Chapter 5
The Fossil Record of Mammalian Carnivores in South America: Bias and Limitations

Abstract South America has a rich fossil record that allows the reconstruction of the continental communities during the Cenozoic. Florentino Ameghino was one of the earliest advocates of a temporal sequence of faunas and biogeographic events, later refined by several authors (e.g., George G. Simpson, Rosendo Pascual, Bryan Patterson). This scheme is continually revised and improved by new faunal, systematic, and chronological studies. The fossil record is always incomplete, and many biases are recognized, some of them—the megabiases affect the interpretation of the global fossil record. For example, in South America, a megabias exists with respect to tropical areas, particularly before the Late Pleistocene. The SA fossil record contains large hiatuses between ages, with some ages being unconstrained by geochronological dates, while others are poorly sampled in terms of fossil recovery, faunal diversity, and identified localities. This form of bias which together with the differential duration of the South American Ages affects interpretation of the evolution of the continental fauna. In this chapter, we examine the spatial distribution of South American fossil localities, their frequency per age in the Cenozoic, and discuss the effect biases in the fossil record by means of a statistical approach.

Keywords Megabias · Taphonomy · Paleogeography · Paleoenvironments

5.1 Introduction

Florentino Ameghino (1854–1911) was one of the earliest researchers to make a substantial contribution to knowledge of SA mammalian faunas, their evolution, and biogeography. His work (e.g., Ameghino 1889, 1906) became the basis for investigations by other authors, for example George G. Simpson (1950, 1980), who recognized three "faunal strata," mainly characterized by biogeographic events (namely isolation, new lineages coming from Africa, and the Great American Biotic Interchange; see Chap. 2). A large volume of work begun in the mid-twentieth century by many different research teams (e.g., Simpson 1950, 1980; Pascual and Odreman Rivas 1971; Patterson and Pascual 1972; Marshall et al. 1977, 1981,

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1983, 1984, 1985; Stehli and Webb 1985; Pascual and Ortiz-Jaureguizar 1990; Cione and Tonni 1995, 1996, 1999, 2001, 2005; Marshall and Cifelli 1990; Webb 1991, 2006; Flynn and Swisher 1995; Kay et al. 1999; Flynn et al. 2003; Pascual 2006; Cerdeño et al. 2008; Tejedor et al. 2009; Tonni 2009; Madden et al. 2010; Woodburne 2010; Vizcaíno et al. 2012; Dunn et al. 2013; Goin et al. 2012, 2016; Deschamps et al. 2013; Tomassini et al. 2013; Wilf et al. 2013; Woodburne et al. 2014a, b; Cione et al. 2015) produced the synthesis that we have to date concerning the biostratigraphy, chronology, biogeography, and evolution of Cenozoic fossil associations in South America (see also Table 1.1).

This copious bibliography is an indication of the amount and richness of the South American fossil record as well as the volume of study. But the record is imperfect and has important systematic biases (e.g., Marshall and Cifelli 1990; Prevosti and Soibelzon 2012; Prevosti et al. 2013; Carrillo et al. 2015). The fossil record is not consistent through different parts of the Cenozoic and across different regions of the continent, creating a megabias (large-scale distortions caused by changes in the quality of the fossil record; Kowalewski and Flessa 1996; Behrensmeyer et al. 2000; Noto 2011; Benton 2015). In addition, large-scale discontinuities in the record and taphonomic conditions of fossil sites are linked to differential intensity of sampling and imprecise limits for several ages (Marshall and Cifelli 1990; Prevosti and Soibelzon 2012; Prevosti et al. 2013).

In this chapter, we provide a short review of the quality of the Cenozoic continental fossil record of South America, with particular reference to the context of change in diversity of sparassodonts and carnivorans. In this and the following chapter, we test hypotheses about competition between clades and extinction and quantitatively evaluate if the bias in the fossil record has an impact on hypotheses.

5.2 Limitations and Bias of the Cenozoic Continental Fossil Record of South America

The biases examined are general problems that affect the fossil record (e.g., Marshall and Cifelli 1990; Kowalewski and Flessa 1996; Behrensmeyer et al. 2000; Noto 2011; Benton 2015) and in particular estimations of diversity, first and last appearances, and the precise calibration of different chronological parameters (e.g., Marshall and Cifelli 1990; Maas et al. 1995; Foote 2000; Prevosti and Soibelzon 2012; Prevosti et al. 2013; Benton 2015).

