the ancestors of the caviomorphs reached South America from Africa in late Mesozoic to early Tertiary, but this view is not followed here. Evolutionary radiation of the caviomorphs in isolation on the southern continent is verified by an extensive fossil record and recent distribution patterns for the group.

Bats.—Partially because of their relative vagility, bats usually have been ignored in dealing with problems of overwater invasion. The specialized families Natalidae, Furipteridae and Thyropteridae may best be explained as having undergone differentiation in isolation in South America. The time of invasion and isolation for these groups must have been prior to Pliocene.

Manatee.—Manatees are marine coastal and lowland river inhabitants. There is a single living genus with one species in tropical West Africa, and one or two forms in Florida, and around the Caribbean into the Amazon and Orinoco river systems. Two South American fossil genera *Potamosiren* (Late Miocene) and *Ribodon* (Middle Pliocene) suggest not overwater, but through water invasion of an ancestor in Eocene-Oligocene. They may be grouped without question as a Young Southern taxon.

Procyonids.—It is assumed by all previous authors that procyonids have invaded South America at least twice. The first time was prior to Middle Pliocene, where, in Argentina, two related fossil genera occur. The second invasion or invasions by essentially the Recent procyonid genera is assumed to have taken place after the connection of the two continents in post-Miocene times. If the connection occurred in Early Pliocene overwater dispersal is not needed to explain the Middle Pliocene fossils. If the bridge emerged in Early Pleistocene the ancestors of the fossil *Cyonasua* and *Chapalmalania* were doubtless overwater waifs from Central America. The earliest procyonids in

North America are from mid-Miocene so the entrance of this group into South America must have been no later than Early Pliocene.

Cricetid Mice.—Herskovitz (1966, 1969) has developed a convincing argument that most of the cricetid mice in South America must have differentiated there. Cricetids occur from Early Oligocene onward in North America. In the Americas two major stocks of the Cricetidae are known, one with all representatives having a complex penis and the second more advanced groups with a simple penial structure. The complex penis group contains around 40 genera, all but *Nyctomys* and *Otonyctomys* of Central America, one Galapagos Island, and one West Indian genus, are known from South America. This group is usually regarded as a distinct tribe Sigmodontini within the Cricetinae. Only two genera of the tribe range into temperate North America, the cotton rats, *Sigmodon* and rice rats, *Oryzomys*. The simple penis group includes peromyscine (7 genera), neotomine (5 genera) and microtine (9 genera) lines in the Americas. Only one peromyscine genus (*Aporodon*) and one neotomine genus (*Tylomys*) reach northern South America.

Herskovitz is convinced that the sigmodontines are derived from over-water invasion of South America by a complex penis ancestor in Oligocene-Miocene. Radiation and differentiation in South America led to the origin of the 40 or 50 genera. According to him, *Nyctomys* and *Otonyctomys* may be relicts north of the Panamanian Portal derived from the common ancestor that passed into South America. Any other allies of the sigmodontines in Central America have become extinct or replaced by the rather more recent intrusion of the simple penis lines. Herskovitz does not believe that the tremendous differentiation of sigmodontines in South America could have taken place in the last 3 million years (Pleistocene) as required by the Simpson (1950, 1969) and Patterson and Pascual (1968) theory of land connection. The latter two authors develop a counter argument that runs like this:

- a. there are no sigmodontine fossils from Miocene in South America, so there were no sigmodontines there,
- b. if sigmodontines were in South America in Miocene, many caviomorphs would have been replaced by competition,
- c. if sigmodontines were there in Miocene they should have differentiated beyond the generic group stage,
- d. the original sigmodontines evolved into multiple genera in Central America, since 17 cricetids live there today, and invaded South America; with little additional proliferation the 40 living genera evolved from the many invaders.

These views seem unacceptable to me. It is correct that no sigmodontines are known in Miocene fossil materials in South America but they are also unknown in the Miocene of North America. Given the predominance of southern Argentina fossil localities and the tendency of paleontologists to

collect larger animals, lack of cricetid remains in Miocene South America is not surprising. Contrary to the second point of Patterson and Pascual, there is no evidence that caviomorphs are currently suffering any ill effects from competition or replacement by cricetids. These authors make this point themselves (1968:443, 447). If a Pleistocene invasion of cricetids had no perceptible effect on the caviomorphs, why would a Miocene one affect caviomorphs adversely? Obviously a Miocene invasion of cricetids is not ruled out by caviomorph rodent history.

The third point is equally fallacious. The evolution of 40 genera since a presumed Miocene invasion and tribal differentiation are major events. They are of an equal or higher order of magnitude than the Miocene invasions and differentiations of murid mice in Australia or cricetid mice in Madagascar documented by Simpson (1961, 1940). In Australia two invaders of probable Miocene age evolved into 10 genera with five more on New Guinea. In Madagascar a group of seven endemic genera of cricetids (the endemic subfamily Nesomyinae of some authors) apparently have evolved from a single Miocene overwater waif.

The final argument is also difficult to accept. Today, 17 genera of cricetids are found in Central America, but only 3 sigmodontines occur north of extreme eastern Panama. It is unlikely that so many diverse genera as are now found in South America evolved post-Pliocene or if derived from a host of Central American ancestors left only three relicts behind. The data of Patterson and Pascual (1968:445-445, Tabs. 11-12) leave little question that sigmodontine mice have been in South America for a long period of time and differentiated there. Four genera of sigmodontines are known from Late Pliocene in Argentina, as compared to one in the Late Pliocene of North America.

The group must be regarded as overwater invaders of more recent origin than primates and caviomorphs, but clearly they arrived in South America prior to the uplift of the Isthmian connection.

Other Invaders.—The many additional groups proposed as overwater invaders by Hershkovitz (1969), appear to be relatively recent overland invaders. None of the genera is known as fossils in South America prior to Late Pliocene. Most do not appear in the record until Pleistocene. Hershkovitz' realization of the relatively early penetration by overwater transport of cricetids into South America and his misunderstanding regarding the extent of the Panamanian Portal and the effect of its reduced section, the Bolivar Trough, led him to overestimate the potential for overwater invasion.

Overwater invasion from the south

Because Hershkovitz regarded the Panamanian Portal as an ineffective barrier to mammal dispersion he proposed that a number of groups passed from the southern continent to Central America prior to re-establishment of the land connection (Table 2, Unit 3). Others including Patterson and Pascual

agree that Pliocene records of ground sloths and armadillos might result from overwater transport from south to north. In my opinion none of the other groups listed by Hershkovitz requires overwater transport prior to reconnection of the land bridge to explain their distributions. All seemed to have entered Central America fairly recently and certainly have had time to move northward since a Pliocene or even Pleistocene land bridge formation. Central and North American differentiation into a number of species as in *Sigmodon* and *Oryzomys* is most easily explained if reconnection occurred in Early Pliocene. If the connection were established in Pliocene no difficulty is encountered in explaining the presence of fossil edentates in North America as well; if it formed in Pleistocene overwater transport is required for these groups.

The age of the Isthmian Link and faunal interchange

The evidence previously discussed (p. 9) supports a concept of closure of the final link of the Panamanian Isthmus by uplift of the Bolivar Trough in Early Pliocene. Simpson (1950) and Patterson and Pascual (1963, 1968) take issue with the interpretation. They argue that the closure was in Early Pleistocene on the basis of mammal fossil data. A review of Pliocene faunas suggests that they have overstated their data. No mammals of the northern element appear in South America prior to Middle Pliocene (procyonids), but four cricetids, a skunk and two peccaries are known from Late Pliocene. Since most Pliocene fossil localities are from Argentina, it is not surprising that an invasion of northerners into northern South America might not affect the fossil record until later in the period several thousand kilometers to the south. Pleistocene localities, of course, abound with northern forms. Pleistocene fossil faunas in North America also show effects of invasion by southerners northward across the Isthmian Link, with about 20 genera represented. Unfortunately all Pliocene samples from North America lie in temperate climatic areas at least 4000 kilometers overland from South America. Generally, these localities are from regions that were semi-arid and affected by frost in Pliocene. They seem on ecologic grounds to be rather unsuitable sites for the ready establishment of the first tropical immigrants. Early Pliocene records of Southerners are to be expected in Middle American fossil faunas, but the only lowland finds of this age are strictly northern in composition (7-8 genera), all of relatively large animals (Olson and McGrew, 1941; McGrew, 1944; Mooser, 1959). Nevertheless, three southern genera, a ground sloth (*Megalonyx*), an armadillo (*Dasypus*) and a cotton rat (*Sigmodon*), are known from Late Pliocene in the United States.

