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Do marsupials make good predators? Insights from predator–prey diversity ratios

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ABSTRACT

Questions: Was mammalian predator diversity in South America unusually low during the Cenozoic before the Great American Biotic Interchange (GABI)? If yes, what factors might account for this? Does a similarly low diversity of predators characterize modern and fossil Australian faunas?

Data studied: Predator and prey diversity for 385 modern mammal faunas, 13 South American paleofaunas, and 15 Australian paleofaunas.

Analysis method: I regressed predator diversity on prey diversity by continent for both modern and fossil faunas and compared slopes and intercepts of the regression lines. I also compared relative predator diversity (= predator–prey ratios) using analysis of variance.

Conclusions: Predator diversity is much lower than expected in pre-GABI South American faunas and in modern and fossil Australian faunas; in all of these, marsupials are the primary predators.

Keywords: Australia, carnivore, Cenozoic, marsupial, paleofauna, phorusrhacid, predator diversity, South America.

INTRODUCTION

Understanding patterns of species distributions is a fundamental theme of macroecological investigations (Brown, 1995). Certainly some of the most well-documented macroecological phenomena are patterns of species diversity in relation to latitude, altitude, productivity, and area (Schluter and Ricklefs, 1993; Rosenzweig, 1995). Many other factors can affect diversity on smaller scales, however, such as disturbance frequency, habitat complexity, competition, and predation (Ricklefs and Schluter, 1993). In island/isolated faunas these factors can influence diversity to different degrees, making these communities highly amenable to investigations of pattern and process.

For most of the past 65 million years, the mammals of South America represented such an isolated fauna; the continent was cut off from all other major land masses and dispersal to and from South America was extremely limited (Simpson, 1980; Houle, 1998; Reguero *et al.*, 2002;

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Scher and Martin, 2006). The result of this isolation was a diverse but totally endemic terrestrial mammal fauna composed of various extinct ungulates (e.g. notoungulates, litopterns, astrapotheres), xenarthrans (armadillos, sloths, anteaters, glyptodonts), marsupials (opossums and a variety of extinct groups), platyrrhine primates, and caviomorph rodents (chinchillas, guinea pigs, agoutis, porcupines, etc.) (Patterson and Pascual, 1968; Simpson, 1980; Flynn and Wyss, 1998). This endemism persisted until a few million years ago when South America rejoined North America via island chains and finally the Isthmus of Panama (Simpson, 1950; Webb, 1976, 1978, 1991; Marshall *et al.*, 1982) (Fig. 1). The resulting Great American Biotic Interchange (GABI) between the two continents significantly changed the composition of South American faunas; today nearly half of the non-volant terrestrial mammals in South America are derived from northern immigrants rather than southern endemics (Wilson and Reeder, 1993).

On an ecological level, one of the most significant results of the GABI was a dramatic shift among mammalian secondary (and higher) consumers. Before the GABI, the carnivorous 'adaptive zone' in South America was primarily occupied by marsupials (extinct sparassodonts and didelphids) and large, non-volant 'terror birds' known as phorusrhacids (Patterson and Pascual, 1968; Marshall, 1977, 1978; Alvarenga and Höfling, 2003) (Fig. 2). Although some of the carnivorous marsupials evolved highly specialized morphologies (e.g. the saber-like canines of *Thylacosmilus*; Fig. 2a), their overall taxonomic diversity (and, potentially, morphological diversity) was apparently much less than that exhibited by placental carnivores on other continents. When the GABI initiated the replacement (either actively or passively) of these endemic marsupial carnivores and phorusrhacids by placental carnivorans (bears, cats, dogs, raccoons, otters, etc.), this trophic level not only changed in taxonomic composition, it also experienced a significant increase in diversity (Croft, 2001, 2002).

I undertook this study to explore patterns of diversity among these South American mammalian carnivores before the GABI. Although the general pattern of low pre-GABI diversity has long been recognized, it had never been quantified or rigorously examined before my earlier analysis (Croft, 2002). I have subsequently expanded my data set of South American paleofaunas, added a new data set of Australian paleofaunas, and applied additional statistical analyses to the examination of these patterns. The present study upholds the preliminary findings of my earlier analysis (Croft, 2002) but does so with more extensive supporting data.

MATERIALS AND METHODS

Definitions

Diversity: the total number of species recorded at a given locality, irrespective of relative abundance (i.e. alpha diversity). Van Valkenburgh and Janis (1993) used this same definition of diversity in their analysis of North American large herbivores and carnivores.

Predator: a non-volant terrestrial mammal that kills and eats other terrestrial mammals. By this definition, vertebrates need not constitute the majority of an animal's diet for it to be considered a predator. I use this term in lieu of 'carnivore' to avoid confusion between that term (a trophic one) and carnivoran (a taxonomic one) and to emphasize that not all of the predators under consideration are placental carnivorans. This term also better accommodates predatory mammals that are more accurately considered omnivores than carnivores (e.g. *Ursus arctos*, the brown bear). Finally, by using a broad definition of a

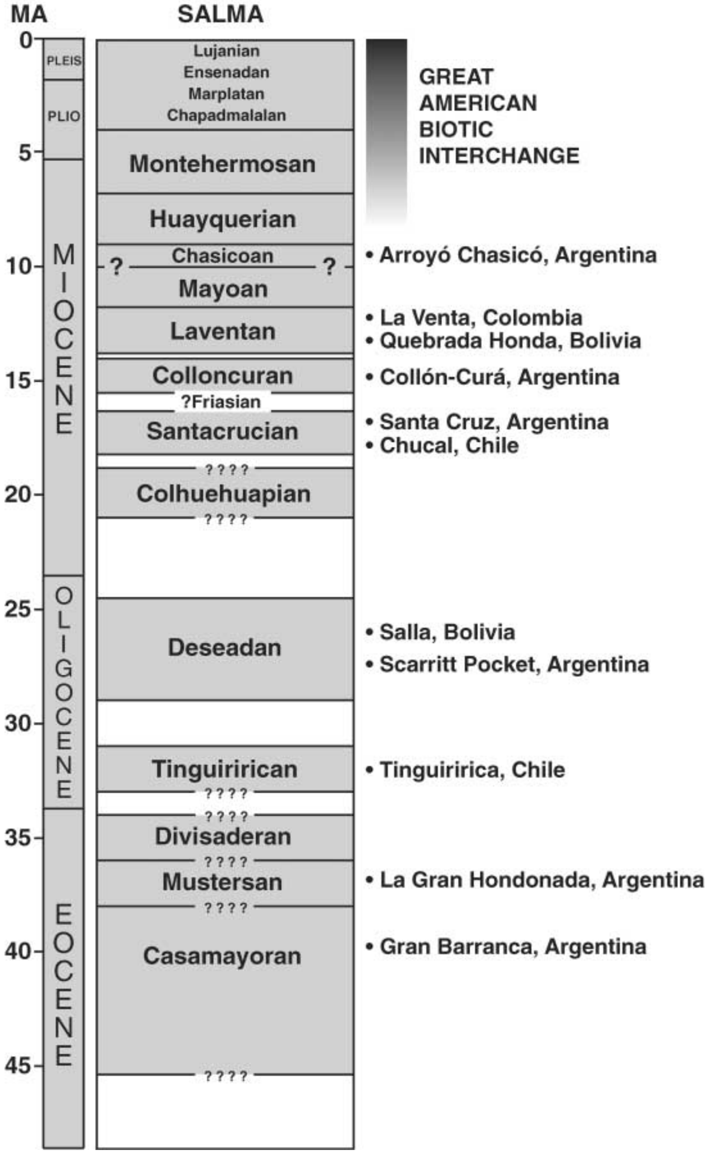

Fig. 1. Sequence of South American Land Mammal 'Ages' (SALMAs) based primarily on Flynn and Swisher (1995) and Flynn *et al.* (2003); the four youngest SALMAs have been condensed for legibility. The approximate ages of the Great American Biotic Interchange (GABI) and the South American paleofaunas examined in this study (Table 1) are indicated to the right of the SALMA sequence. MA = megannum.