5.2.1 Hiatuses and Definition of Ages

Marshall and Cifelli (1990) discussed the importance of hiatuses, particularly in the Paleogene record. Since that time, new information has accumulated (e.g., Flynn et al. 2003; Cerdeño et al. 2008; Tejedor et al. 2009; Madden et al. 2010; Dunn et al. 2013; Clyde et al. 2014; Woodburne et al. 2014a, b), but hiatuses and unconstrained age limits remain in the South American fossil record (Tables 1.1, 5.1).

Major hiatuses in the Paleogene exist between most ages. In the case of the Peligran and the Itaboraian, the Riochican and the Vacan, and within the Casamayoran (Table 1.1) for example, hiatuses are longer than the time span of their corresponding ages (Dunn et al. 2013; Clyde et al. 2014; Woodburne et al. 2014a, b). New mammal associations partially fill those gaps and potentially represent new biochronological units (Tejedor et al. 2009; Madden et al. 2010).

The hiatus problem is less severe in the Neogene, but gaps of about 2 Ma exist, for example, between the Colhuehuapian and Santacrucian (or "Pinturan," Vizcaíno et al. 2012; Perkins et al. 2012).

For the Neogene, the most relevant issues are the lack of definition for some ages (e.g., Colloncuran, Friasian, Mayoan, Huayquerian) (e.g., Prevosti et al. 2013; Cione et al. 2015) and the absence of radiometric constraints.

For the late Miocene, there is an issue with the definition of the Huayquerian, one of the most extensive age units, repeatedly used in South America, from Venezuela to Argentina, and one of the most relevant in terms of the biochronology of the GABI, since this age records the earliest Holarctic immigrants in South America. The Huayquerian age was defined in the badlands of the Huayquerías of Mendoza (Mendoza, Argentina; De Carles 1911; Rovereto 1914), first used by Kraglievich (1934) imploying the concept of faunal association and then by Simpson (1940) as part of his scheme of South American Stages. However, the Huayquerías Formation in its type locality has provided less than a dozen published species (Forasiepi et al. 2014) and is poorly constrained, with a radiometric date of about 5.8 Ma in the upper part of the sequence (Yrigoyen 1994) from a re-deposited ash. Consequently, there are different conceptions in the literature about the Huayquerian that are not linked to the type locality and fauna found at the Huayquerías of Mendoza. Furthermore, the age was divided into a lower and upper Huayquerian intervals. The first was defined on the basis of the *Macrochorobates scalabrinii* biozone from an innominate lithostratigraphic unit exposed in the lower valley of Chasicó Creek, Buenos Aires (Tonni et al. 1998). The second was based on four biochronological units (Verzi et al. 2008) from the Cerro Azul, Irene, and Epecuén formations exposed in eastern La Pampa and southwestern Buenos Aires provinces (Cione et al. 2015).

In an attempt to constrain the age of the Huayquerian, Cione et al. (2015) correlated its fauna with the "Mesopotamiense" in Entre Rios, Argentina (Brandoni and Noriega 2013), constrained by a date of 9.47 Ma obtained for the lower Paraná Formation (Pérez 2013). This sets the age of the Huayquerian between ca. 8.2 and 5.9 Ma. Based on the rodent record of the Cerro Azul Formation and deposits in the southwest of Buenos Aires Province (e.g., Verzi et al. 2008; Verzi and Montalvo 2008), other authors placed the Huayquerian between ca. 6 and ca. 5.3 Ma, although without radiometric or paleomagnetic data (see Prevosti and Pardiñas 2009 for a critique of this scheme). More recently, a date of 5.28 Ma was determined for

Table 5.1 Diversity of predators (carnivorans and sparassodonts) number of fossil localities, time span, and Lazarus taxon for the South American Ages