The geologic and invertebrate paleontologic record, (Olsson, 1956; Nygren, 1950; Parodiz, 1969) tends to be in conflict with mammalian fossil data. Parodiz (1969:189) demonstrated that fossil freshwater mollusks in South America, from nearly the same sites as for fossil mammals, show immigration of northern families into South America for the first time in

Late Miocene-Early Pliocene. These data point unequivocally to an Early Pliocene connection between Central and South America. The mammal record demonstrates a full interchange of groups in Early Pleistocene, some group interchange in Middle to Late Pliocene but tends to discount an Early Pliocene land bridge. Whitmore and Stewart (1965) on the basis of mammal fossils from Panama indicate that by Middle Miocene only the Bolivar Trough remained as a marine barrier to intercontinental exchange with a water gap of no more than 100 kilometers. The view of Patterson and Pascual is that this barrier functioned for 10 to 12 million years to prevent fauna exchange, although a seaway of nearly 1000 kilometers in extent must have been crossed a minimum of six times during the previous 65 million years. If the Bolivar Trough remained a barrier through Pliocene some mammal groups probably crossed the narrow gap overwater. The procyonid, cricetid, skunk and peccary records from South America Pliocene might be accounted for in this manner. Similarly the earliest records for Southerners in North America might have been derived from early Pliocene overwater waifs from south to north.

Exact dating of the time of intercontinental connection (Pliocene versus Early Pleistocene) can only be finally resolved by discovery of additional Pliocene deposits in northern South America and lower Central America. Malfait and Dinkelman (1972) place the time of completion of the land bridge as mid-Pliocene. Nevertheless, my tendency is to accept Early Pliocene as the time of reconnection based upon geologic and invertebrate marine and freshwater paleontologic evidence, my review of the herpetofaunas (Savage, 1966) and Hershkovitz demonstration of significant differentiation in northern mammals that have crossed overland into South America. Among the components of the herpetofauna 37 genera found in Middle America appear to have invaded South America since the restoration of the Isthmian Link; 62 genera of South American origins have moved northward out of 159 genera found in Middle America. Out of the groups of mammals that unquestionably crossed the land bridge, whether in Pliocene or Pleistocene, 27 of the 138 genera in North and Central America passed from south to north, and 40 of the 160 in South America passed from north to south. These data suggest a relatively long history of connection, but do not preclude a Pleistocene date for reconnection of the continents.

The re-establishment of the Isthmian Link by Early Pliocene readily explains the presence of the Pliocene occurrence of procyonids, skunk, and peccaries in Pliocene South America and ground sloth, armadillo, and rice rats in North American Pliocene. It also allows enough time for differentiation of Northern groups in South America and Southern groups to the north, after crossing the land bridge, one of the weak links in any argument for a Pleistocene connection. The refusal of Patterson and Pascual (1968:436) to recognize the evidence from other groups and geology, and suggested by mammal fossils as well, seems to stem from a desire to make spectacularly recent what still is a dramatic, revolutionary meeting of two distinctive faunas

in Pliocene. Their statement "No better example of a geologically sudden meeting of two radically different faunas exists . . ." applies to the Pliocene encounter equally as well as to the presumed Pleistocene one.

Hershkovitz (1966, 1969) took a very original position regarding the role of the Panamanian Portal as a barrier to mammal dispersion. He argued that most genera of mammals crossed the portal with ease and that it had no major effect on regulating north-south or south-north movements into South or Central America, respectively. His interpretation is in marked disagreement with that of vertebrate paleontologists. A major weakness in Hershkovitz' discussion lies in his apparent misunderstanding of the nature of the Bolivar Trough. He seems to regard it as being equal to the Panamanian Portal. As emphasized above, until mid-Miocene, Nuclear Central America and South America were separated by a major seaway. The final portion of the marine portal to close was the Bolivar Trough, as nearly as can be determined in Early Pliocene. From Paleocene to Miocene, at least, any faunal exchange must have been across nearly 1000 kilometers of ocean or by island hopping. Hershkovitz (1969:65) regarded the matter of the timing of the bridge reconnection as academic, because he failed to appreciate the extent of the marine barrier during most of Tertiary. His own data require that the continental exchange begin at least by Pliocene, but by ignoring the history of the link region he is forced to propose a series of multiple, extensive overwater raftings of mammals to explain recent distribution patterns. Instead of being academic the dating of the connection is critical. Hershkovitz' proposed series of overwater waifs (Table 2: units 2, 3), except for those I call Young Southerners (Tab. 3), could all have moved north or south overland when the link was established in Early Pliocene. Since the major weight of evidence favors a Pliocene connection, Hershkovitz' principal objection to Simpson's views is negated. Surely the 10-12 million years since the emergence of the Isthmian Link allows enough time for the evolution of the levels of differentiation seen in both northern and southern immigrants in their new surroundings.

The efficacy of the marine portal as a barrier is fully attested by the fossil mammal record of South America from Cretaceous to Pliocene. Only late in the latter period do northern forms begin to appear. Even the reduced portal of mid-Miocene seems to have been an extremely effective barrier. Two fossil faunas, one just to the west of the Bolivar Trough (Whitmore and Stewart, 1965), another of slightly later age from its eastern border (Stirton, 1953), may be compared to illustrate this point. The faunal components are summarized (Table 4). Every animal in both samples is exclusively northern (Panama) or southern (Colombia). There can be no question but that even the reduced Bolivar Trough was a strong barrier to mammal dispersion. The Trough by Late Miocene was no more than 100 kilometers across. The two fossil sites are separated by a distance of about 350 kilometers and lie very close to the east and west margins of the trough zone. A facet of the effective-

TABLE 4

COMPARISON OF MIOCENE FAUNAS IN REGION OF BOLIVAR TROUGH

MID-MIOCENE	LATE MIOCENE
-------------	--------------

(Cucaracha)	(Friasian)
Central Panama	La Venta, Colombia
Horses	Opossum
<i>Anchitherium</i>	Borhyaenids:
<i>Archaeohippus</i>	<i>Lycopsis</i>
Rhinoceros	<i>Cladosictus</i>
<i>Diceratherium</i>	Bat (Phyllostomatidae)
Oreodont	<i>Notonycteris</i>
<i>Merycochoerus</i>	Monkeys:
Protoceratid	<i>Cebupithecia</i>
	<i>Hommunculus</i>
	<i>Neosaimiri</i>
	<i>Stirtonia</i>
	Condylarth
	Litopterns (2 families)
	Notoungulates (5 families)
	Astrapothere:
	<i>Astrapotherium</i>
	<i>Xenoastropotherium</i>
	Manatee:
	<i>Potamosiren</i>
	Megalanychid sloth
	Megatheriid Ground sloth
	Mylodont
	Anteater
	Armadillos (3 genera)
	Glyptodont
	Porcupine
	Cavy
	Dinomyids:
	<i>Olenopsis</i>
	<i>Scleromys</i>
	Capromyid
	Echimyid

ness of the narrow barrier may have been the result of the current patterns in the region. One of the principal objections to the proposed sea-level canal across the present day isthmus is the tidal difference between Pacific and Caribbean sides. The former has a 6 m amplitude, the latter an 0.5 m amplitude. If a similar pattern held in the past it is easy to imagine the terrific swirling currents that would sweep through a narrow channel such as the Bolivar Trough as the Atlantic poured into the Pacific twice daily and the Pacific into the Atlantic twice daily. Any mammal attempting to cross the channel would stand an excellent chance of being swept far out to sea, without much possibility of reaching the opposite shore. It seems inescapable that the marine barrier was extremely effective until closure and that most of the mammals

regarded by Hershkovitz as overwater waifs actually are overland immigrants into South America. Contrary to his forceful statements (1969:65), the nature of the water gaps and land bridges and their history, age and extent, best explain the data of present mammal distribution.

The major faunal interchange

At the beginning of Pliocene, the South American fauna apparently consisted of marsupials, bats, platyrrhine primates, edentates, a series of ungulates, manatees, caviomorph and sigmodontine rodents. Most, if not all, of the genera of these groups were unique to South America. Central America was populated by a variety of northern mammal lines (Table 3) but must have lacked almost all of the South American groups, except some bats, possibly manatees and perhaps a few relic sigmodontine mice or their ancestral stock. The major faunal exchange involved northward movement of many southern genera and the reverse. The families potentially involved in the interchange and their derivation are summarized (Table 5). Included in the table are all living Southern American mammal families and those extinct but recorded from Early Pliocene onward. All northern families with living representatives, and those that are extinct but with Miocene or later records in Middle America are listed. For purposes of discussion the family Cricetidae has been divided into two divisions; each is counted as a family equivalent in the following comparisons: Out of a total of 71 stocks that might have participated in the exchange from the end of Miocene onward, 39 are southerners and 32 northerners. Of the 71, 45 occurred in temperate South America, 52 in tropical South America; 50 in tropical Middle America and 42 in temperate North America. Of the southern families 30 were found in temperate South America, 33 in tropical South America. Twenty-four southern families ranged into tropical Middle America and 12 have reached temperate North America. Of the northerners 26 reached tropical Middle America, 19 tropical South America, and 15 temperate South America. Out of these groups 5 southern families are extinct in Middle America, although known as fossils in Pliocene or Pleistocene. Nine northern families present during the same time span are also no longer represented in Middle America. Five southern families, formerly represented in temperate North America, are extinct there and 2 northern families, formerly occurring in South America, are extinct in the New World.