predator, I avoid making fine distinctions about the proportion of meat consumed by extinct taxa with no closely related modern analogues.

Prey: a non-volant terrestrial mammal that is not a predator. I use this term in lieu of 'non-predator' merely for the sake of simplicity.

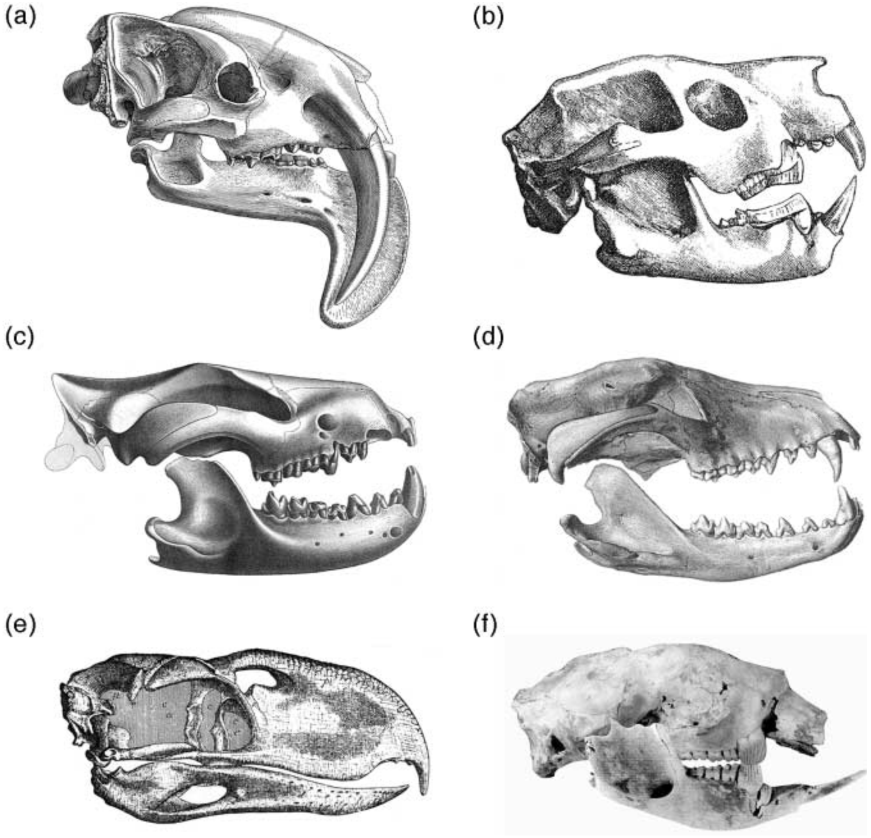

Fig. 2. Skulls of representative extinct South American and Australian taxa discussed in the text, not to scale (approximate skull lengths are provided). (a) *Thylacosmilus atrox*, a saber-toothed marsupial from the Pliocene of Argentina [26 cm (after Riggs, 1934)]; (b) *Thylacoleo carnifex*, a 'marsupial lion' from the Pleistocene of Australia [27 cm (after Zittel, 1893)]; (c) *Borhyaena tuberata* from the early Miocene of Argentina [23 cm (after Sinclair, 1906)]; (d) *Thylacinus cynocephalus*, the 'Tasmanian wolf,' recently extinct in Australia and Tasmania [24 cm (after Sinclair, 1906)]; (e) *Patagornis marshi*, a 'terror bird' from the early Miocene of Argentina [35 cm (after Ameghino, 1895)]; (f) *Ekaltadeta ima*, a giant rat kangaroo from the Miocene of Australia [13 cm (based on Wroe, 1996; Wroe *et al.*, 1998)].

Relative predator diversity: predator diversity divided by prey diversity (i.e. predator–prey ratio, predator–victim ratio) (Van Valkenburgh and Janis, 1993; Rosenzweig, 1995).

Questions

I address three main questions:

1. Was predator diversity in South America unusually low during the Cenozoic prior to the GABI? To answer this question, I examine patterns of relative predator diversity (see rationale below). I first examine a large data set of modern mammal faunas to characterize 'normal' or 'expected' relative predator diversity. I then compare these

data to data from well-sampled South American paleofaunas to assess relative predator diversity before the GABI.

2. If South America was depauperate in predators, what factors might account for this? I do not answer this question unequivocally, but I discuss several possible explanations.
3. Does a similarly low diversity of predators characterize Australian faunas? To test one explanation for low pre-GABI predator diversity in South America – that marsupials are less 'successful' as predators than placentals – I examine relative predator diversity in modern and fossil Australian faunas.

Relative predator diversity

Most previous macroecological studies of marsupial predator diversity have analysed patterns of continent-wide diversity during relatively broad time intervals (up to seven megannum) (Marshall, 1977; Marshall and Cifelli, 1990; Wroe *et al.*, 2004). This approach has several shortcomings. Perhaps most importantly, geographic and temporal binning preclude analyses of local (community) and regional diversity and obscure finer-scale temporal changes in diversity. For example, although Wroe *et al.* (2004) list 12 large carnivorous marsupials as existing in South America between 17 and 10 million years ago, these data give no indication of the average diversity of large carnivores during that period of time; the 12 species could have been part of a single fauna with a diverse predator guild or they could have been distributed geographically and temporally among 12 faunas, each with a solitary predatory marsupial. These two possibilities have very different implications for the paleoecology of predatory marsupials and macroecological patterns of diversity. Analyses of continent-wide diversity also assume that taxon sampling and preservation are comparable both geographically and temporally; this is almost never the case. When differences in sampling are not taken into account, it is impossible to determine whether the observed patterns are real or merely the result of other processes (Barnosky *et al.*, 2005).