Age	Number of sites	Time span (Ma)	Geographic area (km^2)	Predator diversity	Predator Lazarus	Spa. diversity	Spa. Lazarus	Car. diversity	Car. Lazarus
Tiupampan	1	0.7	175	1	0	1	0	0	0
Peligran	1	1.7	175	0	1	0	1	0	0
Itaboraian	2	1.5	21,116	1	0	1	0	0	0
Riochican	1	2	289	0	1	0	1	0	0
Casamayoran	9	10	19,774	9	0	9	0	0	0
Mustersan	3	2.5	234,294	3	0	3	0	0	0
Tinguirirican	1	2.3	5314	0	0	0	0	0	0
Deseadan	11	5.2	5,290,846	8	0	8	0	0	0
Colhuehuapian	5	0.9	270,261	7	0	7	0	0	0
Santacrucian	26	2	348,695	11	0	11	0	0	0
Friasian	2	0.8	370	4	3	4	3	0	0
Colloncuran	6	1.5	200,582	3	1	3	1	0	0
Laventan	14	2	42,961	5	0	5	0	0	0
Mayoan	1	1.8	350	0	1	0	1	0	0
Chasicoan	2	1	291,880	4	0	4	0	0	0
Huayquerian	12	3.72	3,578,542	11	0	7	0	4	0
Montehermosan	1	1.28	29,875	3	1	2	1	1	0
Chapadmalalan	9	1	3,174,916	5	0	2	0	3	0
Barrancalobian	1	0.1	0.65	0	2	0	0	0	2
Vorohuean	3	0.2	11,766	3	1	0	0	3	1
Sanandresian	3	0.92	110,253	2	2	0	0	2	2
Ensenadan	37	1.38	1,412,918	22	0	0	0	22	0

(continued)

Table 5.1 (continued)

Age	Number of sites	Time span (Ma)	Geographic area (km^2)	Predator diversity	Predator Lazarus	Spa. diversity	Spa. Lazarus	Car. diversity	Car. Lazarus
Bonaerian	8	0.274	88,020	1	6	0	0	1	6
Lujanian	108	0.119	15,871,045	36	0	0	0	36	0
Platan	135	0.005508	15,528,203	23	7	0	0	23	7

Spa. = sparassodonts; Car. = carnivorans; Ma. = millions of years the upper Huayquerian levels studied by Verzi and Montalvo (Schultz et al. 2006; Tomassini et al. 2013; Cione et al. 2015) close to the Atlantic coast of Buenos Aires Province, which is a slightly younger upper age limit.

The immediately preceding Chasicoan Age has only one date of 9.24 Ma (Schultz et al. 2006) but its limits are otherwise not constrained.

The Pliocene Montehermosan to Marplatan Ages were defined in the coastal region of Buenos Aires Province. The Montehermosan is based on the *Eumysops laeviplicatus* biozone (Tomassini et al. 2013 = *Trigodon gaudryi* and *Neocavia depressidens* biozones of Cione and Tonni 2005) and at its type locality is neither dated nor constrained. Tomassini et al. (2013) suggested that the Monte Hermoso Formation was deposited over a few hundred thousand years, and point to the existence of hiatuses between the Montehermosan, Huayquerian, and Chapadmalalan Ages. The Chapadmalalan is based on the *Paraglyptodon chapadmalensis* biozone and has a radiometric date of age of 3.3 Ma at the top of its type unit, the Chapadmalal "Formation" (Schultz et al. 1998), three meters below the contact with the overlying Barranca de Los Lobos "Formation," indicating that the Chapadmalalan upper limit is at least younger than 3.3 Ma. The Marplatan includes three Subages, namely the Barrancalobian, Vorohuean, and Sanandresian, based on the *Platygonus scagliai*, *Akodon lorenzinii*, and *Ctenomys chapalmalensis* biozones, respectively (Cione and Tonni 1995, 1999; Cione et al. 2015). There are no confidents limits defined for any of these ages. But a recent paleomagnetic study (Rico and Bidegain 2013) suggested that the upper limit of the Vorohuean Subage is ca. 2.6 Ma, and that Sanandresian is between 1.8 and 2.6 Ma. Recently, Isla et al. (2015) questioned the mammal association used for the definition of the Barrancalobian Subage, suggesting that it could represent a mixture of Chapadmalalan and younger faunas. This challenging argument should be further evaluated.

The ages of the Quaternary South American Ages and biozones were also defined in the Pampean Region. Time constraints, particularly for the Ensenadan, Bonaerian and Lujanian, are tentative (Cione and Tonni 1995, 1999; Prevosti et al. 2009; Cione et al. 2015).