As nearly as can be determined, the recent New World mammal fauna, exclusive of cetaceans and the West Indian forms, is comprised of 332 genera; 191 of these are southern genera, 141 northern genera. Table 7 summarizes the data for generic distributions (based on Hershkovitz, 1958 and Hall and Kelson, 1959). The first line (N) lists the number of genera in each major geographic region. The second line (%) gives the percentage of the total of each fauna comprised of southern and northern genera. The third line gives the percentage of the total genera for the New World as a whole, represented

TABLE 5
MAMMAL FAMILIES INVOLVED IN FAUNAL INTERCHANGE ACROSS ISTHMIAN LINK LAND BRIDGE

Southern Families	South America Temperate	South America Tropical	Middle America Tropical	North America Temperate	Northern Families
Didelphidae				↑	
* Borhyaenidae					
Caenolestidae					
* Argyrolagidae		↓			Soricidae Talpidae
Emballonuridae			↑		
Noctilionidae			↑		
Phyllostomatidae				↑	
Desmodidae				↑	
Natalidae			↑		
Furipteridae					
Thyropteridae		↑			
	↓				Vespertilionidae Molossidae Hominidae
Callithricidae					
Cebidae		↑			
Dasyopodidae			↑		
* Glyptodontidae				↑	
* Megalonychidae				↑	
* Megatheriidae				↑	
Bradypodidae			↑		
* Mylodontidae				↑	
Myrmecophagidae					
	↓		↑		Ochotonidae Leporidae Aplodontidae
		↓			Sciuridae Castoridae Geomyidae
					Heteromyidae Cricetidae (Peromyscini, Neotomini.

MAMMAL FAMILIES INVOLVED IN FAUNAL INTERCHANGE ACROSS ISTHMIAN LINK LAND BRIDGE

29

etidae
infidae
idae
dae

by genera in the region. For example, in temperate South America there are 53 southern genera; these comprise 69% of the fauna for the region; the 53 genera represent 28% of the southern genera in the New World. In addition, data for all South American genera are pooled for an overall evaluation and totals for the four mainland regions are pooled and summarized in the same table.

These figures (Tables 5-6-7) provide a basis for testing the conclusion of Simpson (1950) that the major faunal movement was from north to south and the assertion of Hershkovitz (1969) of the reverse.

TABLE 6

FAMILIAL EXCHANGE BETWEEN MIDDLE AND SOUTH AMERICA ACROSS ISTHMIAN LINK

FAMILIES		TROPICAL SOUTH AMERICA			MIDDLE AMERICA		
		Total	Southern	Northern	Total	Southern	Northern
Prior to	N	33	33	0	25	0	25
Land Bridge	%	100	100	0	100	0	100
Additions	N	19	0	19	25	24	1
Extinctions	N	9	7	2	14	5	9
Net Gain	N	10	-7	17	11	19	-8
Today	N	43	26	17	36	19	17
	%	100	60	40	100	53	47
Enrichment	%	30	-21	51	44	76	-32

At the time the bridge was established 39 southern families occurred in South America, 33 in the region of the marine portal. To the north 25 northern families occurred in the adjacent Central American area. After the faunal exchange and extinctions 43 groups occur in the South American area and 36 in Central America. On this basis (Table 6) both regions were enriched by the interchange, a net gain of 10 families in South America (a 30% enrichment) and a net gain of 11 families in Central America (a 44% enrichment). The figures demonstrate a basically balanced exchange, but 51% of the enrichment in South America comes from northern additions and 76% of the enrichment in Middle America from southern invaders.

At the generic level (Table 7) a similar pattern in faunal composition for the tropic bases of the Isthmian Link is indicated. From south to north (southerners) as a % of total number of southern genera show the following pattern: 28-76-40-17; from north to south the percentage of northerners to total number of northern genera is: 59-44-35-17. On this basis the equivalent of 40% of the southern genera have invaded tropical Middle America; 35% of the northern genera have invaded tropical South America. If the faunas nearest to the Bolivar Trough are used for comparison, the equivalent of 53% of the southern genera invaded Central America from tropical South

TABLE 7
NUMBERS OF LIVING MAMMAL GENERA IN THE NEW WORLD BY MAJOR REGION

TEMPERATE SOUTH AMERICA			TROPICAL SOUTH AMERICA			MIDDLE AMERICA			NORTH AMERICA		
Southern	North- ern	Total	South- ern	North- ern	Total	South- ern	North- ern	Endemic	South- ern	North- ern	Total
N	53	24	77	146	49	195	77	3	8	62	139
%	69	31	100	75	25	100	56	2.2	5.8	44	100
% Total	28	17	23	76	35	59	40	1.6	5.7	44	42
									17	59	35

Total South American				Total New World				
		Southern Northern		Southern Northern		Total		
N		183	53	236	N	191	141	332
%		78	22	100	%	58	42	100
% Total		96	37.5	76	% Total	100	100	100

America; the equivalent of 79% of the northern genera in Central America immigrated across the land link. Essentially most of the Central American northerners (49 out of 62 genera) have invaded South America and about half of the southerners (77 out of 146 genera) have crossed into Central America. A higher percentage of northern genera moved southward than southerners northward, but many more (actual numbers) southern genera immigrated northward. Any of Simpson's or Hershkovitz', or Darlington's ideas can be supported by these data, depending upon which ones are selected.

As a further attempt to evaluate the situation, I have tried other means of faunal comparison. At the family level (Table 8) 62% of the southern stocks reached Central America, but only half of these reached temperate North America. Of the groups present in tropical South America at the time of Isthmian uplift 73% invaded Central America. Out of the northern families 59% reached South America and 47% passed through the tropical area to South America. Out of the northerners in Central America at the time of connection of the continents 72% ranged into South America. Slightly fewer northern lines (19) invaded South America than South American stocks (24) invaded Central America. In the region of interchange the two elements are almost balanced. Seventy-seven of 146 tropical southern genera have invaded Central America, 49/62 of the northern genera in Middle America have immigrated to South America. Only when temperate North and South America are compared is there any suggestion of one of the two elements being more successful invaders than the other. Out of the total number of northern families a higher percentage (47%) have reached temperate South America than southern families have reached temperate North America. Of the families in the region adjacent to the Isthmian Link at the time of intercontinental connection 14 of 25 (56%) northerners have penetrated into temperate South America and 12 of 33 (36%) southerners have reached temperate North America.

The ratio of southern to northern families in each region (Table 8) provides another measure of the effect of the interchange. In temperate and tropical South America there are 2 southern families to each northern family, in Middle America the families are in a nearly 1:1 ratio and in North America the northerners are 2.5:1 to southern families. These ratios again demonstrate the almost equal familial exchange in the Isthmian region and the slightly greater success of northern families in reaching temperate South America over southern families affecting the North American fauna.

A similar ratio comparison for genera (Table 8) follows an almost identical pattern. In temperate South America southerners are in a ratio of about 2:1 to northerners, 3:1 to northerners in the tropic regions of the continent and nearly 1:1 with northerners in Middle America. In North America the number of northern genera approaches 3:1 southern. This method indicates that somewhat more southern genera have invaded Middle America from tropic areas to the south than northern genera have crossed from Central into South

America. Again fewer southerners contribute to the North American fauna, than northern genera contribute to the mammalian fauna of temperate South America.

Another comparison (Table 8) uses the maximum number of genera of a particular element in one region as a basis for determining faunal exchange. If the number (146) of recent southern genera in tropical South America is taken as 100%, it is seen that 53% have invaded Middle America and 22% have reached North America. If the number (84) of northern genera in temperate North America is taken as 100%, 58% have invaded tropical South America and 29% have reached temperate South America. This comparison supports the concept of a balanced faunal exchange.

