Was southern Central America an archipelago or a peninsula in the middle Miocene? A test using land-mammal body size

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Abstract

There has been considerable discussion about the complex geological history of southern Central America in the late Cenozoic prior to the closing of the Isthmus of Panama during the Pliocene. It is particularly unclear how far nuclear Central America extended southward as a continuous land connection with North America versus the alternate paleogeographic reconstruction of an extensive island-arc system during this time. In modern faunas, terrestrial mammal body sizes have fundamentally different patterns within regions of continuous land-mass versus island populations as a result of the "island rule." Variation in body size is relatively limited in species with continent-wide distributions, whereas, relative to mainland populations, those on islands can have as much as a four-fold increase, or decrease, in body size. Using tooth molar dimensions as a proxy for body mass, tooth size is compared from a middle Miocene land-mammal fauna from Panama (Gaillard Cut Local Fauna) relative to contemporaneous faunas in North America. Among six species, there is no significant difference in tooth size between Panama and North America. A second test comparing the artiodactyl *Paratoceras wardi* between Panama and Texas shows a significant difference in tooth size, with *P. wardi* from Panama having slightly larger teeth (104% to 112% larger) than *P. wardi* from Texas. This difference in size, however, is small compared to that predicted from insular evolution and is more consistent with the amount of variation seen in continent-wide species distributions. Results from both tests are consistent with the hypothesis that southern Central America had a dry-land connection to North America during the middle Miocene. Based on these data, there is no support for the alternate hypothesis of an extensive archipelago in southern Central America during this time.
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1. Introduction

The paleogeography of southern Central America has changed profoundly over the past 20 million

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years (Ma), from a volcanic arc separated from South America by a wide seaway, to an isthmus that connected North and South America only 3 Ma (Duque-Caro, 1990; Coates et al., 1992, 2003, 2004; Coates and Obando, 1996). The formation of the Isthmus of Panama was important because it facilitated the mixing of terrestrial faunas between the two continents (Webb, 1976; Stehli and Webb, 1985), as well as physically separating a once continuous marine province into separate and distinct Pacific and Caribbean communities (Woodring, 1965, 1966; Vermeij, 1978; Vermeij and Petuch, 1986; Jackson et al., 1993, 1996). Although several studies have clarified the geologic history of the formation of the isthmus (Emiliani et al., 1972; Keigwin, 1978; Duque-Caro, 1990; Coates et al., 1992, 2003, 2004; Coates and Obando, 1996; Collins and Coates, 1999), the paleogeography of southern Central America before the isthmus has remained unclear. Evidence from marine rocks and volcanic terranes suggest that the volcanic arc during the Miocene consisted of an archipelago sepa-
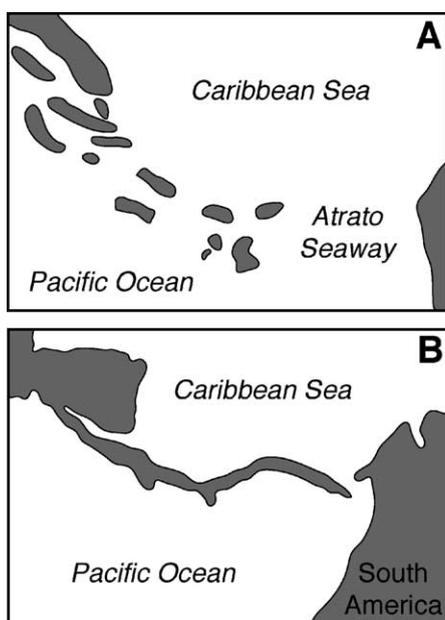

Fig. 1. The two paleogeographic models that have been proposed for Central America during the middle Miocene. (A) Archipelago model (Coates and Obando, 1996). (B) Peninsula model (Whitmore and Stewart, 1965). Emergent land is represented by gray.