To avoid (as much as possible) the various sampling biases that can plague macroecological studies such as this, I use an alternative approach to examining absolute diversity: relative predator diversity [= predator–prey diversity ratio (see Van Valkenburgh and Janis, 1993)]. Factors such as habitat area, habitat heterogeneity, sampling intensity, and preservation potential should similarly affect predator and prey diversity at a single locality; therefore, examining the *ratio* of predator to prey diversity should provide a measure that is relatively independent of these confounding factors. Assessing relative predator diversity on a locality by locality basis has the added benefit of preserving spatial and temporal patterns of diversity, resulting in data that can be used in other sorts of analyses. Since the local fauna is the point of comparison, it permits 'apples-to-apples' comparisons despite significant geographic and/or temporal distances.

Predators and prey

Sorting taxa into well-defined categories is a key challenge of most macroecological studies and the present study is no exception; diet can be a particularly difficult attribute to quantify, especially given daily and seasonal variation. The definition of predator I use here is intentionally broad in that it does not exclude species by body size or amount of meat in the diet. Wesley-Hunt (2005) used a similarly inclusive definition in her investigation of morphological disparity among North American carnivoramorphans and creodonts. This definition contrasts with similar studies that have investigated evolution within the large carnivore guild [i.e. mammals ≥ 7 kg (Van Valkenburgh, 1985, 1988, 1989; Van Valkenburgh and Janis, 1993)] and those that have focused on large hypercarnivores [i.e. mammals ≥ 2.5 kg (Flannery, 1994; Wroe *et al.*, 2004)]. A key advantage of a broad definition for modern taxa is that it permits equally broad interpretations of diet in fossil taxa; this is especially appropriate for taxa that have no close living relatives and/or ecological analogues (e.g. borhyaenids, propleopines, etc.).

My rationale for excluding body size as a predator criterion stems primarily from the observation that many weasels (Carnivora: Mustelidae: *Mustela* spp.) are quite small (≪1 kg) and yet are hypercarnivorous (Ewer, 1973; Werdelin, 1986; King, 1989; Johnson *et al.*, 2000). Similarly, although smaller quolls (*Dasyurus hallucatus*, *D. viverrinus*) may be less carnivorous than the spotted quoll (*D. maculatus*), character displacement among these species suggests they are members of the same guild and are partitioning available prey resources (Jones, 1997). Not counting smaller predators such as these would not accurately represent predator diversity in modern faunas and might also misrepresent predator diversity in pre-GABI South American faunas.

Based on the above definition, I classify most extant carnivorans as predators except: aardwolf (Hyaenidae: *Proteles cristatus*; insectivorous); kinkajou (Procyonidae: *Potos flavus*; frugivorous); otters (Mustelidae: Lutrinae spp.; piscivorous); panda (Ailuridae: *Ailuropoda melanoleuca*; folivorous); seals (Phocidae spp.; piscivorous/marine); sea lions (Otariidae spp.; piscivorous/marine); sloth bear (Ursidae: *Melursus ursinus*; insectivorous); walrus (*Odobenus rosmarus*; molluscivorous/marine).

Among Recent Australian marsupials, the thylacine (Thylacinidae: *Thylacinus cynocephalus*; Fig. 2d) and some dasyurids are included as predators: kowari (*Dasyuroides byrnei*); mulgara (*Dasycercus cristicauda*); phascogale (two species of *Phascogale*); quolls (four species of *Dasyurus*); Tasmanian devil (*Sarcophilus laniarius*). The inclusion of these smaller dasyurids as predators is supported by the following studies: Chen *et al.* (1998), *Dasycercus*; Baynes and Jones (1993), *Dasycercus, Phascogale*; and Jones (1997), *Dasyurus* spp. Fossil Australian marsupial predators include thylacinids, thylacoleonids (Fig. 2b), some dasyurids (i.e. those resembling modern forms classified as predators), and some propleopine hypsiprymnodontids (e.g. *Ekaltadeta*; Fig. 2f). All currently recognized extinct carnivorous marsupials (i.e. those from Wroe, 2003: table 1) are counted as predators.

Recent New World marsupials are categorized as predators based primarily on the classification of Vieira and Astúa de Moraes (2003). Didelphid marsupials in their category V and those in their categories III–IV larger than 100 g are counted as predators: brown four-eyed opossum (*Metachirus nudicaudatus*); common opossums (*Didelphis* spp.); grey four-eyed opossum (*Philander opossum*); lutrine opossum (*Lutreolina crassicaudata*); Patagonian opossum (*Lestodelphys halli*). Species in categories III–IV smaller than 100 g are excluded because they probably take few vertebrates (Vieira and Astúa de Moraes, 2003). I count all fossil sparassodont marsupials as predators (e.g. borhyaenids, thylacosmilids) and some didelphids (i.e. those resembling modern forms classified as predators). Some authors have suggested that certain non-marsupial mammals (e.g. large ground sloths) might have been predators or scavengers in South American paleoecosystems (Fariña and Blanco, 1996; Bargo *et al.*, 2004, 2006). These analyses have focused exclusively on Pleistocene (post-GABI) taxa (Fig. 1), however, and thus do not apply to the paleofaunas considered here.

The platypus (*Ornithorhynchus anatinus*), otters, pinnipeds (seals, sea lions, etc.), and other semi-aquatic species are included as prey. My justification for this is that at least some of these are eaten by terrestrial predators (e.g. polar bears feed extensively on seals) and therefore should positively affect carnivore diversity/distributions, at least in some habitats.

Faunal lists

I compiled a data set of modern non-volant terrestrial mammal faunas for all continents except Antarctica, which has no exclusively terrestrial mammals (see online Appendix; http://www.evolutionary-ecology.com/data/2088appendix.pdf). Although these lists cover a variety of geographic areas and habitats, the relative scarcity of faunal lists for certain areas (e.g. tropical Africa, Asia, and South America) resulted in some regions being better represented than others. Most faunal lists for continents other than Australia were taken from the Information Center for the Environment's Biological Inventory Database (http://www.ice.ucdavis.edu/bioinventory/bioinventory.html) and the Species in Parks NPFauna Database (http://ice.ucdavis.edu/nps/). For the most part, I included only faunal lists from these databases described as 'essentially complete'. Not all 'essentially complete' lists were used, however; I excluded any which obviously were missing significant faunal components (e.g. small rodents). I also included lists with no completeness data when no faunal components obviously were missing and total diversity was comparable to that of other faunas in the area. Australian faunal lists were taken exclusively from published scientific literature. I also used published inventories to supplement the number of Central and South American faunas represented.

Because a primary goal of the present study is to determine 'normal' ranges of relative diversity for continental faunas, I excluded all island faunas (e.g. UK, Japan, Madagascar) from the analyses. I grouped the remaining faunas by continent (Europe and Asia were considered together) and identified and excluded any obvious outliers within each continental group. Outliers were defined as faunas in which predator or prey diversity was more than three standard deviations beyond the continental mean. Using this criterion, two outliers were identified: Kahuzi-Biéga (Congo) and Dja (Cameroon). The resulting data set included a total of 385 faunal lists distributed among Africa ($n = 33$), Australia ($n = 102$), Eurasia ($n = 92$), North America ($n = 105$), and South America ($n = 53$) (see online Appendix; http://www.evolutionary-ecology.com/data/2088appendix.pdf).