In short, although there is not a continuous sedimentary record in most sites of the Pampean Region, the late Miocene-Pleistocene SA Stages/Ages—with the exception of the Huayquerian—were defined in this area. Most sites are geographically isolated with few datable elements, which lead to uncertainty, in particular to the time span represented by the units. More continuous sequences with classical fossil sites are present in western Argentina (e.g., Catamarca Province; Riggs and Patterson 1939; Marshall and Patterson 1981; Esteban et al. 2014). Independent biozones have been recently defined and constrained by several radiometric dates and magnetostratigraphic data (Reguero and Candela 2011; Esteban et al. 2014), but these schemes are difficult to correlate with the biostratigraphic scheme of the Pampean Region. A recent proposition suggests avoiding the use of "ages" in favor of using the international timescale (Brandoni 2013; Esteban et al. 2014), but this is only possible when accurate independent methods of dating are available and the faunal ages are precisely delimited.

5.2.2 Age Time Span

Durations of SA Ages are extremely unequal. Some ages comprise several million years (ca. 5 Ma for the Deseadan), while others are less than 200,000 years (ca. 120 ka for the Lujanian and less than 10 ka for the Platan) (Tables 1.1, 5.1, and Fig. 5.1). Increasing the duration of an age naturally increases the number of fossil sites and finds with a potential consequent increase in diversity (Marshall and Cifelli 1990; Maas et al. 1995; Palombo et al. 2009; Figueirido et al. 2012; Prevosti and Soibelzon 2012). However, this effect has been recently statistically tested for SA associations with studies focused on the carnivoran fossil record since the late Miocene to Present (number of species against time span of each age; Prevosti and Soibelzon 2012), and on the sparassodont and carnivoran fossil record for the entire Cenozoic (Prevosti et al. 2013). Despite the inequality of the duration of the ages, these studies produced non-significant correlations, suggesting that the major pattern of diversity through time has not been strongly affected by fossil recovery biases.

The updated dataset of Prevosti et al. (2013) (Table 5.1) provides a similar result (Spearman rank correlation) whether the analysis was done with the total sample (*R*: −0.047, *p* 0.825), or for only sparassodonts (*R*: 0.268, *p* 0.283), or only carnivorans (*R*: −0.134, *p* 0.713) (Fig. 5.1). This relationship was confirmed using Quantile Regression and the Durbin–Watson test that indicated the absence of autocorrelation in the data.

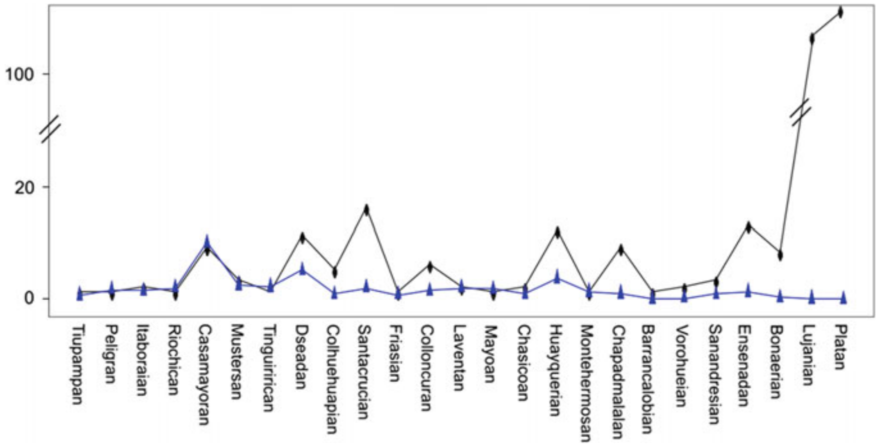

Fig. 5.1 Number of localities (a proxy of sampling effort) and time span of each South American Age. Black diamonds and line: number of localities; blue triangles and line: time span (millions of years)

5.2.3 Geographic Bias

The SA fossil record has a strong geographic megabias against tropical or low-latitude areas (e.g., Pascual and Odreman Rivas 1971; Patterson and Pascual 1972; Marshall et al. 1982; Marshall and Cifelli 1990; Prevosti and Soibelzon 2012; Carrillo et al. 2015; Goin et al. 2016). This bias is more extreme for the Paleogene and early–middle Miocene, because other than a few exceptions (e.g., Campbell 2004; Antoine et al. 2015), fossil sites are limited to high-latitude areas, especially in Patagonia (e.g., Pascual and Odreman Rivas 1971; Patterson and Pascual 1972; Marshall et al. 1982; Prevosti and Soibelzon 2012; Carrillo et al. 2015; Goin et al. 2016; Figs. 3.1, 4.1 and 5.2).