rated by shallow straits (Fig. 1A; Coates and Obando, 1996). Alternatively, evidence of terrestrial mammals with only North American affinities suggests a dry-land connection with North America by 16 Ma (Fig. 1B), effectively making the Central American volcanic arc a peninsula of North America during this time (Whitmore and Stewart, 1965). It remains unclear, however, just how strong this connection was before formation of the isthmus. Specifically, did North American mammals (1) disperse over dry land between North and Central America, or (2) were there narrow straits that allowed some, but not all, North American land mammals to swim across? If the former hypothesis is correct, in which there was continuous dispersal between North and Central America as a result of a peninsula, then we may expect little to no isolation and, therefore, little to no divergent evolution in body size between population centers. If the latter hypothesis is correct, then we may expect a greater degree of isolation and, therefore, divergent evolution in body size of the populations reaching islands in Central America via swimming or some other sweepstakes event, relative to dispersal across dry land. The purpose of this study is to test these two hypotheses by comparing differences in tooth size, here used as a proxy for body size, between Miocene land mammals from Panama and their conspecifics from North America. Testing for differences in tooth size allows us to constrain the strength of a peninsular connection to North America.

2. Cast of characters: Miocene land-mammals from Panama

Fossil land mammals are poorly known from Central America. One of the few reported localities containing fossil land mammals is the "Gaillard Cut Local Fauna" (L.F.) in the middle Miocene Cucaracha Formation (Ferrusquía-Villafranca, 1978; Rich and Rich, 1983; Tedford et al., 1987, 2004), which lies within the Panama Canal Basin in central Panama (Fig. 2). Whitmore and Stewart (1965) presented a preliminary faunal list for the Gaillard Cut L.F., and MacFadden (in press) formally described the assemblage, which now includes 10 species comprising four orders and eight families
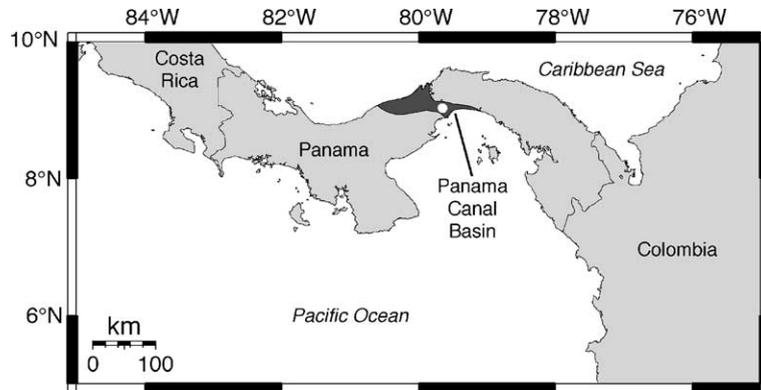
Fig. 2. Location of the Gaillard Cut Local Fauna (open circle) within the Panama Canal Basin in central Panama.

of mammals (Table 1). The Gaillard Cut L.F. is of great paleobiogeographic significance because it is located 2000 km south of the closest similar aged fauna in central Mexico (Ferrusquía-Villafranca, 1978), and about 500 km northwest of middle Miocene faunas from Colombia (Kay et al., 1997). Despite the relative proximity to South America, the Gaillard Cut L.F. is of completely North American taxonomic affinity (Table 1; Fig. 3), suggesting a seaway barrier to the east of the Panama Canal Basin. This fauna is particularly important because it indicates that a diverse continental-like community was already well established by the middle Miocene in Panama (Whitmore and Stewart, 1965; MacFadden and Higgins, 2004). These land mammals, therefore, represent the southernmost North American fauna before the great American biotic interchange about 3 Ma.