Australia's terrestrial mammal fauna has undergone dramatic changes in historical times due, at least in part, to human-mediated introduction of various non-native mammals (e.g. cat, *Felis silvestris*; fox, *Vulpes vulpes*; rabbit, *Oryctolagus cuniculus*). Present-day Australian mammal faunas therefore may not accurately represent recent predator and prey diversity levels. To explore these potential differences in relative predator diversity, I distinguish between modern faunas (which include only presently recorded species) and 'reconstructed' faunas (which use photographs, museum specimens, reliable observations, and/or sub-fossil osteological remains to reconstruct the recent mammal fauna). Reconstructed faunas may somewhat under-represent the original fauna of the area if none of the data precede introductions of non-native mammals to the region.

Species lists for South American and Australian paleofaunas were gathered from the literature (Archive Tables 1, 2; http://www.evolutionary-ecology.com/data/2088archive.pdf). They only include faunas that are reasonably well sampled (at least 15 species for South America, 10 species for Australia), include good locality and stratigraphic information, and for which faunal lists have been published. Thus, although South America has a rich Cenozoic fossil record (Patterson and Pascual, 1968; Flynn and Wyss, 1998), only a small number of faunas were deemed suitable for this analysis. The 13 South American faunas examined in this study are an expanded version of the data set I have used in previous studies (Croft, 2001, 2002).

Analyses

I examined relative predator diversity using least-squares regression and analysis of variance (ANOVA). Both simple (unconstrained and constrained through the origin) and second-order polynomial regression analyses of predator diversity on prey diversity were explored (Van Valkenburgh and Janis, 1993; Rosenzweig, 1995). For unconstrained simple linear regressions, a method equivalent to analysis of covariance (ANCOVA) was used to identify groups of faunas whose slopes and intercepts were not significantly different (Zar, 1984). Ninety-five percent confidence intervals for slopes and intercepts were also calculated. I used the arcsine transformation to normalize relative predator diversity data prior to the ANOVA. All analyses were conducted on an Apple PowerBook G4 using Prism 4.0 (GraphPad Software, Inc.), SPSS (SPSS, Inc.), or StatView 4.51 (Abacus Concepts).

RESULTS

Modern faunas

Among the four largest continents (i.e. Africa, Eurasia, North America, and South America), r^2 values for simple linear regressions of predator diversity on prey diversity approximate 0.5 (range: 0.468–0.557; Table 1). Second-order polynomial regressions have similar r^2 values (range 0.448–0.563; Archive Table 3; http://www.evolutionary-ecology.com/data/2088archive.pdf) and thus do not fit the data appreciably better. The slopes of simple linear regressions are not statistically different among these four continents ($P > 0.05$) but the intercepts are ($P < 0.0001$; Table 1). If South America is excluded, neither the slopes nor intercepts of the remaining three continents differ statistically (for pooled data, slope = 0.271, intercept = 3.55). Simple linear regressions constrained through the origin demonstrate a similar pattern; slopes for Africa, Eurasia, and North America are all similar (0.371 for pooled data), but the slope for South America is lower (0.294) and its 95% confidence interval does not overlap that of any of the other three continents (Table 1). Based on ANOVA, however, relative predator diversity does not differ significantly among the four continents (Table 2).

For modern and reconstructed Australian faunas, r^2 values for simple linear regressions of predator diversity on prey diversity differ appreciably (Table 1); the r^2 value for modern faunas (0.475) falls within the range of that of the larger continents, but that for reconstructed faunas is close to zero (0.078). Second-order polynomial regressions fit the data only slightly better than simple linear regressions (Archive Table 3; http://www.evolutionary-ecology.com/data/2088archive.pdf). Neither the slopes nor the intercepts of simple linear regressions differ between modern and reconstructed Australian faunas ($P > 0.30$), though the slope for reconstructed faunas does not differ significantly from zero, either. Slopes for simple linear regressions constrained through the origin are similar for modern and reconstructed faunas (pooled slope = 0.141) but this value is well below the range of the larger continents (Table 1). Analysis of variance of relative predator diversity supports this pattern; no significant difference exists between modern and reconstructed Australian faunas, but relative predator diversity is much lower than that of the larger continents (Table 2).

Table 1. Coefficients (including 95% confidence intervals) of simple least squares regression equations of predator diversity on prey diversity

	N	UCR slope	UCR intercept	UCR r^2	CTO slope
AF	33	0.258 (0.173 to 0.342)	4.60 (0.829 to 8.37)	0.557	0.354 (0.323 to 0.385)
AU (FOS)	15	0.0980 (0.009 to 0.188)	0.303 (−1.55 to 2.15)	0.304	0.112 (0.074 to 0.149)
AU (MOD)	87	0.122 (0.095 to 0.150)	0.445 (−0.0051 to 0.895)	0.475	0.146 (0.132 to 0.160)
AU (REC)	15	0.0486 (−0.051 to 0.148)	1.943 (−0.426 to 4.31)	0.078	0.128 (0.104 to 0.152)
AU (MOD + REC)	102	0.115 (0.090 to 0.139)	0.537 (0.109 to 0.965)	0.463	0.141 (0.130 to 0.153)
EA	92	0.246 (0.191 to 0.301)	3.68 (2.04 to 5.32)	0.468	0.362 (0.337 to 0.386)
NA	105	0.278 (0.225 to 0.332)	3.67 (1.95 to 5.38)	0.506	0.388 (0.370 to 0.406)
AF + EA + NA	230	0.271 (0.293 to 0.302)	3.55 (2.50 to 4.60)	0.555	0.371 (0.357 to 0.384)
SA (FOS)	13	0.104 (0.029 to 0.178)	−1.242 (−4.01 to 1.52)	0.460	0.072 (0.048 to 0.096)
SA (MOD)	53	0.184 (0.135 to 0.232)	4.41 (2.73 to 6.10)	0.532	0.294 (0.265 to 0.323)

Note: Results for both unconstrained regressions (UCR) and those constrained through the origin (CTO) are provided. The unconstrained regression line of AU (REC) is the only one with a slope not significantly different from zero.

Abbreviations: AF, Africa; AU, Australia; EA, Eurasia; FOS, fossil faunas; MOD, modern faunas; *N*, number of faunas; NA, North America; REC, reconstructed faunas; SA, South America.

South American paleofaunas

Unconstrained simple and second-order polynomial regressions fit the South American paleofauna data equally well; r^2 values for both are between 0.45 and 0.5, comparable to those of modern faunas (Table 1, Archive Table 3; http://www.evolutionary-ecology.com/data/2088archive.pdf). The slope of the simple linear regression line is significantly lower than that of Africa, Eurasia, and North America but does not differ statistically from that of modern South America. The regression equation does differ from modern South America in its much lower intercept, however. The line also does not differ from pooled modern Australian faunas in slope, but does differ in having a lower intercept. For simple linear regression through the origin, the slope (0.072) is lower than for any modern continent and the 95% confidence interval is non-overlapping (Table 1). The ANOVA of relative predator diversity supports statistical differences between South American paleofaunas and modern large continents but not between them and modern Australia (Table 2).