In contrast, post-middle Miocene fossil sites are generally found north of Patagonia. The distribution of late Miocene Huayquerian outcrops is wider, but still there are few records from lowland tropical South America or Patagonia. In this context, Prevosti and Soibelzon (2012) demonstrated that for the late Huayquerian–Platan time span, localities with fossil carnivorans are mostly restricted to the southern half of the continent and only since the Late Pleistocene (Lujanian) is there a wider coverage of the continent, including tropical and low-latitude areas. Similarly, Carrillo et al. (2015), in an analysis that included the complete faunal lists from 13 middle Miocene to Pleistocene associations, detected a differentiation between temperate and tropical faunas with a megabias toward higher latitudes and younger ages.

In order to test this megabias, we analyze the correlation between the geographic coverage of each biochronological unit vs its taxonomic diversity by considering the number of carnivorous species, both sparassodont and SA carnivoran. We

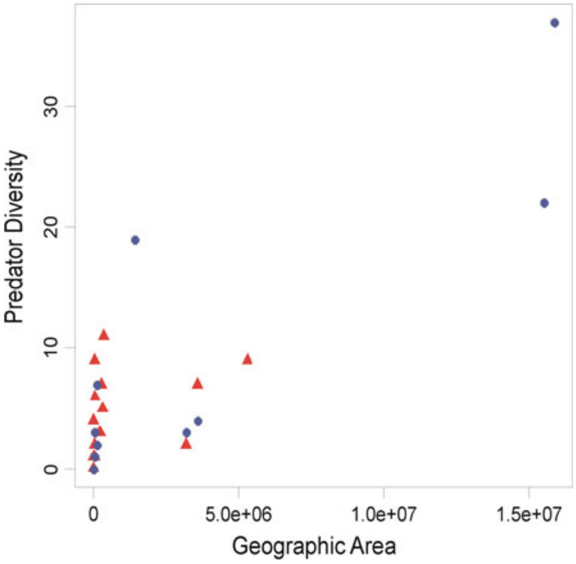

Fig. 5.2 Biplot of geographic area (km^2) and predator diversity in each South American Age. Circles: carnivorans; triangles: sparassodonts

estimated the geographic area covered by each SA Age, using localities that are the furthest apart localities in the west, east, south, and north, and applying the software gvSIG (http://www.gvsig.org); Table 5.1; raw data available on request). For ages with only one or two fossil localities, we duplicated or triplicated their geographic coordinates, and their first decimal was randomly changed. The analysis of these data indicates that there is a positive and significant correlation between the area covered by the sites of each age and the species richness of the whole sample (sparassodonts + carnivorans; Spearman R: 0.829, $p < 0.0000004$), only sparassodonts (Spearman R: 0.688, $p < 0.0016$), and only carnivorans (R: 0.844, $p < 0.0022$). These results indicate that ages covering larger geographic areas produced larger diversities (Fig. 5.2). This relationship was also confirmed using Quantile Regression (whole sample, sparassodonts + carnivorans: r^2 0.686, $p = 0.00342$; carnivoran sample: r^2: 0.687, $p = 0.015$), but not for the sparassodont sample, which gave a non-significant result (r^2: 0.126, $p = 0.09530$). The Durbin–Watson tests were not significant, indicating the absence of autocorrelation in the data.

5.2.4 Sampling

Differences in sampling between ages is an issue for a wide range of analyses, since it is likely that well-sampled ages provide larger diversities than those poorly sampled (e.g., Benton et al. 2000). Several proxies were used to evaluate the impact of sampling on the diversity counts: number of fossil localities, number of geological formations, geological exposure area, and skeletal completeness (e.g., Figueirido et al. 2012; Benton 2015; Cleary et al. 2015), but these measurements are also affected by differential sampling efforts, taphonomic processes, fossil site exposures, and specimen availability and/or taxonomic work. A non-significant relationship between diversity and one of these sampling proxies cannot completely rule out the presence of a bias, but a significant correlation may be interpreted as evidence of bias.

The sampling bias of the SA fossil record was tested by Prevosti and Soibelzon (2012) and Prevosti et al. (2013) using the nonparametric Spearman rank correlation between the diversity of carnivorans and sparassodonts and the number of localities per age (see also Marshall and Cifelli 1990). The results demonstrated the presence of a strong and significant correlation, congruent with the presence of a sampling bias, when carnivorans, sparassodonts, and both groups together were considered. The "range-through taxa" (="Lazarus taxa") were included in the tests (Fig. 5.3).