TABLE 8

INCREASE AND DECREASE IN PROPORTIONS OF SOUTHERN AND
NORTHERN GROUPS OF MAMMALS
(Recent and Fossil Families, Living Genera)

	TEMPERATE South America	TROPICAL South America	MIDDLE America	NORTH America
% Total Southern Families	77	85	62	31
% Total Northern Families	47	59	81	94
Ratios:				
Southern:Northern Families (maximum)	2:1	1.7:1	1:1.1	1:2.5
Southern:Northern Genera	22:1	3:1	1.2:1	1:2.6
% Southern Genera (100% = 146)	36	100	53	22
% Northern Genera (100% = 84)	29	58	74	100

Certain conclusions emerge from the evaluation of the comparative data. Some data can be interpreted to favor each of the three possible hypotheses: a) primary movement from North into South America (Simpson's view), b) primary movement from south to north (Herskovitz' position), or c) that the faunal exchange was balanced. Nevertheless the 10 comparisons made in the preceding paragraphs support the following conclusions:

1. a higher proportion of northern families were able to invade South America and penetrate to the temperate zone of the continent than the reverse (47% of northern families, 31% of southern families); almost equal numbers of genera of northerners (24) and southerners (32) reached temperate areas on the opposite continents and each of these values is about 17% of the total northern or southern genera in the New World

2. in the region of the Isthmian Link the picture is mixed but points to a balanced faunal exchange

a. in favor of greatest south to north movement, at the family level, southerners affected Middle America more profoundly than northerners affected tropical South America: 48% of the Middle American families are of southern origin; 37% of the tropical South American families are of northern origin, 56% of the genera in Middle America are of southern origin, only 25% of the genera in tropical South America are of northern origin,

b. in favor of greatest north to south movement at the generic level, northerners invaded tropical South America more than southerners invaded Middle America: 79% of the northern genera in Middle America have reached South America, while 53% of the southerners in tropical South America have reached Central America or beyond

c. all other measures of contributions to the interchange indicate a balanced situation:

24 southern families moved north, 19 northern families moved south;

65% of all southern families now occur in Middle America, 58% of all northern families now occur in tropical South America;

73% of the southern families in tropical South America reached Central America, 72% of the northern families in Central America reached South America;

ratios of southern to northern families for tropical South America compared to Middle America are 1.7:1 and 1:1.1, respectively;

35% of all New World northern genera have reached tropical South America, 40% of all New World southern genera have reached Central America;

ratios of southern to northern genera for tropical South and Middle America are 3:1 and 2:1, respectively;

53% of the southern and 58% of the northern genera, when the greatest number of genera in any one region is used as 100%, are found in Middle America and tropical South America, respectively.

3. faunal enrichment also was generally balanced; in Middle America before faunal exchange and extinction the area had 25 northern families, today the total is 17 northern and 19 southern; in tropical South America before the exchange there were 33 southern families, today there are 26 southern and 17 northern families in the region; the Middle American fauna was enriched by 44%, the South American by 30%. The enrichment in both cases involved a disproportionate extinction of native families and enrichment by invader lines (Table 6).

The hypothesis of Simpson (1950) regarding a greater immigration and effect on South America of northern groups than southern effects on North America is not supported. His views are strongly biased by his comparisons between temperate North America or North and Central America combined versus South America, which obscured the degree to which South American groups contributed to the fauna of tropical Middle America. It is true that 79% of the northern genera in Central America have reached South America

while only 53% of the southern genera in tropical areas have passed into Central America. However, 77 southern genera have moved northward and 48 northern genera southward. Of the 141 northern genera in the New World only 35% have reached South America and only 25% of the tropical South American fauna is of northern origin. Emphasis on the one point of substantial immigration of northern genera into South America from Central America creates a false picture of the situation. Other evidence supports the concept of balanced interchange.

Hershkovitz' (1969) hypothesis that southern immigration northward is dominant also is supported by the following data, at the family level 51% of the Middle American mammal fauna is of southern origin, 35% of the tropical Southern American fauna of northern origin. 56% of the Middle American genera are of southern groups, 25% of the tropical South American genera are from the north. These values are considerably biased, since many southern groups only occur in extreme lower Central America, a region indeed dominated by recent southern invaders. The remaining evidence supports a concept of balanced interchange.

Darlington (1957:367) suggested a possible balanced exchange, but was handicapped by his acceptance of Simpson's views. He finally concluded that the South American fauna was profoundly changed by the exchange, North America much less so. A balanced exchange is strongly indicated by my analysis. At the family level more southern groups moved northward than the reverse; at the generic level the northerners had greater impact. In terms of total New World families and genera, in short the total pattern of mammalian faunal distribution, the exchange was balanced, 62% of all New World southern families and 40% of the genera have invaded Middle America; 59% of all New World northern families and 35% of the genera have reached South America. Other comparisons (Tables 5-6-7) confirm the equilibrium established between northern and southern invaders and endemic stocks. The essential pattern of approximately equal interchange between the continents is reiterated by each comparison (see 2c above). Only in the immediate region of the Bolivar Trough does the general balance seem to break down. The view of this breakdown depends upon the data selected for evaluation. On one basis southern families have been more successful invaders than northern families, 25 southerners to 19 northerners involved in the exchange; 51% of Middle America families are southern in origin, 35% of tropical South American are northern. In terms of total number of families 62% of southern families and 59% of northern families were involved; 73% of the southern families in tropical South America and 72% of the northern families in Central America were involved in the exchange. At the generic level on one basis the apparent breakdown of balance is the reverse of the pattern for families, since 79% of the northern genera in Middle America have crossed into South America and only 53% of the southerners have ranged north, but 77 southern genera occur in Middle America and only 45 northern genera in tropical South

America. Which values indicate the dominant movement and effect? The other comparisons show a balance of generic exchanges when total numbers of New World genera are considered; for example, 34% northerners, 40.5% southerners, are involved in the exchange. When faunal enrichment for tropical America as a whole is evaluated, the enrichment of Middle America at the family level was 44%, for South America 30%, confirming the present overall balance following the interchange and maximum exchange during the last 10-12 million years.

The role of Middle America

When I began this study, it was with the full expectation that the Middle American mammal fauna would prove to be as distinctive and significant to understanding of origins and history as is the herpetofauna (Savage, 1966). In my paper I demonstrated that the Middle American herpetofauna is unique, mostly endemic and only slightly influenced by northern and southern invaders. Of 159 genera of amphibians and reptiles in Central America 67 are Middle American in origin. Only 14% of the genera north of Panama are South American in origin and less than 12% are of northern affinities. The expectation for the mammal fauna has not been fulfilled.

The herpetofauna of Middle America is dominated by autochthonous tropical groups, (Middle American Element) that apparently are allied to South American tropical stocks (South American Element). The two elements underwent independent evolution north and south of the Panamanian Portal during Eocene-Pliocene and have been involved in the intercontinental interchange across the Isthmian Link. Temperate North America has its own herpetofauna made up of stocks (Old Northern Element) associated with the history of temperate forest climates and a more recent series (Young Northern Element) derived from tropical ancestors in association with development of temperate subhumid to arid climates. Neither of these latter two stocks profoundly affected tropical Middle America. Three major recent herpetofaunas occur in the New World, a North and temperate Middle American fauna (Nearctic), a tropical Middle American fauna (Mesoamerican) and a tropical and temperate South American fauna (Neotropical).

The mammal situation is quite different. Two major recent faunas are recognized (Herskovitz, 1958) a North American temperate unit (Nearctic) and a Middle and South American unit (Neotropical). Only two principal historical units, a Southern Element and a Northern Element seem to be involved in mammal history (Table 3). These differences partially reflect the relative ages and evolutionary patterns for amphibians-reptiles and mammals. All orders and probably most families of living amphibians and reptiles were represented in Cretaceous. Some orders (marsupials, insectivores, multituberculates, condylarths, and creodonts) of mammals are known from Early Paleocene, but most do not appear until Eocene. Among Southern Element groups many of the families appeared by Eocene, but most of those still extant

appeared in Oligocene. Many Northern Element families are Oligocene in age, but a number, about 10, did not appear until Miocene or later. The northern mammal lines seem to have had little difficulty in populating and replacing more primitive stocks in Central America. The slower pace of amphibian and reptile evolution allowed *in situ* differentiation of ancient groups in Middle America. The Cenozoic mammal situation conforms to the concept of Matthew (1915), Simpson (1950) and Darlington (1957) of northern origins and southward immigration of higher placental mammal families. The more temperature sensitive amphibians and reptiles do not follow this pattern. Their centers of evolutionary radiation are tropical or warm temperate, with construction of family ranges by Late Cenozoic temperature effects, immigration reduced and more likely to involve south to north movement than the reverse.

Simpson (1950) viewed tropical Middle America as being at present a complex transition zone, barrier and pathway for immigration with its combined roles acting to form a filter to faunal interchange across the Isthmian Link. In his view, during the past, Middle America was populated by tropically adapted northerners that were in position geographically and ecologically to invade South America. He aptly pointed out that most of the groups regarded as North Tropical (Table 3) types by me, were probably differentiated in the Middle American tropics and thus could rapidly and successfully invade South America when the land connection was formed. Darlington (1957:459) also regarded Central America as a transitional zone between temperate North America and tropical South America.