Table 2. Mean relative predator diversity by continent and results of ANOVA of arcsine-transformed relative predator diversity data

	N	Mean	SD	AF	AU (FOS)	AU (MOD)	AU (REC)	EU	NA	SA (FOS)	SA (MOD)
AF	33	0.388	0.119	×	s	s	s	—	—	s	—
AU (FOS)	15	0.117	0.086	s	×	—	—	s	s	—	s
AU (MOD)	87	0.158	0.100	s	—	×	—	s	s	—	s
AU (REC)	15	0.137	0.048	s	—	—	×	s	s	—	s
EA	92	0.417	0.167	—	s	s	s	×	—	s	—
NA	105	0.412	0.104	—	s	s	s	—	×	s	—
SA (FOS)	12	0.065	0.048	s	—	—	—	s	s	×	s
SA (MOD)	53	0.386	0.187	—	s	s	s	—	—	s	×

Note: Statistically different pairings ($P < 0.0001$ level; Scheffé's test) are designated by 's'.

Abbreviations: AF, Africa; AU, Australia; EA, Eurasia; FOS, fossil faunas; MOD, modern faunas; *N*, number of faunas; NA, North America; REC, reconstructed faunas; SA, South America; SD, standard deviation.

Australian paleofaunas

As for South America, unconstrained simple and second-order polynomial regressions fit the Australian paleofauna data equally well, though the r^2 values are much lower (0.304 and 0.305, respectively; Table 1, Archive Table 3; http://www.evolutionary-ecology.com/data/2088archive.pdf). When constrained through the origin, the slope of the linear regression is quite low (0.112), and the 95% confidence intervals overlap the constrained slopes for modern and reconstructed Australian faunas as well as fossil South American faunas (Table 1). Based on ANOVA, relative predator diversity in Australian paleofaunas is no different from that in modern Australian faunas or fossil South American faunas (Table 2).

DISCUSSION

Predator–victim diversity ratios

Rosenzweig (1995) suggested that predator–victim diversity ratios (= relative predator diversity) tend to approximate 1/3, though they may be lower in more diverse faunas. To my knowledge, the modern faunal data presented here constitute the largest vertebrate data set yet brought to bear on patterns of predator–victim diversity ratios and therefore may provide useful insights into whether mammal faunas follow these predictions.

For regressions constrained through the origin for large continents, slopes (= ratios) do indeed approximate 0.333, though most are slightly higher (combined Africa, Eurasia, and North America = 0.371; South America = 0.294; Table 1). The slope for modern Australia is much lower (modern + reconstructed = 0.141) as might be expected given its isolated nature and paucity of carnivorous marsupials. Similarly low values typify South American and Australian paleofaunas. Thus, although predator–victim ratios are generally close to 0.333 in modern mammal faunas, factors such as isolation and taxonomic composition can result in significant deviations from this value.

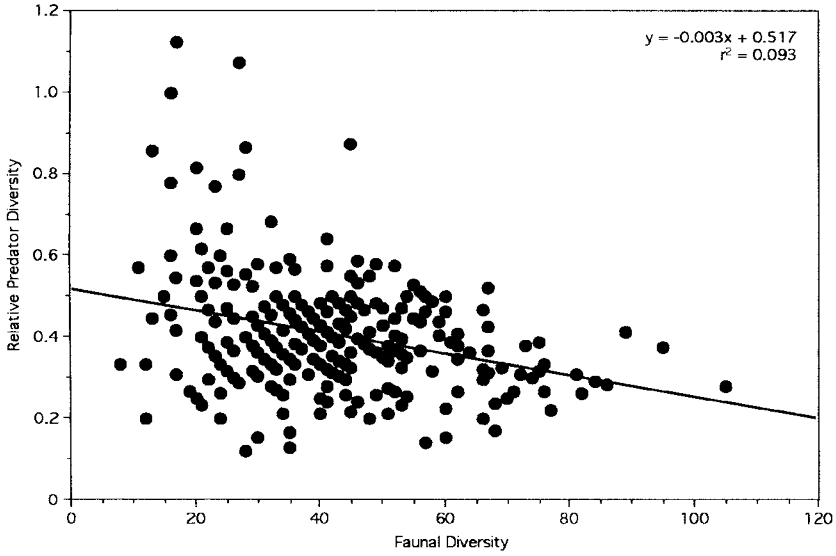

Fig. 3. Bivariate plot of relative predator diversity versus faunal diversity (= predator diversity + prey diversity) for the four largest continents (pooled). The simple least-squares regression line is included.

Predator diversity apparently decreases in more diverse mammal faunas, but this relationship is not strong (Fig. 3). A regression of relative predator diversity on faunal diversity (= predator diversity + prey diversity) is significant ($P < 0.001$) and inverse (slope = –0.003). A second-order polynomial regression results in only a slightly better fit ($r^2 = 0.094$). A discussion of the potential reasons for this relationship is beyond the scope of the present study, but would be an interesting area of future research.

Pre-GABI relative predator diversity

The primary goal of the present study was to determine whether relative predator diversity in South America was unusually low during the Cenozoic prior to the GABI. The results presented above from both regression analyses and ANOVA provide an unequivocal answer of 'yes'. The disparity in predator diversity between South American paleofaunas and modern faunas from large continents is perhaps most easily seen in a visual comparison of regression lines (Fig. 4); at all levels of prey diversity, South American paleofaunas exhibit dramatically lower predator diversity. Based on data from modern faunas, South American paleofaunas should include anywhere from approximately two to fourteen times as many species of predators as are observed (Table 3, Archive Table 4; http://www.evolutionary-ecology.com/data/2088archive.pdf).

In addition to being represented by few species, pre-GABI South American predators are represented by remarkably few specimens. In a recent study of the borhyaenid *Arctodictis*, Forasiepi *et al.* (2004) noted that out of more than 500 specimens recently collected from the Santa Cruz Formation, only two pertained to borhyaenids (< 1%). Cladera *et al.* (2004) calculated the minimum number of individuals (MNI) for La Gran Hondonada; only two out of 253 mammals were borhyaenids (< 1%). I surveyed several large museum collections from South American localities and found these percentages to be typical; in pre-GABI