3. Mammalian body size variation on islands and continents

Body size is an extremely important trait of any species and is highly predictive of ecology, adaptation, and life-history characteristics (e.g., Eisenberg, 1981; Peters, 1983). Likewise, phenotypic variability in body size is plastic and can vary within certain limits given changes in the ecology of local populations. In this section, we briefly review the degree to which variation occurs within a recognizable species of mammals, both on islands relative to mainland

Table 1
Land mammal taxa from the Gaillard Cut Local Fauna, Cucaracha Formation, Panama

Order	Family	Genus and species	Common name	Biogeographic affinity
Rodentia	–	*Texomys stewarti*	Geomyoid rodent	North America
Carnivora	Canidae	*Tomarctus brevirostris*	Dog	North America
Carnivora	Amphicyonidae or Hemicyonidae	–	Bear dog	North America
Artiodactyla	Tayassuidae	*Cynorca* sp.[a]	Peccary	North America
Artiodactyla	Oreodontidae	*Merycochoerus matthewi*	Oreodont	North America
Artiodactyla	Protoceratidae	*Paratoceras wardi*	Protoceratid	North America
Perissodactyla	Equidae	*Anchitherium clarencei*	Horse	North America
Perissodactyla	Equidae	*Archaeohippus* sp.	Horse	North America
Perissodactyla	Rhinocerotidae	*Menoceras barbouri*	Rhinoceros	North America
Perissodactyla	Rhinocerotidae	*Floridaceras whitei*	Rhinoceros	North America

Source: Whitmore and Stewart (1965), Slaughter (1981), MacFadden and Higgins (2004), MacFadden (in press), this study.
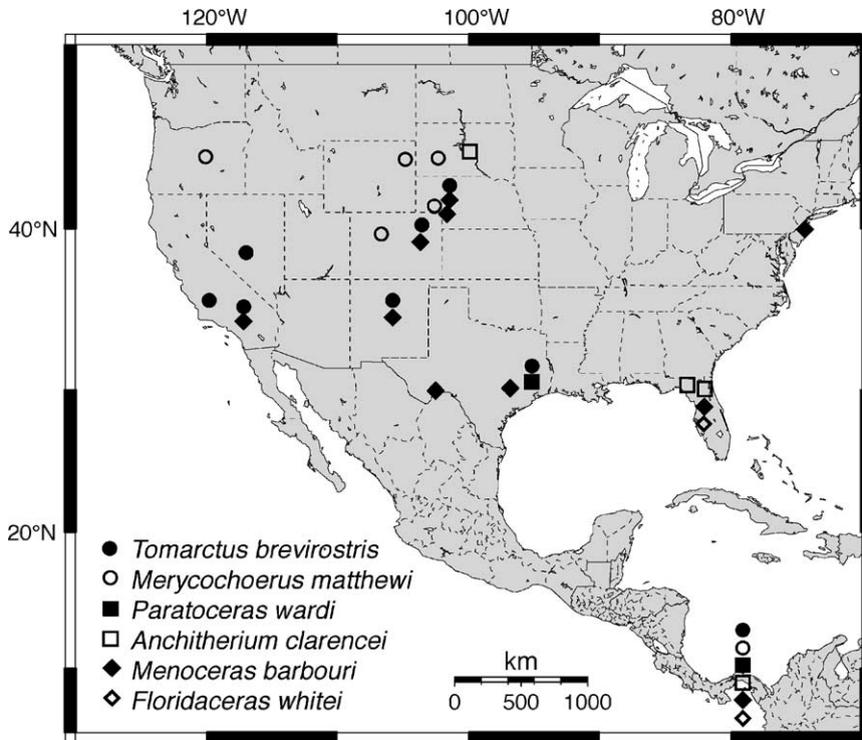[a] New discovery.

Fig. 3. Paleobiogeographic distribution of land mammals from the Gaillard Cut Local Fauna, Cucaracha Formation, Panama Canal Basin, and their conspecifics in North America. Data from Whitmore and Stewart (1965), MacFadden and Higgins (2004), MacFadden (in press) and the Paleobiology Database (http://paleodb.org/).

counterparts, and within species that are widespread on continents.