A new analysis of the data (Table 5.1; Figs. 5.1, 5.4) supports previous results, with a positive correlation between the number of sites and diversity for the SA Ages, whether the correlation is tested with the whole sample: sparassodonts + carnivorans (Spearman R: 0.817, $p < 0.0000006$), only with sparassodonts (Spearman R: 0.745, $p < 0.0004$), or only with carnivorans (Spearman R: 0.893, $p < 0.0005$). These results indicate that better-sampled ages provide larger

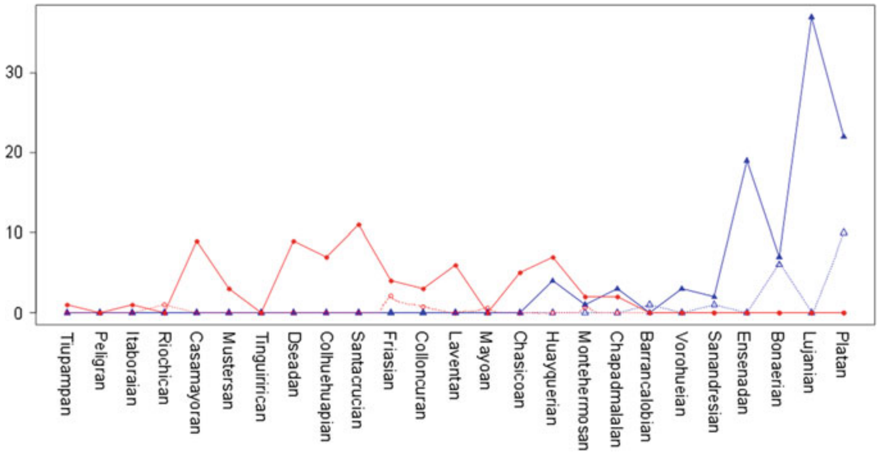

Fig. 5.3 Diversity of predators (number of taxa) and number of Lazarus taxa in each South American Age. Red circles and lines: sparassodonts; blue triangles and lines: carnivorans; solid lines: diversity; broken lines: Lazarus taxa

diversities. A relationship was also confirmed using Quantile Regression and the Durbin–Watson test, indicating lack of autocorrelation in the data. Consequently, the low diversity found for most of the Paleogene, and Colloncuran, Friasian, Chasicoan, Montehermosan, Marplatan, and Bonaerian Ages could be explained by this sampling bias (Figs. 5.1 and 5.4). “Lazarus taxa” showed a low negative relationship against diversity (Spearman R between −0.177 and −0.314), but this is non-significant ($p > 0.05$).

The number of localities and geographic areas covered by each age is strongly and significantly correlated, especially when considering the whole sample (sparassodonts + carnivorans) or the carnivoran sample alone (Spearman R: 0.84 and $p < 0.0000002$, and Spearman R: 0.84 $p < 0.0022$, respectively). The sparassodont sample had a lower but still significant correlation between these variables (Spearman R: 0.77, $p < 0.000185$). This high positive correlation indicates that geographic area and number of localities are redundant. In this sense, better-sampled ages will have more localities and a wider geographic covered area than the less sampled.

Because there is a clear recovery bias in the fossil record, we examined how this has affected observed sparassodont and carnivoran diversity during the late Miocene and Pliocene, which is the period of crucial relevance to understand the demise of sparassodonts. Using re-sampling techniques (Manly 1997), the sampling effort was tested with the number of localities and specimens as proxies, of each clade by age (Tables 5.1 and 5.2). We reduced the sample of the better-known associations (Santacrucian, the combination of Friasian to Chasicoan, and Huayquerian for sparassodonts; Ensenadan for carnivorans) to test if these approximate the sampling effort observed for the Huayquerian to Chapadmalalan