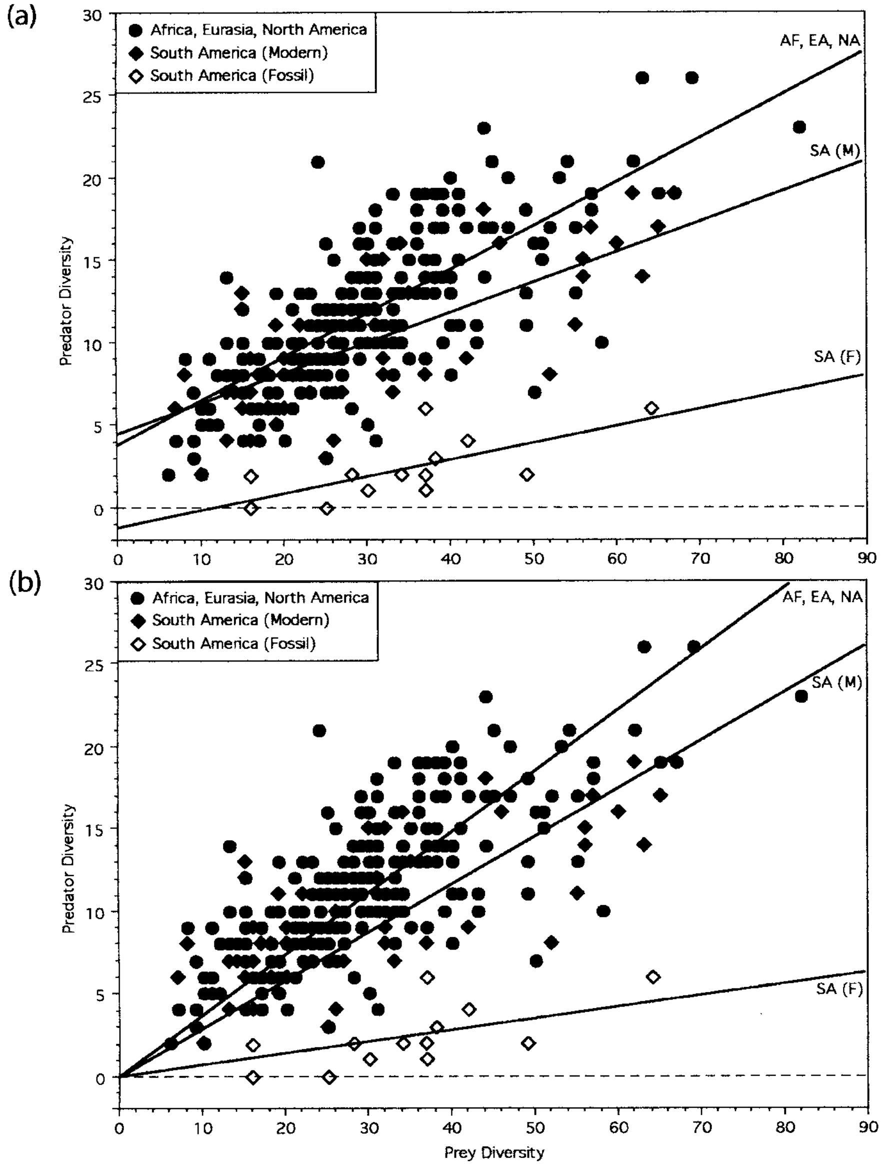

Fig. 4. Bivariate plots of predator diversity versus prey diversity for modern faunas from large continents (pooled) and South American paleofaunas including (a) unconstrained least-squares regression lines and (b) least-squares regression lines constrained through the origin.

faunas, specimens of predators account for less than about 2% of identified specimens, with the average across all faunas of just under 1% (Archive Table 5; http://www.evolutionary-ecology.com/data/2088archive.pdf). This low representation is especially noteworthy given the excellent preservation in many of these faunas; most localities also include rare animals such as small marsupials, primates, and/or anteaters. In contrast, predatory mammals

Table 3. Predicted predator diversity of South American paleofaunas based on simple least-squares regressions of predator diversity on prey diversity for the unconstrained regression of Africa, Eurasia, and North America

Fauna	Prey spp.	Predator spp.	Predicted no. of predator spp.
Arroyo Chasicó	38	3	13.8
Monkey Beds, La Venta, Colombia	49	2	16.8
Entire fauna, La Venta, Colombia	64	6	20.9
Quebrada Honda, Bolivia	28	2	11.1
Collón Curá, Argentina	37	1	13.6
P. australe Zone, Santa Cruz, Argentina	34	2	12.8
P. attenuatum Zone, Santa Cruz, Argentina	30	1	11.7
Chucal, Chile	17	0	8.2
Scarritt Pocket, Argentina	17	2	8.2
Salla, Bolivia	37	6	13.6
Tinguiririca, Chile	25	0	10.3
La Gran Hondonada, Argentina	37	2	13.6
Gran Barranca, Argentina	42	4	14.9

Note: Predictions based on other regressions are presented in Archive Table 4 (http://www.evolutionary-ecology.com/data/2088archive.pdf).

account for 4.5–5.0% of identified specimens from the late Eocene/early Oligocene White River Group of South Dakota (Clark *et al.*, 1967), about 7–10% of specimens from the early Miocene Thomas Farm locality of Florida (Florida Museum of Natural History on-line catalogue), and nearly 10% of specimens (nearly 6% of MNI) from the late Miocene Middle Siwalik rocks of Pakistan (Badgley, 1986). Many more data could be collected to test whether these localities are representative of Holarctic paleofaunas in general, but these few samples serve to illustrate the relative rarity of predator specimens in pre-GABI South American faunas. Assuming no fundamental taphonomic differences exist between South America and other continents, these data imply that predatory mammals were represented by very few individuals in pre-GABI South America in addition to being represented by very few species.

The lack of South American predators

A variety of explanations could account for the observed pattern of low predator diversity in pre-GABI South America. In a paleontological study such as this, the first that must be considered is whether such a pattern is merely due to taphonomic bias: Is it possible that the predators were there, they just aren't being sampled? With the caveat that negative evidence such as the apparent lack of predators can never be verified – only falsified – available evidence suggests that taphonomic bias is not primarily responsible for low predator diversity.

The 13 paleofaunas included in this study span some 30 million years, range over approximately 55° of latitude, and include a variety of geological settings (Archive Table 1; Fig. 1, Archive Fig. 1; http://www.evolutionary-ecology.com/data/2088archive.pdf); it is difficult to envision a preservational bias that could exert a similar negative effect on predator diversity across such diverse conditions. Moreover, there is no evidence that these faunas sample only a restricted set of habitats or ecological conditions which might be expected to bias relative predator diversity in one direction or the other (e.g. Birney and Monjeau, 2003; Dickman, 2003). No significant taphonomic size bias appears to be present among these faunas; all include both large and small mammals (see sources in Archive Table 1; http://www.evolutionary.com/data/2088archive.pdf). Even if a size bias were present, it would more likely fail to sample small prey than large predators, thus biasing these faunas towards high rather than low relative predator diversity. Although predatory marsupials are very rare in South American paleofaunas (as noted above), the presence of other rare taxa such as small marsupials and primates in many of these faunas suggests that the rarity of predatory marsupials (potentially due to low abundance) is not responsible for their apparent low diversity (Archive Table 5; http://www.evolutionary-ecology.com/data/2088archive.pdf); low diversity and low abundance appear to be separate issues. Additionally, poor sampling of faunas in general (which would fail to record rare taxa) should have little affect on the present analysis, in contrast to those focused on absolute predator diversity; poor sampling would decrease the apparent diversity of both predators and prey and would not be expected to systematically bias relative predator diversity in one direction or the other.