Herskovitz (1958) concluded that tropical Middle America was dominated by Neotropical groups and that it is not a transitional zone between North and South American faunas. He (1966, 1969) expanded on this view and related it to his idea that the Panamanian Portal was ineffective as a dispersion barrier and that Middle America was a region of differentiation, primarily for southern groups (Table 2, unit 3) and as a staging area for northern groups that invaded South America overwater (unit 2) and overland (unit 8).

Patterson and Pascual (1968) regarded tropical Middle America as the area of differentiation of numerous northern stocks (particularly cricetid mice) that rolled into South America, while disappearing to the North, after an Early Pleistocene land-bridge was established. The data presented in their paper and in the previous sections of this report seem clearly to define the role of Central America in faunal history. From earliest Cenozoic it has been closely tied to North America and populated with tropical groups of northern origins. It is from these latter stocks that additional groups passed across the marine portals to South America from Cretaceous to Miocene (Table 3, Young Southern Complex). These stocks underwent evolution in isolation in South America as their tropical Middle American allies became extinct. Even as early as Late Eocene, Nuclear Central America was almost completely domi-

nated by derivative northern lines. By Late Miocene 25 northern families were in the region, underwent differentiation into groups still present there, and became the earliest post-Miocene invaders of South America (Table 3, North Tropical Complex). All evidence suggests that no southern stocks or a very few were in Middle America at this time. The idea of Patterson and Pascual (1969) that 40 sigmodontine mice genera differentiated in Central America and immigrated *en masse* into South America, leaving behind only 4 or 5 stocks is a drastic overextension of this view. Since the intercontinental connection was established many northern genera in Central America have moved southward and at least 77 southern genera have moved into Central America. No evidence suggests wholesale immigration by one group, but rather movement by representatives of many different genera.

It seems in this instance that tropical Middle America served several functions in the periods just before, during and after formation of the Isthmian Link:

1. North Tropical groups underwent differentiation there prior to uplift;
2. These groups moved southward into tropical South America and new stocks (North American) began to filter into the region after the bridge was established;
3. Southern groups moved northward across the connection;
4. The region today has a mixed fauna: 19 southern families to 17 northern families; 77 southern genera to 62 northern genera; it has acted and continues to act as a barrier, pathway and filter to northward and southward movements by South American and North American mammals, respectively. Its role as a center of differentiation is past, since only 11 genera are endemics, 8 southern and 3 northern.
5. The region today forms a complex filter to faunal interchange and its mammal fauna (families: 53% southern, 47% northern; genera: 56% southern, 44% northern) reflects the modern role as a transitional zone, forming both a barrier and a pathway for immigration.

The distribution patterns of mammals and the actual operation of the filter effects in Middle America have never been analyzed in depth, although Simpson (1950, 1956) realized the need and significance of such a study. It may well be that the apparent transitional nature of the region, at least as far as mammals are involved, is overemphasized by a treatment of it as a single unit. In my study of the herpetofauna (Savage, 1966) the Central American fauna, taken as a whole, appeared to be a transitional mixture of South American post-Miocene immigrants (42% of the genera) and northern groups (58%). Detailed analysis, however, demonstrated that southern genera are predominant only in the southern portion of the Isthmian Link (Panama). In Nuclear Central America less than 15% of the genera are of southern origin.

The mammals of the West Indies

In the discussion of the major patterns of New World mammal distribu-

tion and history I have not included families and genera from the West Indies, since they are peripheral to the central problem. A summary of living (Hershkovitz, 1958) and fossil groups (Simpson, 1956) provides the data for the following observations. It is clear that the islands have been populated by overwater waifs, principally if not exclusively of tropical origins. The lesser Antilles mammal fauna is small, but seems to be mostly derived from northern Venezuela-Trinidad in late Cenozoic. Only the caviomorph heptaxodontid genus *Amblyrhiza* (Anguilla and St. Martin) and the sigmodontine mouse *Megalomys* (Curaçao, Martinique, St. Lucia, Barbuda, and possibly Tobago), are endemic (both are apparently extinct). In addition the phyllostomatid bat genus *Ardops*, with four nominal species, is endemic to the lesser Antilles and the West Indian endemic genera *Brachyphylla* and *Monophyllus* of the same family also occur there.

The situation in the Greater Antilles is very different. The recent fauna consists of endemic insectivores, bats, several endemic caviomorphs and one sigmodontine mouse. In the fossil record an endemic insectivore, several bats, an endemic monkey, several endemic ground sloths and a number of endemic caviomorphs are known from Pleistocene and many of these survived on the island almost to the present (Table 9). Simpson (1956) regarded the fauna as composed of three overwater groups of invaders:

1. the insectivores from North America in Early Tertiary;
2. most of the fauna from South America in Miocene-Pliocene;
3. the sigmodontine mouse from Central America recently. According to his view the ancestors of group 2, arrived by overwater waif dispersion from Colombia.

Darlington (1957) disagreed. He viewed the Greater Antillean mammal fauna as derived primarily by overwater waif dispersal from Central America to Cuba or Jamaica.

Hershkovitz developed another hypothesis, associated with his general theme of the inefficacy of the Panamanian Marine Portal as a barrier to intercontinental mammal dispersal. Four separate invasions by overwater transport were suggested:

1. the ancestor of the insectivores from Central America in Cretaceous or early Tertiary (possibly by a land bridge, Fig. 5A);
2. immigrants from the south in Middle Tertiary, while South America was separated from Middle America (endemic bats, edentates, and caviomorphs);
3. bats from Central America, derived from overwater transport from South to Central America in earlier times;
4. recent species from Central America.

Although he stated that the total fauna seems to be South American in origin, Hershkovitz (1969:10, Fig. 5) concluded that the Greater Antillean mammal fauna is a relict representative of a tropical Tertiary Middle American fauna. This view is another example of the confusion caused by Hershkovitz'

underestimate of the effect of the Panamanian Portal. It is clear that mid-Tertiary mammals in Central America did not include representatives of Southern Element stocks and that the West Indian fauna shows virtually no effect of North Tropical genera.

TABLE 9
MAMMAL FAUNA OF THE GREATER ANTILLES

GROUP	ORIGIN					Total (Extinct)
	SOUTHERN South American	ELEMENT Young Southern	West Indian	NORTHERN North Tropical	ELEMENT North American	
Insectivores			3(1)			3(1)
Primates		1(1)				1(1)
Bats	15(2)	1		3	4	23(2)
Edentates	5(5)					5(5)
Caviomorphs		18(15)				18(15)
Sigmodontines		1				1
Total	20	21	3	3	4	51
%	39	41	6	6	8	100
Extinct	7	16	1			24
Living	13	5	2	3		27
%	48	18.5	7	11		100

The accompanying table (Table 9) makes the situation clear. The bulk of Greater Antillean genera are South American in origin and most of them probably reached the islands prior to the invasion of Central America by the southern lines in Pliocene onwards. The peculiar insectivores are ancient relicts of North America origin and their ancestors may have crossed to Cuba (portions land positive throughout Tertiary, according to Malfait and Dinkelman, 1972) from Central America or Gulf coastal North America early in Tertiary. For this reason they cannot be grouped with any of the four historical units recognized for continental forms and I have separated them as a West Indian unit. Seven northern bat genera and the very recent sigmodontine invader (*Oryzomys*) seem to have come from Central America. *Oryzomys* is a Young Southern Element genus that spread very rapidly into Central America after the Isthmian Link was established in Pliocene. The Antillean species *O. antillarum* belongs to a Central American species group (*palustris*) that ranges from Panama to New Jersey and is an example of the immigration of southern genera across the land link.

My analysis supports the hypothesis of Simpson (1956) in most respects. If Darlington (1957:510-517) and Hershkovitz (1969:10) are correct that the Greater Antillean fauna came mostly by overwater transport from Central America then this occurred well back in Tertiary. This idea suggests that the insectivores, primate, most bats, edentates and caviomorphs are relicts of a hypothetical ancestral tropical fauna in Central America that gave rise to

Antillean and South American stocks, but is now extinct in Middle America, except for descendant groups that re-invaded from South America. Only the presence of insectivores supports this concept. The Antillean primate, bats, edentates, and caviomorphs all appear to be advanced derivative groups rather than near the ancestral stocks that originally reached South America. One subfamily of phyllostomatid bats and two families of caviomorphs are endemic to the islands, but all close relatives are South American. For terrestrial mammals Simpson's three strata of overwater waifs cited at the beginning of this section agree with available evidence. Perhaps some of the bats of southern derivation have reached the Antilles from Central America since Pliocene.