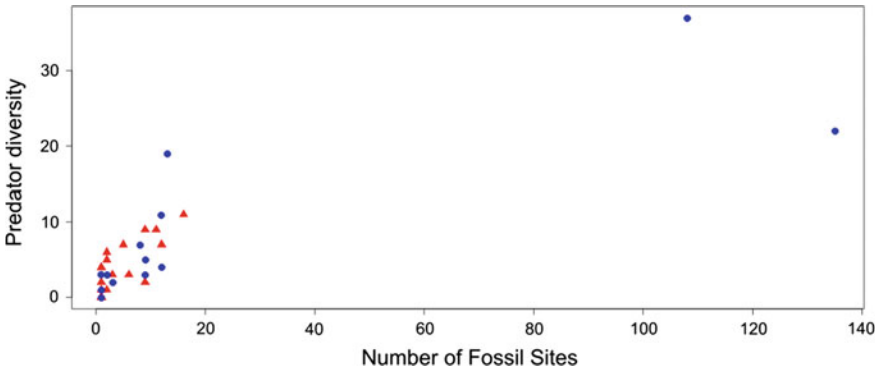

Fig. 5.4 Biplot of the number of localities and the diversity of predators (number of species) in each South American Age. Circles: carnivorans; triangles: sparassodonts

for sparassodonts and Huayquerian to Sanandresian for carnivorans. For sparassodonts, the Huayquerian was also used as a proxy to test the diversity of the Montehermosan and Chapadmalalan. If the diversity displayed by the fossil record is significantly different from the re-sampling exercise ($p < 0.05$), we can assume that difference in the sampling effort does not explain the low diversity observed for the late Miocene–Pliocene and should indicate a real pattern.

The result of our analysis demonstrated that the observed diversity of sparassodonts for the Huayquerian is lower than expected (except when it is compared with the Santacrucian) and for the Chapadmalalan (except when it is compared with the Huayquerian using the specimens as proxy for the sampling effort). In contrast, the difference in diversity in the Montehermosan is lower and non-significant (except when it is compared with the Santacrucian using the localities as proxy for the sampling effort). The observed carnivoran diversity is significantly lower during

Table 5.2 Number of specimens of carnivorans and sparassodonts during the Santacrucian–Ensenadan

Age	Carnivorans	Sparassodonts
Santacrucian	0	220
Friasian	0	8
Colloncuran	0	5
Laventan	0	26
Mayoan	0	0
Chasicoan	0	7
Huayquerian	16	31
Montehermosan	4	2
Chapadmalalan	18	9
Barrancalobian	0	0
Vorohuean	3	0
Sanandresian	2	0
Ensenadan	189	0

the Huayquerian, Montehermosan, and Chapadmalalan. But during the Vorohuean and Sanandresian, the difference in diversity is only significant when localities are used as proxy. Using the number of localities and re-sampling the Santacrucian and Huayquerian faunas, we calculated a median number of sparassodonts in 2–4, 3–6, 4–6, and 4–10 species bins for the Barrancalobian, Vorohuean, Sanandresian, and Ensenadan, respectively. Conversely, the median random expected number of carnivorans for the Barrancalobian is four species, twice the number of ghost lineages recorded in this Subage.

Finally, we examined the situation considering three carnivorans (*Conepatus altiramus*, *Smilodontidion riggii*, and *"Felis" pumoides*) with dubious Chapadmalalan stratigraphic procedence (see Chap. 4), as a simulation of potential new records that could increase the diversity of carnivorans for that age. However, we understand that is not possible to corroborate that these fossil were effectively recovered from Pliocene beds (Berman 1994; Cione and Tonni 1995, 2001, 2005, Prevosti and Soibelzon 2012). In only considering a diversity of six carnivores, the result is marginally non-significant, suggesting that the observed low diversity is a product of taphonomic biases. However, removing any one of these taxa results in a significant difference from random expectation.

5.3 Discussion and Conclusions

The review of several potential biases in the South American fossil record highlights the limitations and complications in interpretation of diversity and related variables. Important issues regarding the SA biochronological scheme and major biases are the lack of definition for some units and lack of radiometric constraints for others, the presence of large hiatuses in the biochronological sequence, especially for the Paleogene, the difference in interval length, from the Deseadan covering ca. 5 Ma to the Platan covering less than 10 ka, a geographic bias in the fossil record disfavoring the tropics, and differential sampling.

In this context, sampling biases are probably a major reason for the difference between the high diversity and ecological disparity of the Santacrucian Age in comparison to the low values recovered for the Chasicoan. A relevant issue is to determine whether the long interval between the last record of the large hypercarnivorous Sparassodonta in the Chapadmalalan and the first records of the large hypercarnivorous Carnivora (Felidae and some clades of Canidae) in the Ensenadan (Fig. 4.2) is a real pattern or a product of the bias of the record (Prevosti et al. 2013).