A further line of evidence that can be brought to bear on the question of sampling comes from the study of Van Valkenburgh and Janis (1993). Their analysis of predator–prey diversity ratios in North American paleocommunities produced ratios much greater than those observed in South American and Australian paleofaunas, comparable to those observed in modern faunas from large continents (mean = 0.373, standard deviation = 0.206). Although their study only focused on large carnivores and herbivores (i.e. no rodents, rabbits, or carnivores smaller than the grey fox), it suggests that the general rarity of carnivores relative to herbivores (due to trophic level) does not significantly bias estimates of relative predator diversity in fossil faunas.

If I am correct in my assertion that the observed pattern of low predator diversity in South American paleofaunas is real and not an artifact of sampling, then potential explanations for this pattern must be considered. One possible explanation stems from the observation that the terrestrial predator niche was likely partly filled by phorusrhacid birds in addition to sparassodont marsupials (Marshall, 1977, 1978; Croft, 2001; Alvarenga and Höfling, 2003; Wroe *et al.*, 2004) (Fig. 2e). Competition with these birds may have limited the absolute diversity of predatory marsupials, thus resulting in low relative diversity of mammalian predators, especially in open habitats (Marshall, 1977, 1978). Counting phorusrhacids as predators has a negligible effect on relative predator diversity, however; one phorusrhacid occurs at Salla and Arroyo Chasicó and two occur at La Gran Hondonada and in the lower Santa Cruz (*P. attenuatum* Zone) based on the faunal lists used in this study. Only 11 species of phorusrhacids have been recorded in pre-GABI South American faunas, most from the Deseado (three) and Santa Cruz (five) formations (Archive Table 6; http://www.evolutionary-ecology.com/data/2088archive.pdf). If all the species known from these two formations are added to the predator counts for Scarritt Pocket and Santa Cruz (which come from the Deseado and Santa Cruz formations, respectively), relative predator diversity does approach the low end of the range observed in modern faunas. This would not be consistent with the methods used in this study, of course, which would require that unrepresented prey species from these formations also be added, pushing relative diversity levels back down. Adding only phorusrhacids (and not unrepresented mammalian prey) to diversity counts could possibly be justified if it were a taphonomic ‘correction factor’; perhaps the fragility of bird bones has resulted in phorusrhacids being under-represented in the fossil record relative to mammals. The large to very large body size of most phorusrhacids, however, would increase the preservation potential of their bones relative to most birds (Behrensmeyer *et al.*, 2003); this would decrease the magnitude of any taphonomic bias, thus minimizing the need for such a correction factor. Indeed, in many large fossil collections, the number of phorusrhacid specimens is not dramatically different from the number of predatory mammal specimens (Archive Table 5; http://www.evolutionary-ecology.com/data/2088archive.pdf). Overall, these data are ambiguous as to whether the presence of phorusrhacids might have been a causal factor in the low diversity of pre-GABI mammalian predators. Even if a correlation between low mammal predator diversity and high phorusrhacid diversity could be established, an equally plausible argument could be made that phorusrhacids were filling niche space left vacant by sparassodonts (perhaps due to changing environmental conditions or other factors) rather than limiting sparassodont diversity through competition (Marshall, 1977, 1978).

The idea that phorusrhacids were filling empty niche space accords well with the proposal that carnivorous marsupials are functionally constrained by peculiarities of their tooth replacement (Werdelin, 1987; see also Van Nievelt and Smith, 2005). Although some marsupial lineages have circumvented this constraint [e.g. *Thylacoleo* (Werdelin, 1988)], the lesser degree of morphological diversity/specialization in their dentition relative to carnivorans (e.g. Jones, 2003, figs. 1, 3) may be a primary causal factor in their apparent low taxonomic diversity. Is it possible that this constraint or some other aspect of marsupial biology has resulted in their being unsuccessful predators by placental standards? To answer this question, data from Australia are especially relevant.

Evidence from Australia

Besides South America, Australia is the only other continent in which marsupials have dominated the terrestrial predator niche. Like South America, various non-mammalian predators also may have filled this niche [e.g. birds, snakes, lizards (Hecht, 1975; Flannery, 1991, 1994; Burness *et al.*, 2001)], although the paleobiology of these animals has been disputed (Wroe, 2002). The low diversity of modern predatory marsupials (as defined here) in Australia is universally recognized. In contrast, the notion that similarly low diversities of marsupial predators have characterized Australian Cenozoic paleofaunas in general has been the subject of debate (Wroe, 2002, 2003, 2004; Wroe *et al.*, 2004). The data presented above unequivocally support the notion that low relative predator diversity characterizes not only modern Australian faunas, but also those of at least the past 30 million years (Tables 1, 2; Fig. 5; Archive Tables 2, 3; http://www.evolutionary-ecology.com/data/2088archive.pdf). Moreover, these low levels of relative predator diversity are statistically indistinguishable from those of pre-GABI South America. Given that the only relevant characteristics shared by all of these faunas appear to be the presence of marsupial predators and the absence of placental predators (at least until recently in Australia), these data suggest that low relative predator diversity primarily results from the limited taxonomic diversity of marsupial predators.

In a recent study focusing on the historical diversity of large mammalian carnivores in Australia and South America, Wroe *et al.* (2004) examined continental diversity patterns over the past 25 million years. The results obtained by that study were broadly similar to those obtained here, despite having been generated using very different methods and definitions: predator diversity was similar in South America and Australia before the GABI. Wroe *et al.*