3.1. Island mammals

Numerous studies have demonstrated that populations inhabiting islands rapidly diverge in body size relative to mainland populations of the same, or closely related sibling, species. Commonly known as the "island rule" (Van Valen, 1973), within an island community of terrestrial mammals, species with large body sizes will evolve smaller body sizes relative to their mainland counterparts (dwarfism or nanism); whereas species with small body sizes will evolve larger body sizes (gigantism) (Foster, 1964; Gould and MacFadden, 2004). The explanations for dramatic and rapid size changes in insular mammal populations are complex and appear to generally relate to changes and limitations in resource availability (Lomolino, 1985; McNab, 1994), or to release from

competition and predation that allows evolution toward an optimum body size for energy acquisition (Case, 1978; Lomolino, 1985; Damuth, 1993). Numerous examples of these phenomena are reported from extinct Miocene through Pleistocene mammalian faunas of the Mediterranean islands. At one end of the spectrum, the fox-sized Miocene insectivore *Deinogalerix koenigswaldi* from the Gargano peninsula of Italy (which was an island during the Neogene) is the largest insectivore ever reported, extinct or living (Freudenthal, 1972). In contrast, the tiny elephant *Elephas falconeri* from the Pleistocene of Sicily is about four times smaller in skull size than its congener, and presumed ancestor, *E. namadicus* from the adjacent mainland (Sondaar, 1977). Size reduction in extinct proboscideans is in fact pervasive in island faunas. In addition to the Mediterranean during the Pleistocene, similar examples of "dwarf" proboscideans are known from *Stegodon* of Indonesia (Hooijer, 1962) and the pygmy mammoth (*Mammuthus*

exilis) of the Channel Islands off the coast of California (Johnson, 1978).

An excellent example of insular dwarfism is also seen in the modern three-toed sloth *Bradypus* from the Bocas del Toro archipelago of Panama (Anderson and Handley, 2002). This series of islands has been sequentially isolated at various times over the past 10,000 years since the latest Pleistocene. Relative to mainland populations of *Bradypus*, the degree of dwarfism is proportional to the amount of time the particular island populations have been isolated (i.e., populations from older islands have significantly smaller body sizes relative to populations from younger islands). Likewise, the recent discovery of *Homo floresiensis* from the island of Flores in Indonesia offers an intriguing example of dwarfism from within our own genus (Brown et al., 2004).

3.2. Continental mammals

When there are few barriers to dispersal and consequently ready gene flow between populations within a species, body size is known to vary, but considerably less than what is seen for insular mammals relative to their mainland counterparts. Yablokov (1974) presented an exhaustive analysis of variation of soft and hard anatomical characters in modern mammals. Linear measurements (e.g., body lengths), normally vary within a coefficient of variation (V) of <10%; whereas, body mass can have significantly more variation within species, with V's frequently approaching 30%, or in some cases more in highly dimorphic species of mammals. As a general rule, Mayr (1969) stated that V's of taxonomic relevance (i.e., within a given species), are usually less than 30%. Simpson et al. (1960) found that the great majority of linear anatomical dimensions have V's between 4% and 10%. Several studies reported in MacFadden (1989) have shown that for morphologically recognizable "morphospecies" of fossil mammals (e.g., horses), linear measurable characters, such as tooth lengths and widths, will demonstrate V's between 5% and 10%.

3.3. Predictive test of insularity versus continental mammals

The foregoing discussion indicates that linear tooth dimensions measured from the Gaillard Cut L.F. as compared to similar-aged faunas from mainland North America can be used as a proxy for understanding whether Panama was an archipelago or a southern peninsular extension of North America during the middle Miocene. On the one hand, if we find significant differences between the Panamanian and North American samples, such that the Panamanian mammals are significantly smaller, then the archipelago hypothesis is supported. Alternatively, if there is no significant difference in tooth size, then the hypothesis of a contiguous mainland connection with ready gene flow is supported.

4. Methods

Samples were analyzed for six of the 10 taxa represented in the Gaillard Cut L.F. as compared to their North American counterparts; specifically, the canid *Tomarctus brevirostris*, oreodont *Merycochoerus matthewi*, protoceratid *Paratoceras wardi*, horse *Anchitherium clarenci*, and rhinos *Menoceras barbouri* and *Floridaceras whitei* (Table 1). Four other taxa from the Gaillard Cut L.F. were not included in this analysis because they were not identifiable to species (indeterminant amphicyonid or hemicyonid, peccary *Cynorca* sp., horse *Archaeohippus* sp.) or they were endemic to Panama (*Texomys stewarti*).

