Diversity and disparity of sparassodonts (Metatheria) reveal non-analogue nature of ancient South American mammalian carnivore guilds

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This study investigates whether terrestrial mammalian carnivore guilds of ancient South America, which developed in relative isolation, were similar to those of other continents. We do so through analyses of clade diversification, ecomorphology and guild structure in the Sparassodonta, metatherians that were the predominant mammalian carnivores of pre-Pleistocene South America. Body mass and 16 characters of the dentition are used to quantify morphological diversity (disparity) in sparassodonts and to compare them to extant marsupial and placental carnivores and extinct North American carnivoramorphans. We also compare trophic diversity of the Early Miocene terrestrial carnivore guild of Santa Cruz, Argentina to that of 14 modern and fossil guilds from other continents. We find that sparassodonts had comparatively low ecomorphological disparity throughout their history and that South American carnivore palaeoguilds, as represented by that of Santa Cruz, Argentina, were unlike modern or fossil carnivore guilds of other continents in their lack of mesocarnivores and hypocarnivores. Our results add to a growing body of evidence highlighting non-analogue aspects of extinct South American mammals and illustrate the dramatic effects that historical contingency can have on the evolution of mammalian palaeocommunities.

1. Introduction

The evolution of mammals during South America’s protracted Cenozoic geographical isolation is well documented [1–3]. Nevertheless, few studies have attempted to examine how such ‘Splendid Isolation’ may have affected the structure of mammalian ecological communities. Herein, we quantify and analyse the taxonomic diversity and morphological disparity of sparassodont metatherians, the predominant carnivorous land mammals of ancient South America, in order to characterize their evolutionary history and examine dietary resource partitioning among members of the terrestrial carnivore guild. Sparassodonts represent a radiation of mammals into the carnivore/predator niche independent of those on other continents [4]. Thus, their fossil record provides an opportunity to test whether patterns of clade evolution and niche partitioning in carnivoramorphs primarily reflect ecological factors affecting all carnivorous mammals or morphological adaptations unique to Carnivora.

Sparassodonts are organized into five family-level groups: Borhyaenidae, Proboryhaenidae, Thylacosmilidae, Hathliacynidae and the monotypic Hondurasphidae, the first three of which comprise Borhyaenoidea [5–7]. They ranged in size from less than 1 kg to approximately 150 kg, and their fossil record extends from the early Cenozoic to the Pliocene (electronic supplementary material, table S1). Although sparassodonts as a group were clearly carnivorous...
in South America including: (i) did the diversification of sparassodonts in South America resemble that of carnivoramorphans in North America? (ii) how did the late Cenozoic decline of sparassodonts affect the group’s disparity? and (iii) how do diversity and disparity of sparassodonts compare to Cenozoic North American carnivoramorphans and modern carnivorans as a whole?

2. Material and methods

(a) Terminology

‘Diversity’ (without any qualifier) refers to taxonomic diversity (richness) and ‘disparity’ refers to morphological diversity [15] or functional richness [16]. We measure diversity using operational taxonomic units (OTUs) and disparity using occupied morphospace. ‘Carnivorous’ refers to animals that feed on vertebrates (not simply secondary consumers). ‘Omnivorous’ refers to animals that consume significant plant material and/or invertebrates in addition to vertebrates.

(b) Sparassodont data

OTUs are genera or purported genera, primarily following Forasiepi [5]. Additional details are provided in the electronic supplementary material, table S4. To describe sparassodont dental ecomorphology, we scored all OTUs for 16 characters used by several previous studies [17–19] to quantify carnivoramorphan and ‘creodont’ dental ecomorphology (electronic supplementary material, tables S6–S7). M3 and M4 were considered the carnassials in sparassodonts; as they are the largest and least-worn slicing teeth and are thought to be the closest functional analogues of ‘creodont’ and carnivoran carnassials (e.g. [19,20]). Relative grinding area (Character no. 16) was scored following Werdelin & Wesley-Hunt [17] but with one bin subdivided into order to better distinguish extant mesocarnivores and hypocarnivores. Body mass (Character no. 17) was scored following Wesley-Hunt [19] but with the smallest body size state divided into two; OTUs were coded using body mass ranges in the electronic supplementary material, table S1, and scored for the larger state in cases where the body mass spanned two categories. Scoring was based on original material where possible (electronic supplementary material, table S5). Owing to incomplete fossil preservation, most OTUs could not be scored for at least some characters. In some cases, character states were scored based on homologous or analogous teeth or morphologically similar OTUs (noted in the electronic supplementary material, table S7).