As was mentioned in Chapter 4, small hypercarnivorous carnivorans (e.g., *Galictis* spp.) are known since the Vorohuean but are more diverse since the Ensenadan. Foxes are known since the Vorohuean but have a better fossil record during the Ensenadan–Lujanian Ages. On the other hand, sabertooth cats and other large hypercarnivorous placentals (e.g., canids, *Puma*, *Panthera*) appear in the SA fossil record during the Ensenadan and are the most frequently recovered carnivorans during the last 1.8 Ma. The absence of large hypercarnivorous carnivorans in the Chapadmalalan–Marplatan could be due a strong bias against medium- and large-sized carnivorans, a conclusion congruent with the recent suggestion that the glyptodont *Panochthus* is a Lazarus taxon during the Marplatan (Zamorano et al. 2014; Cione et al. 2015; see also Isla et al. 2015). However, medium- and large-sized mammals, for example, equids, other glyptodonts, ground sloths, mesotheriids, and one large carnivoran (*Chapalmalania*), are recorded for the Marplatan (Cione and Tonni 2005; Cione et al. 2015). In this context, we expect that if *Smilodon* was present before the Ensenadan in the Pampean Region, it should have been found together with mustelids and foxes. This reasoning could also be applied to justify the absence of *Thylacosmilus* in the Marplatan. Additionally, carnivorous didelphimorphians are also recorded in the Barrancalobian and Vorohuean (Zimicz 2014) and, since they have small body sizes, this suggests that small hypercarnivore sparassodonts should be found in the Marplatan if they were not extinct. New collections with controlled provenance are needed to test the presence of this type of bias.

The Chapadmalalan Age is well known, particularly through the very rich outcrops of the Chapadmalal "Formation," which have been extensively explored for more than a century (see Cione and Tonni 1995). Several specimens of *Cyonasua*, some of *Chapalmalania* and *Thylacosmilus*, one specimen of *Borhyaenidium*, and "terror birds" have been collected here (see Chaps. 3 and 4; Tambussi and Degrange 2011; Degrange et al. 2015). The possible presence of felids in the Chapadmalalan has been refuted (see Prevosti 2006; Prevosti et al. 2006; Prevosti and Pomi 2007), and the presence of mephitids (*Conepatus*) is dubious (Cione and Tonni 1995; Woodburne et al. 2006; Woodburne 2010). The large sampling effort and the amount of taxonomic and biostratigraphic work on the Chapadmalal "Formation" indicate that the mammalian diversity would not increase significantly with new fossil collections. Sparassodont and carnivoran diversity is presently very low in the Chapadmalalan, but this does not appear to be related to a bias in the fossil record (Table 5.1). Additionally, several key relevant Ages (i.e., Chapadmalalan, Ensenadan–Recent) are well represented and well sampled, locally or regionally. Consequently, we interpret that the low diversity and narrow morphological disparity of carnivorans during the Huayquerian–Sanandresian is not an artifact of the sampling effort (see also Prevosti and Soibelzon (2012), and similarly the high diversity and broad disparity observed since the Ensenadan is a real pattern.

Our re-sampling analysis (using number of fossil localities and specimens as proxies) tested the impact of the sampling effort on the observed diversity. The re-sampling analysis indicates that the observed carnivoran diversity is significantly lower than random expectation for the Huayquerian–Chapadmalalan, something that suggests that the observed diversity is a real pattern and not a product of a low sample size for these Ages. The same is the case for sparassodonts for the Chapadmalalan, and less certain for the Huayquerian, but the results for the Montehermosan are dubious. As happens with the Montehermosan, the results about carnivoran diversity in the Vorohuean and Sanandresian are also ambiguous because there are fewer than three localities or predator specimens (2–4) and consequently the diversity could increase with larger samples. In addition, it is not possible to exclude the presence of other biases obscuring the real diversity (such as systematic biases against specific body sizes, ecological groups, or taxa). However, in the absence of other evidence, we conclude that the biases in the fossil record are not enough to explain the low diversity observed during the late Miocene–Pliocene.

In summary, big structural issues and biases are relevant to interpreting the SA biochronological framework and particularly the Paleogene ages. With the available data, it is not possible to definitively exclude the possibility that taphonomic and sampling biases mask a significant overlap in time between ecologically equivalent sparassodonts and carnivorans. However, in light of the arguments and statistical predictions discussed, it is probable that the lack of temporal and ecological overlap actually reflects the real pattern.

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