4.1. Tooth dimensions as a proxy for body size

The above discussion concerning possible differences in mammalian body size is predicated on the assumption that this character is a known quantity. In the fossil record, however, true body size is rarely preserved. Thus, inferences about body size must be made from characters that readily preserve in the fossil record. For extinct mammals, teeth provide one of the most frequently preserved clues to estimating general body size. Studies have shown that within taxonomic groups, such as fossil horses, molar dimensions are highly correlated ($R^2 > 0.90$) to body mass (MacFadden, 1986). We, therefore, infer that teeth can be used as a reliable proxy for relative body size (Damuth and MacFadden, 1991). In this study, premolar and molar lengths were used as a proxy to estimate differences in relative body size between the six mammalian species from Pan-
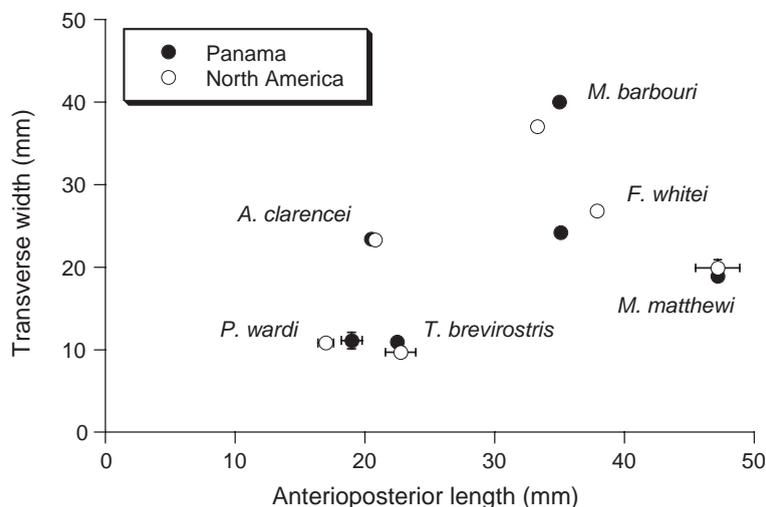
Fig. 4. Bivariate plot comparing tooth size of six species between Panama and North America. Error bars represent one standard deviation.

ama and their counterparts in continental North America.

4.2. Measurements, comparisons, and statistical tests

We performed two separate analyses on the land-mammal teeth from the Cucaracha Formation. First, we compared tooth size between all six species from Panama and North America. Teeth were measured along their greatest transverse width and anterioposterior length with dial calipers. In the case of tapering teeth, such as in artiodactyls, the measurement was taken from the base. Tooth size of some of the North American conspecifics was derived from the litera-

ture. In the second analysis, we compared tooth size within a single species (*P. wardi*) from Panama and Texas, for which we have adequate data. In both analyses, we used paired sign tests to test for significant differences in tooth size (Sokal and Rohlf, 1995).

5. Results

Comparison between the six species from Panama and North America shows no overall significant difference in tooth size (paired sign test, $p > 0.6874$; Fig. 4; Table 2). One Panamanian taxon (*F. whitei*) was 91

Table 2
Comparison of tooth size of six species from Panama and North America

Taxon	Tooth position	Panama			North America			Apl percent difference	Trn percent difference
		Count	Apl (mm)	Trn (mm)	Count	Apl (mm)	Trn (mm)		
Tomarctus brevirostris	m1	1	22.5	10.9	5	22.8 ± 1.2	9.7 ± 0.6	99	113
Merycochoerus matthewi	m3	1	47.2	18.9	3	47.2 ± 1.7	19.9 ± 1.0	100	95
Paratoceras wardi	m3	9	19.0 ± 0.8	11.2 ± 1.0	12	17.0 ± 0.6	10.8 ± 0.5	112	104
Anchitherium clarencei	M1?	1	20.5	23.4	5	20.8	23.3	99	100
Menoceras barbouri	RI1	1	35.0	40.0	1	33.3	37.0	105	108
Floridaceras whitei	p4	1	35.7	24.3	1	37.9	26.8	94	91