ORIGINS OF NEW WORLD TROPICAL MAMMAL ASSEMBLAGES: A SUMMARY

The purpose of this section is to summarize the ideas developed in the preceding pages in the form of a general theory (Savage, 1960:184).

At the beginning of Cenozoic relatively few major mammal stocks populated the world. In South America marsupials, edentates, condylarths and protonotungulates were already established as an isolated fauna probably derived from the Gondwanaland mammal fauna of Late Triassic. That these stocks were already in South America and did not arrive there from the north as proposed by Simpson (1950, 1969) and Patterson and Pascual (1963, 1968) seems likely (Fooden, 1972). Some question still persists as to whether the basic South American lines reached Central and North America by waif-overwater or overland migration and if the latter where the land connection was geographically located. Evidence from geology, invertebrate paleontology and distribution of the herpetofauna suggests the presence of a Paleocene intercontinental connection but not in the present day Isthmian Link region. The latest new tectonic studies (Freeland and Dietz, 1971; Malfait and Dinkelman, 1972), while equivocal, tend to rule out such a proto-Antillean land-bridge. The original mammal groups underwent independent evolution in isolation in South America until Pliocene, (Fig. 1) since the Panamanian Marine Portal separated Nuclear Central America from South America from Late Cretaceous to Pliocene, their closest allies to the north became extinct during this time interval in Central and North America. The descendent stocks of this ancient assemblage form the South American Complex of the Southern Element (Table 3).

From Cretaceous to Miocene (Fig. 2) a number of additional mammal stocks appear to have invaded South America from Nuclear Central America, across the marine barrier. In chronological order from earliest to latest these are: primates, caviomorph rodents, manatees, bats, and sigmodontine mice of the family Cricetidae. The latter series of waif invaders are grouped as the Young Southern Complex of the Southern Element (Table 3). These stocks also underwent evolution in isolation in South America and the two complexes are responsible for the unique composition of the mammal fauna on

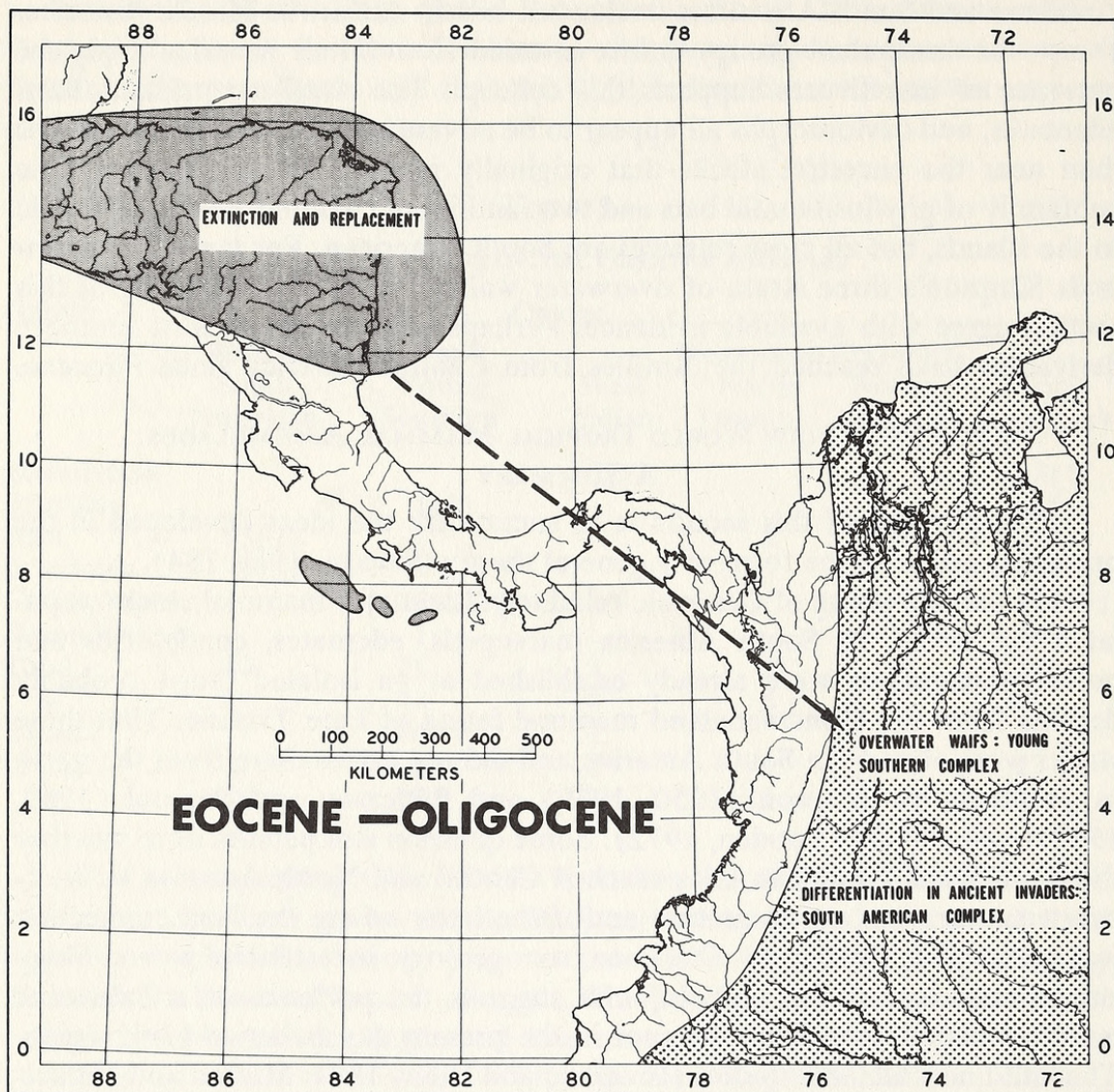


FIGURE 1. Probable Eocene-Oligocene distribution of historical units of Neotropical mammal fauna, indicating events taking place concurrently in Nuclear Central America and South America. Dashed arrow indicates source of overseas waifs.

that continent. These stocks too were replaced and disappeared in Central America.

During mid-Tertiary a series of northern mammal groups invaded Middle America and underwent some differentiation there to form the North Tropical Complex of the Northern Element (Table 3). Contrary to the views of Hershkovitz (1966, 1969) the Panamanian Portal prevented any substantial overwater interchange between South America and Nuclear Central America. Thus, until Pliocene, Northern and Southern Elements remained geographically isolated from one another. In Miocene the portal became reduced from north to south and an elongate peninsula was established. The final waterway to be closed was the Bolivar Trough. The evidence of fossil Miocene mammals in Panama and northern Colombia demonstrates that even



FIGURE 2. Probable Early Miocene distribution of historical units of tropical American mammal faunas.

this relatively narrow (100 km) marine barrier was extremely effective, since no southern groups occurred north of it and no northern groups to the south.

In earliest Pliocene (Fig. 3) the Isthmian Link was completed with the uplift of the Bolivar Trough region. At this time began a dramatic and rapid faunal interchange that continues today. Although Simpson (1950, 1969), Darlington (1957), and Patterson and Pascual (1968) place the time of intercontinental connection as Early Pleistocene, the geologic data, invertebrate paleontologic evidence, distribution of recent herpetofaunas and the South American mammal fossil record with northern groups (procyonids, a skunk and two peccaries) present in Pliocene make it clear that an Early Pliocene connection occurred.

The interchange was complex and continuous from Pliocene onwards and involved both Southern complexes, the North Tropical Complex and in