(c) Non-sparassodont data

We coded nine additional carnivorous metatherian genera for comparative purposes: three extant Australian dasyuromorphians and six extinct South American didelphimorphians (electronic supplementary material, table S1). The former may be the closest extant ecomorphological analogues for sparassodonts, whereas the latter coexisted with sparassodonts during the late Neogene and have been suggested to have occupied similar niches and/or competitively replaced some species [10,21]. Metatherian codings were combined with the extant carnivoran dataset of Werdelin & Wesley-Hunt [17], which includes approximately 85% of modern carnivoran species, and the North American Cenozoic carnivoramorphan dataset of Wesley-Hunt [19], which was recoded to be congruent with the present study.

(d) Time bins

For analyses of diversity and disparity through time, sparassodonts were allocated to 2-million-year time bins based on the
South American Land Mammal Age(s) (SALMAs) or informal equivalents in which the taxon has been recorded (electronic supplementary material, table S8). These bins (intervals) were used rather than absolute ages because the ages of most South American fossil sites are not known with greater precision.

(e) Carnivore guilds

Taxonomic lists of non-volant terrestrial carnivore guilds were compiled from the literature for the late Early Miocene site of Santa Cruz, Argentina [22,23] and three modern ecosystems: the lowland rainforest of Malaysia, the savannah-woodland of Serengeti National Park, Tanzania, and the temperate coniferous forest of Yellowstone National Park, USA (electronic supplementary material, table S9). Santa Cruz was chosen as representative of a South American fossil carnivore guild because it is the most diverse guild presently known, and the palaeobiology of many species has been studied in detail. The three modern sites are those used by Van Valkenburgh in her classic studies of large carnivore guilds [24,25]; small carnivorans were added based on other sources. Modern carnivorans were categorized as hypercarnivorous, mesocarnivorous or hypocarnivorous based primarily on Van Valkenburgh [25] (large species) and Friscia et al. [26] (small species). A comparative set of 11 Northern Hemisphere fossil carnivore guilds (including ‘creodonts’, mogenychians, carnivoramorphans and other groups) were compiled from Morlo et al. [27] and the primary literature (electronic supplementary material, table S9).

(f) Analytical methods

Analytical methods for calculating disparity follow Werdelin & Lewis [28] and Werdelin & Wesley-Hunt [18]. Disparity (occupied morphospace [29]) was calculated as the convex hull area encompassing the taxa on a bivariate plot of the first two axes of a correspondence analysis. All OTUs (sparassodonts, dasyuramorphans, didelphimorphans, North American Cenozoic carnivoramorphans and modern carnivorans) were included in a single analysis to obtain individual scores that were subsequently used to determine occupied morphospace. Morphospace analyses were performed in PAST v. 3.10 for Mac [30], which uses column average substitution to accommodate missing data. Other statistical analyses and data visualization were conducted in JMP Pro® 13.0 for Mac [31].

3. Results

(a) Diversification and decline of sparassodonts

Sparassodont disparity is positively correlated with diversity (Spearman’s $r = 0.8350$ excluding intervals with $<3$ OTUs; $p < 0.0002$), and maximal disparity coincides with maximal diversity during the late Early Miocene (Santacrucian interval; figure 2). Disparity increases from the Early to Middle Eocene (Barrancan interval), drops during the Late Eocene (Mustersian interval) and gradually increases up to the late Early Miocene peak. It decreases gradually during the Middle Miocene, drops during the early-Late Miocene, subsequently rebounds and then drops again by the end of the Miocene (see also Discussion). Diversity shows a similar but exaggerated trend, particularly when intervals with less than three OTUs are ignored (i.e. those for which disparity cannot be calculated). Disparity relative to diversity is highest during the Late Miocene (Huayquerian interval), which plots as an outlier relative to other points based on Mahalanobis and jackknife distances at $\alpha = 0.05$ (but not $\alpha = 0.01$).

(b) Diversification of carnivoramorphans

Carnivoramorph disparity is also positively correlated with diversity (Spearman’s $r = 0.8922$; $p < 0.0001$). Disparity decreases after the Early Eocene and reaches a low point during the Late Eocene (40–38 Ma) but generally increases throughout the remainder of the Cenozoic. Dips in disparity occur during the Oligocene (30–26 Ma), Early Miocene (20–18 Ma) and Middle Miocene (14–10 Ma), and disparity rises steeply in the Late Miocene (after 6 Ma). Diversity outpaces disparity 29–27 Ma but decreases during the Late Oligocene and Early Miocene (26–20 Ma), while disparity remains generally constant. Disparity and diversity show congruent patterns in the Early to Middle Miocene (20–12 Ma), but a decrease in disparity coincides with an increase in diversity in the late Middle Miocene (12–10 Ma), and the opposite occurs during the Late Miocene (after 6 Ma). This final interval (6–4 Ma) plots as an outlier relative to other points based on Mahalanobis and jackknife distances ($p < 0.01$).