Reported as mean ± 1 standard deviation.
North American data from Patton and Taylor (1973) and MacFadden (in press).
Apl = Anteroposterior length.
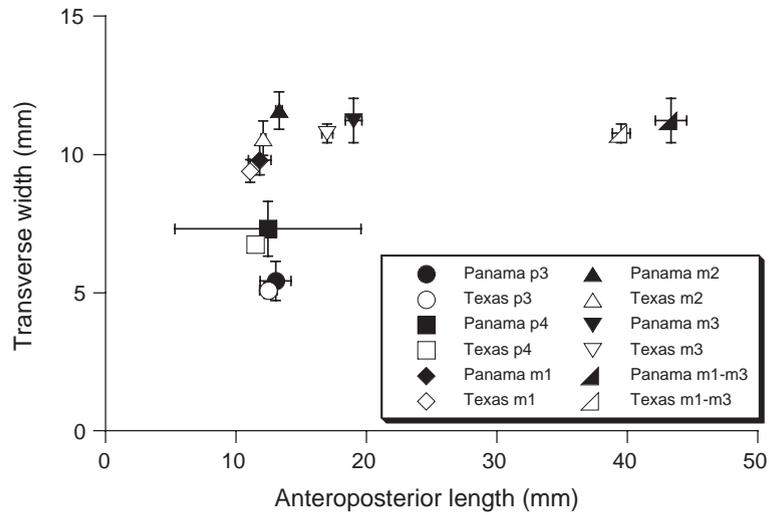Trn = Transverse width.

Fig. 5. Bivariate plot comparing tooth size of *Paratoceras wardi* between Panama and Texas. Error bars represent 95% confidence intervals.

to 94% smaller than its North American conspecific. Three taxa from Panama (*T. brevirostris*, *P. wardi* and *M. barbouri*) were as much as 113% larger than their North American conspecifics. Two taxa (*M. matthewi*, and *A. clarencei*) were too close in size to differentiate. The second test, the comparison of *P. wardi* between Panama and Texas, shows a significant difference in tooth sizes, with *P. wardi* from Panama having significantly larger teeth ($p < 0.001$; Fig. 5; Table 3). All five lower premolars and molars (p3, p4, m1, m2, m3), as well as the anteroposterior length of m1–m3, are larger in *P. wardi* from Panama. There is a greater difference in anteroposterior length than

there is in transverse width for m3 and m1–m3, but the difference appears about equal for the other teeth (Fig. 5; Table 3). Based on these data, *P. wardi* from Panama is at most 112% larger than *P. wardi* from Texas.

6. Discussion

The island rule predicts that populations of large mammals isolated on islands from their mainland counterparts will evolve smaller body sizes, whereas populations of small mammals similarly isolated will

Table 3
Comparison of tooth size of *Paratoceras wardi* from Panama and Texas

Tooth position	Panama			Texas			Apl percent difference	Trn percent difference
	Count	Apl (mm)	Trn (mm)	Count	Apl (mm)	Trn (mm)		
p3	5	13.1 ± 1.0	5.4 ± 0.6	3	12.5 ± 0.3	5.1 ± 0.1	104	107
p4	3	12.5 ± 2.9	7.3 ± 0.4	8	11.5 ± 0.3	6.7 ± 0.4	108	108
m1	8	11.8 ± 1.0	9.8 ± 0.6	11	11.1 ± 0.3	9.4 ± 0.6	106	104
m2	9	13.3 ± 0.3	11.6 ± 0.9	12	12.1 ± 0.3	10.6 ± 0.9	110	110
m3	9	19.0 ± 0.8	11.2 ± 1.0	12	17.0 ± 0.7	10.8 ± 0.5	112	104
m1–m3	7	43.4 ± 1.3	11.5 ± 1.0	11	39.6 ± 1.0	10.8 ± 0.5	110	106