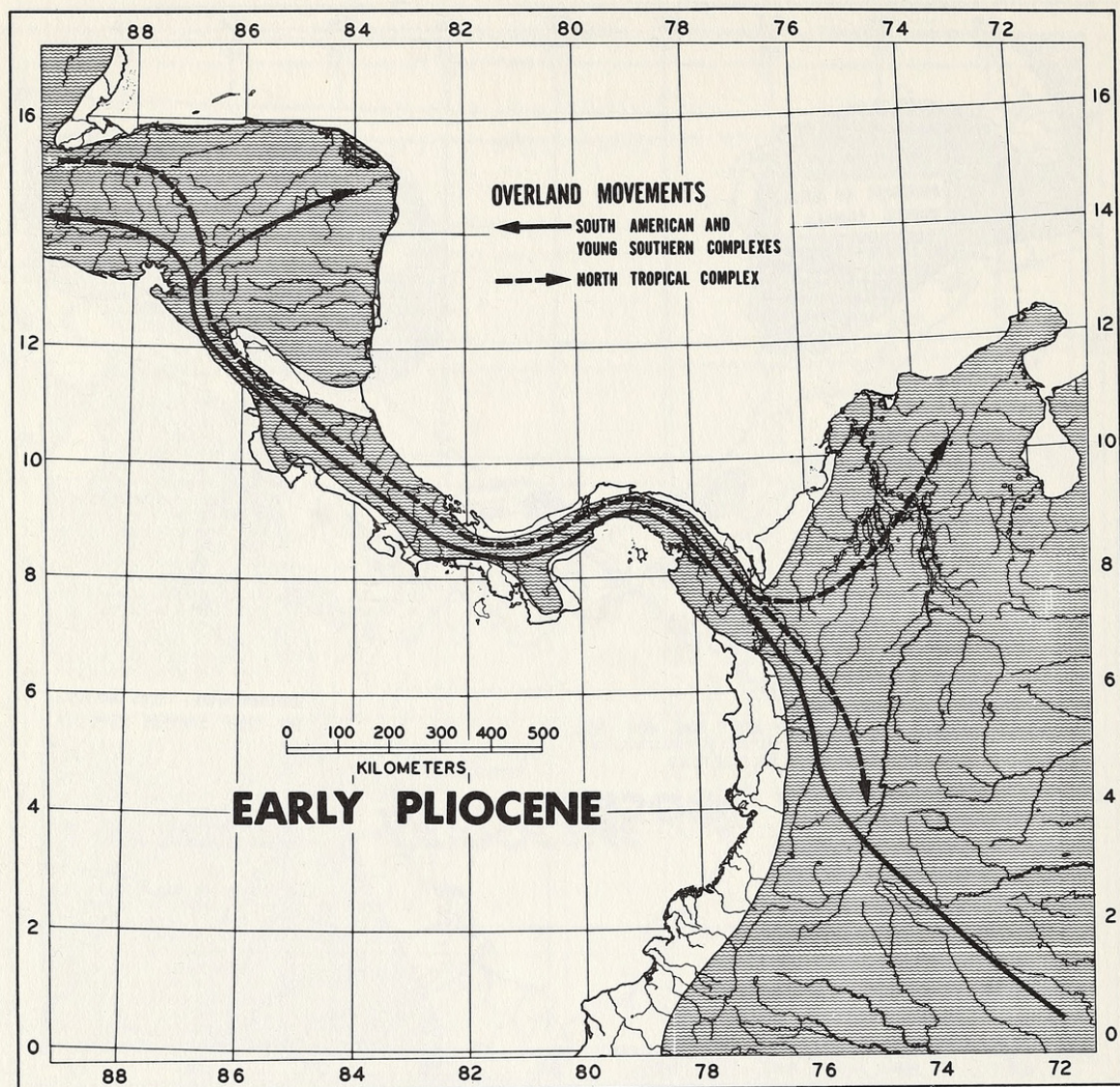


FIGURE 3. Probable Early Pliocene overland movements of historical units of tropical American mammal faunas.

Pleistocene a second northern faunal unit, the North American Complex (Table 3). Members of this complex are allied to the tropical northerners, but are derived from temperate stocks established in North America no later than the time the land connection was formed in the Isthmian region, or are Pleistocene invaders from eastern Asia (Fig. 4). Derivatives of these lines comprised a second wave of northerners that penetrated the tropics of Middle America in Pleistocene and some have extended their ranges into South America (Table 3).

Following the establishment of the Isthmian Link 24 southern families have entered Central America, 12 reached temperate North America; 19 northern families entered South America, 15 reached the temperate areas of the continent. Today, out of 191 southern genera, 40% occur in Central America, 17% in temperate North America; of 141 northern genera, 44% occur in Middle America, 35% in tropical South America and 17% to the

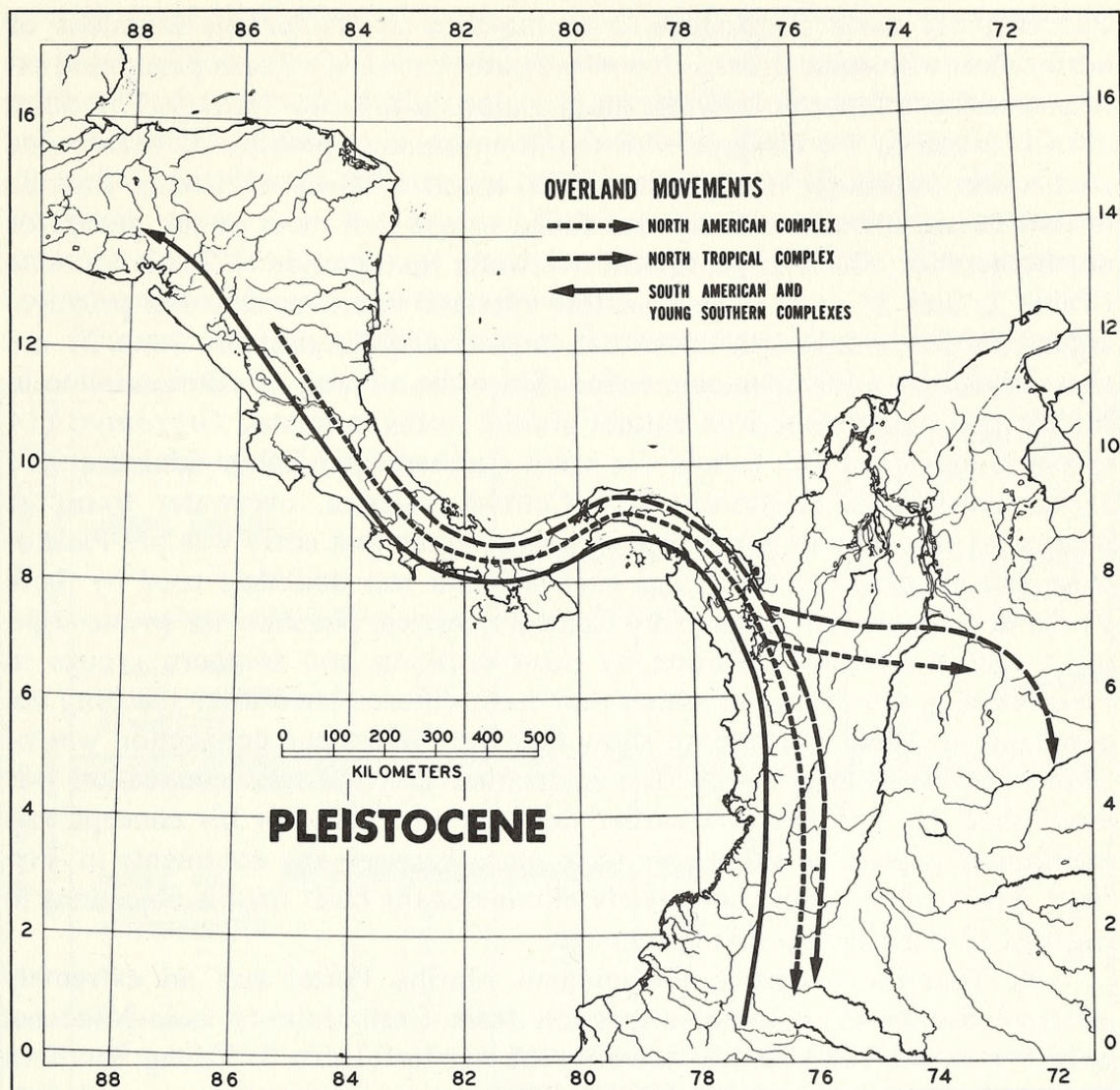


FIGURE 4. General patterns of overland migrations in Pleistocene for historical units of tropical American mammal faunas.

south. Contrary to the views of Simpson (1950), Darlington (1957), and Patterson and Pascual (1968) the immigration has not been predominantly from north to south. Nor can I agree with Hershkovitz (1969) that the heaviest flow was from south to north. Taken in totality, northern families and genera contribute to about the same degree to the fauna of South America as southern families and genera to the fauna of tropic Middle America. The most impressive feature of the interchange is the almost equal effects of north-south and south-north post-Miocene immigrations in modifying the faunal structure in both regions.