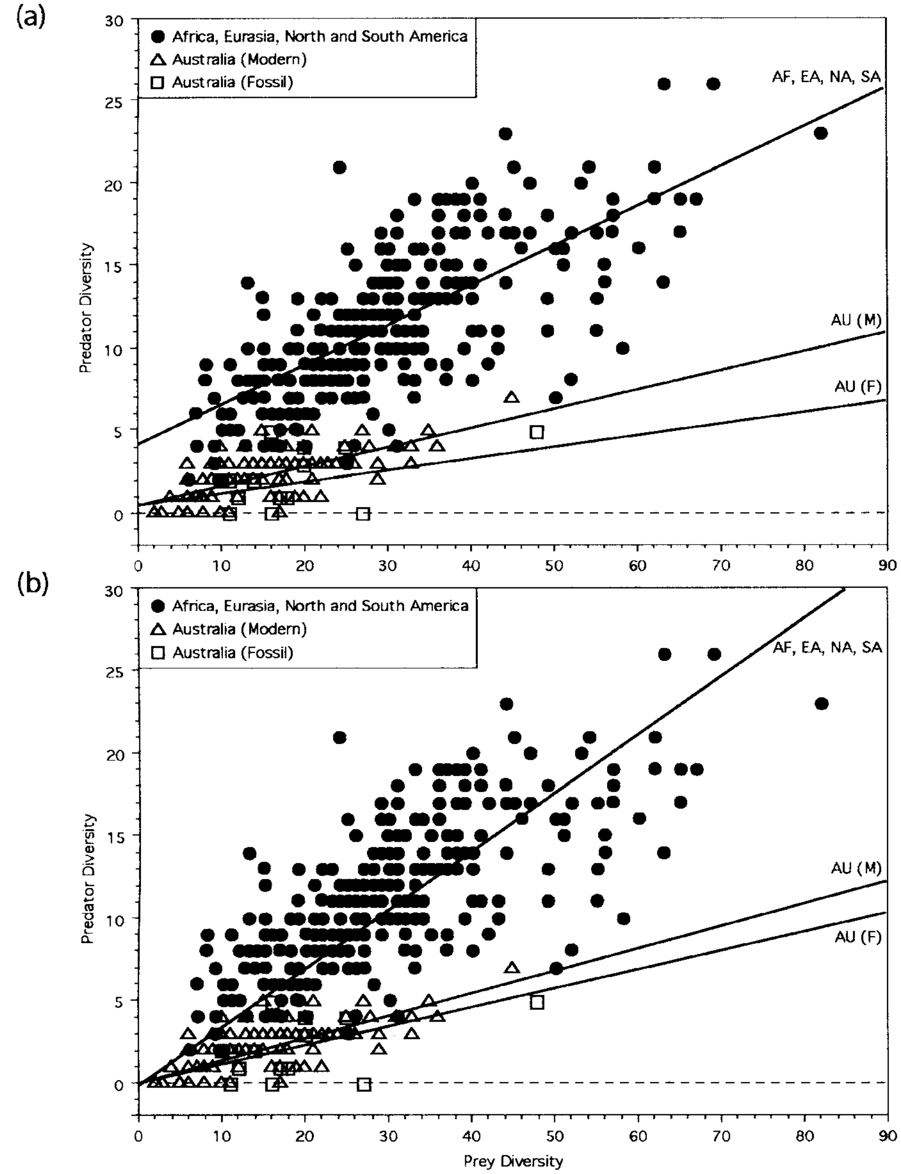

Fig. 5. Bivariate plots of predator diversity versus prey diversity for modern faunas from large continents (pooled) and Australia including (a) unconstrained least-squares regression lines and (b) least-squares regression lines constrained through the origin.

(2004) suggested that pre-GABI diversity was typically higher in Australia than in South America if corrected for continental area, but I do not believe that this is a valid comparison, primarily due to sampling issues; unless fossil localities are distributed throughout the entire area of a continent for each time interval sampled, then using the entire area of the continent as a correction factor is not accurate (Barnosky *et al.*, 2005). Perhaps using a minimum area polygon would be more appropriate, but this still might not accurately represent the data; in a country like South America, localities in Colombia, Bolivia, and southern Argentina would encompass a large geographic range but these three faunas would still fail to sample much of the area of South America. It is because of issues like this that relative predator diversity is especially appropriate; factors such as continental area should similarly affect the alpha diversity of both predator and prey, permitting reasonable comparisons among differently sampled continents of different size.

CONCLUSIONS

The data presented in this analysis indicate that pre-GABI South American paleofaunas and modern and fossil Australian faunas all share the common attribute of low relative predator diversity. Because they also share a lack of placental carnivores, a correlation between marsupial predators and low relative predator diversity is a reasonable conclusion. Competition with non-mammalian predators may have served to limit marsupial diversity or these other predators may have filled niche space left vacant by marsupial predators. Competitive inferiority of marsupial predators is implied in the former case and a limited potential for marsupial predator diversification is implied in the latter. In either circumstance, marsupials as a group appear to make sub-par predators, at least by placental standards.

The rarity of fossil specimens suggests that marsupial predators may have been uncommon components of South American paleocommunities in addition to being relatively species poor. This low abundance is particularly surprising in light of their low diversity; one might reasonably expect a greater number of individuals per species would be present in order to maintain a similar biomass at higher trophic levels. The lower energy requirements of marsupial predators compared to placental predators [about 20% less for animals of equal mass (Burness *et al.*, 2001)] would further be expected to push abundance levels higher, all other things being equal. Not only is greater abundance of marsupials not the case, the exact opposite seems to be true. Further discussion of this apparent contradiction must await a more thorough analysis of species abundances in South American paleocommunities in a taphonomic context.

A topic that I did not address explicitly in this study is trophic differentiation among predatory marsupials. It has been suggested that most fossil predatory marsupials were hypercarnivores and that the real question is why there aren't more large marsupial omnivores (Wroe *et al.*, 2004). Although this may be an accurate assessment of most extinct predatory marsupials (*Thylacoleo* certainly comes to mind), determining whether an extinct mammal was hypercarnivorous (i.e. whether its diet included more or less than 70% meat) seems overly optimistic to me in many cases, especially given the absence of modern analogues and/or close living relatives for most of these taxa. Moreover, a lack of trophic diversity among marsupial carnivores is not an adequate explanation for their lack of taxonomic diversity; a comparison of dinosaurian and (placental) mammalian predators found similar diversity in the two groups despite the apparent preponderance of hypercarnivorous forms among dinosaurs (Van Valkenburgh and Molnar, 2002). The bottom line seems to be that relatively few species of marsupials have successfully ventured into the trophic realm of killing and eating other mammals, regardless of whether they do so as a primary food source or as a supplement to another dietary staple.

The potential role of dental constraints in limiting the diversity of predatory marsupials has been discussed previously, but this may be a developmental red herring. Although the dentitions of marsupial predators are generally assumed to be less diverse than those of placentals, several lineages nonetheless evolved remarkably specialized carnivorous dentitions (e.g. the saber-toothed sparassodont marsupial, *Thylacosmilus*; the phalangeroid marsupial 'lion', *Thylacoleo*; the macropodoid 'killer kangaroo', *Ekaltadeta*). Even the relatively small number of Recent Australian marsupicarnivores show morphological diversity within the dentition, perhaps greater than might be expected if constraint were a significant limiting factor (Jones, 2003). In contrast, the postcranial diversity of Recent marsupicarnivores is much less than that exhibited by modern placental carnivorans (Jones, 2003, figs. 4, 5), potentially due to developmental constraints on forelimb morphology related to marsupial reproduction (Lillegraven, 1975; Sears, 2004). Perhaps it is postcranial constraints – or maybe the combination of dental and postcranial constraints – that has resulted in the low diversity of marsupial predators in South America and Australia. A quantitative comparison of postcranial morphological diversity in extinct marsupial predators and modern carnivores (*sensu* Foote, 1993) would be especially enlightening in this regard. A similar comparison of the dentitions of these two groups is also needed; I am unaware of any study that has explicitly compared the dental diversity of extinct marsupial predators and carnivorans.

On a community level, even if one assumes that phorusrhacids were active predators and were relatively undersampled by the fossil record, the total diversity of predators in South American paleofaunas (and Australian paleofaunas) is still unusually low compared with modern faunas. Such low predator diversities might also have affected prey abundances and/or diversities in these paleofaunas, potentially resulting in changes in vegetational structure (e.g. Oksanen, 1988). This nonanalog characteristic of these paleofaunas is another attribute – in addition to the taxonomic composition of the fauna – that must be taken into account in paleoenvironmental and paleoecological analyses based on modern communities (Croft, 2001; Flynn *et al.*, 2003; Croft and Townsend, 2005).

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