Reported as mean $\pm$ 1 standard deviation.
North American data from Patton and Taylor (1973).
Apl = Anteroposterior length.
Trn = Transverse width.

evolve larger body sizes (Foster, 1964; Van Valen, 1973; Case, 1978; Lomolino, 1985). The threshold between larger and smaller body-size evolution has been in dispute, but probably lies around 1 kg in body size (Lomolino, 1985; Damuth, 1993). This body size reflects an optimum body size for energy acquisition, such that, if on islands a species' usual competitors and predators are absent, then the species should tend to evolve toward the optimum body size of 1 kg (Damuth, 1993).

The present study uses tooth size as a proxy for body size to test for the effect of insular evolution on an island among six species of land mammals. The data offer no support for insular evolution on an island, but they are consistent with evolution on a peninsula where populations had easy dispersal and intermixing with populations in North America. The first test shows that there is no overall difference in tooth size among the six species. Some species from Panama are slightly larger than North American conspecifics, whereas some are smaller. However, none of these slight differences (<113%) in tooth size are as large as what would be expected after insular evolution on an island. The second test shows that *P. wardi* from Panama had significantly larger teeth, but the difference is only at most 112% larger. Furthermore, this difference is in the opposite direction from what the island rule would predict for a large mammal, such as *P. wardi*. *P. wardi* has only been described from one other location: The upper part of the Fleming Formation (early Bartovian) in San Jacinto and Walker counties, Texas (Patton and Taylor, 1973). It is not understood why *P. wardi* from Panama would have evolved a significantly larger body size compared to its conspecific in Texas.

The paleogeography of southern Central America before formation of the Panamanian isthmus has remained poorly known, despite advances in understanding the timing and formation of the Isthmus. The results from this study are consistent with the view that southern Central America existed as a peninsula during the middle Miocene. Nevertheless, there is geologic evidence that narrow straits once crossed southern Central America before and after this time. Paleoenvironmental analysis of the underlying Culebra Formation (older than the Gaillard Cut L.F.) shows that a narrow strait connected the Pacific Ocean with the Caribbean Sea across the Panama

Canal Basin (Kirby, submitted for publication). This strait had a maximum width of 60 km during deposition of the lower Culebra Formation, based on the present distribution of pre-Miocene volcanic terranes (Kirby, submitted for publication). The upper Culebra and Cucaracha formations, the latter containing the land mammals of the Gaillard Cut L.F., represent a prograding delta that filled in this strait in part or completely during the middle Miocene (Kirby, submitted for publication). A second, even younger strait across the Panama Canal Basin formed again about 6 Ma, based on benthic foraminifera showing Pacific affinities in the Caribbean Chagres Formation (Collins et al., 1996). During these two episodes, when a strait formed across southern Central America, insular evolution may have occurred in land-mammal populations cut off from continental populations. But during the middle Miocene, our study found no evidence for straits or other significant barriers to gene flow separating the Gaillard Cut L.F. from related faunas living in North America.

7. Conclusions

Before the formation of the Isthmus of Panama in the Pliocene, southern Central America either existed as an island-arc archipelago or as a long peninsula that was connected to North America. We tested these alternate paleogeographic models by comparing the size of teeth (as a proxy for body size) of middle Miocene land mammals from the Cucaracha Formation in Panama with their conspecifics in North America. Of the six species examined, there is no significant difference in tooth size. A further test of the artiodactyl *P. wardi* showed a significant difference in tooth size, with *P. wardi* from Panama having as much as 112% larger teeth than their conspecific from Texas. However, this difference in tooth size is opposite, as well as smaller, to that predicted from the "island rule," where insular evolution on an island should have produced up to a four-fold smaller body size relative to conspecifics on the mainland. Results from both tests are inconsistent with insular evolution on an island-arc and we, therefore, conclude that the land mammals from Panama had ready gene flow with populations in North America across a continuous peninsula during the middle Miocene.

Acknowledgements

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