In terms of the controversy between the views of Simpson (1950), as supported by Patterson and Pascual (1968) and those of Hershkovitz (1966, 1969) as reviewed in an earlier section of this paper, my analysis indicates:

A. That the time of reconnection between the continents was early

Pliocene, *not* early Pleistocene, a timing that allows for the invasions of northerners with some differentiation in South America, without presuming extensive and continuous overwater immigration during mid-Tertiary. This point is critical and in it I disagree with the Simpsonian hypothesis of Pleistocene connection. Although Hershkovitz (1969) favors a Miocene-Pliocene link, he missed its significance entirely and failed to see that most of the groups of northerners for which he postulated overwater immigration to South America (Table 2, unit 2) must have used this overland route instead. His principal arguments for south-north overwater invasions by southerners (unit 3) are also vitiated by a Pliocene connection. Since the amount of differentiation in Middle and North American extinct ground sloths, primates, *Oryzomys*, (14 species) and *Sigmodon* (about the same number) and Echimyidae required earlier entry than Pleistocene into Central America, overwater transport seemed to Hershkovitz a reasonable view. I agree that entry was pre-Pleistocene, but an overland route was available and was doubtless used by these stocks in Pliocene movements into Central America. Hershkovitz' prime argument against overland invasion by most northern and southern groups in Pleistocene is the degree to which they have differentiated after reaching the new land area. He attempts to show that the Pleistocene connection was of little significance as a result. The realization that the land connection was established 10 million years earlier destroys any basis for his concept that continuous overwater exchanges took place between the continents in Tertiary. The revised timing completely eliminates the basis for his objections to the idea of extensive overland exchange.

B. That the extensive Panamanian Marine Portal was an extremely effective barrier to mammal dispersion from Cretaceous to Late Miocene; only five stocks succeeded in crossing the barrier (Table 3, Young Southern Complex) from north to south, none in the opposite direction; even the reduced portal, restricted to the Bolivar Trough, of Late Miocene was a remarkable barrier to mammal dispersion. In this regard I concur completely with Simpson. Much of Hershkovitz' theory of the history of mammals in his region is negated by his failure to appreciate the barrier effect of the 1000 km extent of the great seaway of Eocene to Miocene and the amazing effectiveness of the 100 km wide Bolivar Trough of Miocene times.

C. That Middle America was an area of differentiation for groups of mammals at infrafamilial levels during middle Tertiary, but not as a center for the origin of new families of northerners; it was clearly isolated from the south during this time, contrary to Hershkovitz (1969), by the seaway and did not have any, or had at most a few southern overwater waif components. The Tropical Northern Complex developed here and formed the initial wave of southward invaders when the Isthmian Link was forged. These views do not substantiate either Simpson (Middle America a major center of differentiation) or Hershkovitz (Middle America with a mixed fauna) in their ideas of tropical Middle America in pre-Pliocene times.

D. That the effect of Isthmian connection produced a dramatic and rapid faunal interchange in both directions with profound effects on the composition and structure of the faunas of North, Middle, and South America and that these effects were essentially balanced. Simpson claimed an even more dramatic change (Pleistocene) with northerners affecting South America much more than the reverse. Herskovitz minimized the extent and amount of overland exchange after the linkage and thought that maximum movement was of southerners into the north.

The role of the Isthmian Link in these events is summarized (Fig. 5).

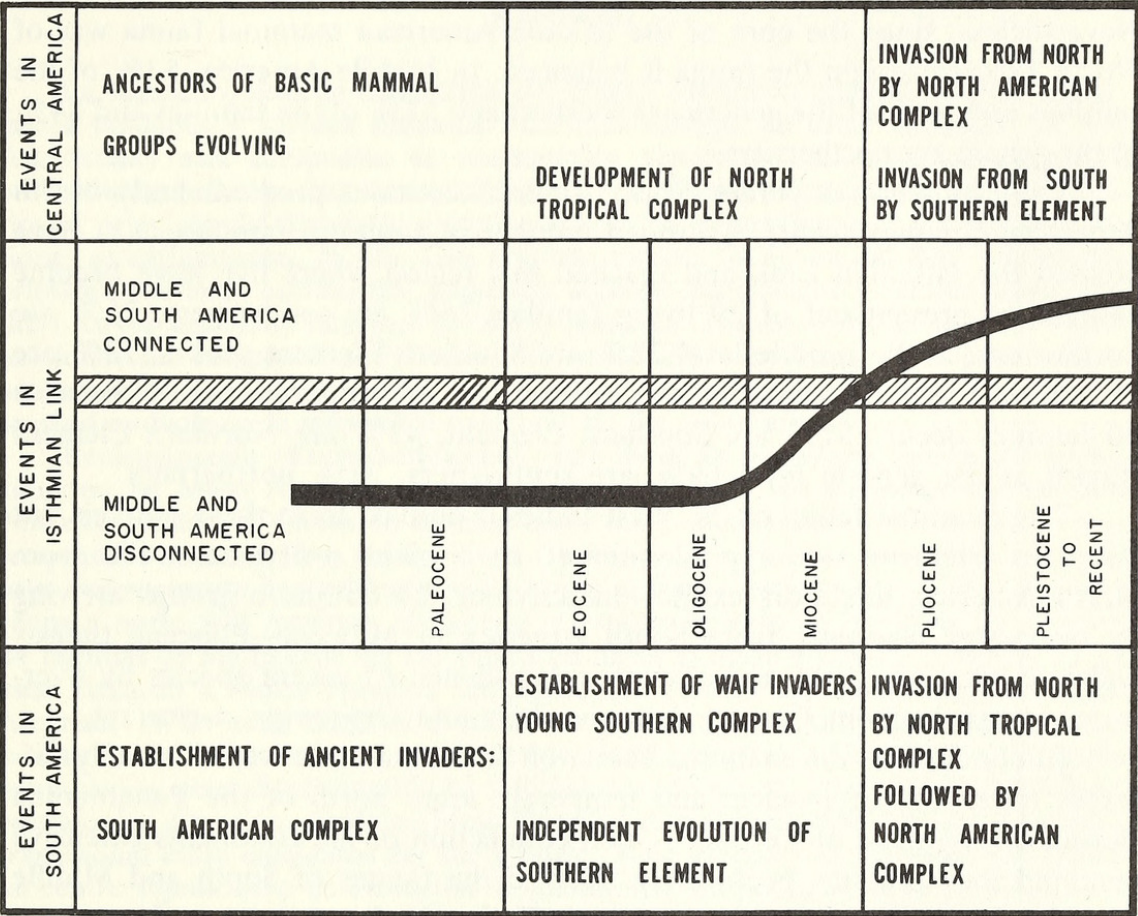


FIGURE 5. Geological history of Isthmian Link—Panamanian Portal region and effects on historical units of tropical American mammal faunas.

The present day South American mammal fauna is composed of two major historical elements, each with two components. The South American and Young Southern groups have a long independent history on the continent. Two waves of Northern Element lines have invaded South America since Miocene across the Isthmian Link. The first, North Tropical groups, were in Central America when the connection was established; the second is a more recent wave of temperate North American stocks that arrived in Early Pleistocene in Middle America, and some continued southward. In the total South

American fauna 60% of the families and 78% of the genera are of the Southern Element; 40% of the families and 22% of the genera are of the Northern Element.

The Middle American mammal fauna contains groups from both Southern Element complexes and both Northern Element complexes. Since Early Pliocene it has had invaders from the south (South American and Young Southern groups) and north (North American groups) add to its basic structure of North Tropical stocks. The southern invaders crossed the Isthmian Link, the northern stocks the land mass of Central America. Many more southern groups reached Central America than did North American types. Nevertheless, since the core of the Middle American mammal fauna was of North Tropical origin the fauna is balanced. In Middle America, 53% of the families and 56% of the genera are southerners; 57% of the families and 44% of the genera are northerners.

The fauna of temperate North America contains predominantly North American complex forms. A limited number of southern families (12) have crossed the Isthmian Link and reached this region where five have become extinct. At present out of 29 living families 24% are southerners, 76% are northerners; at the generic level 28% are Southern Element genera, 72% are of the Northern Element. By way of contrast in temperate South America 30 families occur: 57% are Southern Element, 43% are Northern Element stocks; at the generic level 69% are southerners, 31% northerners.

The mammal fauna of the West Indies is derived from these sources, but Southern Element stocks predominate: a) ancient overwater waifs from North America, ancestors extinct—insectivores; b) Southern groups arriving by overwater transport from South America in Miocene–Pliocene times—endemic bats, edentates and caviomorph rodents; c) recent species by overwater transport from Central America—bats and *Oryzomys*, a rice rat.

In conclusion, the mammal fauna of South America was extremely different from that of tropical and temperate areas north of the Panamanian Portal, during most of Tertiary. Upon connection of the continents extensive overland immigrations profoundly affected the faunas of South and Middle America from Early Pliocene onward. Today both southern and northern faunas have been significantly modified by the increments, but the effects are essentially equalized. Both faunas have been substantially enriched by the exchange, but neither has been disproportionally influenced by the recent immigrants.

The role of Middle America in the history of the mammal faunas has been overemphasized by most authors. It served as a staging ground for North Tropical differentiation (no more than generic or species group level in most cases) and invasion across the link; also as the region most strongly affected by southern invaders. It is today primarily a complex, transitional zone, forming both a barrier to and a pathway for immigration and acting within these combined roles as a filter to faunal interchange across the link region. A



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