(c) Sparassodonts and North American carnivoramorphans compared

Carnivoramorph disparity exceeds that of sparassodonts throughout the Cenozoic except during the late Middle Eocene (42–40 Ma; Barrancan interval), when five OTUs are recorded in South America and only four in North America. In nearly every other interval in which a direct comparison is possible, carnivoramorph disparity is at least twice that of sparassodonts. The only notable exception to this pattern is the Early Miocene (Colhuehuapian and Santacrucian intervals), when carnivoramorph disparity is only approximately 1.3–1.5 times that of sparassodonts.

Disparity displays a similar pattern to diversity. Carnivoramorph disparity exceeds that of sparassodonts throughout the Cenozoic, though values are nearly identical during the late Middle Eocene (Barrancan interval; 0.66163 versus 0.64365, respectively). Carnivoramorph disparity is 2–2.3 times that of sparassodonts prior to this time and generally approximately 4–7 times that of sparassodonts thereafter. Much greater discrepancies (approx. 26–29 times) correspond to the two late Cenozoic dips in sparassodont disparity (Chasicoan and Montehermosan intervals).

Total disparity of Cenozoic North American carnivoramorphs (14.046; $n = 95$) is approximately 85% of that of extant carnivoramorphs worldwide (16.536; $n = 216$). Total disparity of sparassodonts (2.2386; $n = 41$) is approximately 15% that of carnivoramorphs today and throughout the Cenozoic.

(d) Morphospace occupation (disparity)

The first two canonical axes (CAs) encompass 55.3% of the variation among taxa (figure 3). The distributions of taxa and characters strongly resemble the results of Werdelin & Wesley-Hunt [17]; the x-axis is inversely correlated with carnivory (hypercarnivores towards the left, hypocarnivores towards the right), whereas the y-axis correlates negatively with body mass and upper carnassial occlusal angle, and positively with the number of upper premolars anterior to the carnassial and shape of the largest upper premolar anterior to the carnassial. Nearly all metatherians plot negatively on CA1; exceptions include Pseudolycopsis, IGM 251108, Stylcyon and
Sparassodonts scored for all or nearly all (12 out of 13) characters (n = 14) plot most closely to modern hypercarnivorous species (figure 3b). Most occupy a morphospace between felids and hypercarnivorous canids that overlaps hyaenids and highly carnivorous mustelids including the honey badger (Mellivora capensis), African striped weasel (Pocicogale albinucha), beech martin (Martes foina), wolverine (Gulo gulo) and weasels of the genus Mustela. Hondadelphys is an outlier among sparassodonts, plotting near hypercarnivorous canids and a variety of carnivorous to omnivorous feliforms (herpestids, viverrids and Nandinia). Dasyuromorphians largely overlap sparassodonts, occupying positions relative to placentals similar to those found by Jones [33].

(f) Carnivore guilds
Disparity of the Santa Cruz carnivore guild (0.74619) is far less than that of the modern carnivore guild of Malaysia (11.409), the Serengeti (5.5325) and Yellowstone (11.566). This fits with the low trophic diversity inferred for the Santa Cruz carnivore guild; all sparassodonts from the site have been interpreted as hypercarnivores, congruent with their positions in figure 3, whereas only one-half to two-thirds of species in modern and fossil carnivore guilds from other continents are hypercarnivores (figure 4; electronic supplementary material, table S9). If the four Santa Cruz phorusrhacids (terror birds) are included, trophic diversity remains unchanged, as phorusrhacids are also interpreted as hypercarnivores [10,22]. Species diversity of the Santa Cruz carnivore guild is 40–65% that of the modern guilds analysed and 40–75% that of most fossil guilds; with phorusrhacids, this increases to 55–90% compared to modern guilds and 55–100% for most fossil guilds. The number of hypercarnivores at Santa Cruz (15 including phorusrhacids) is comparable to that of Malaysia (n = 17) and Serengeti (n = 14) but 1.5–5× the number recorded at other fossil sites.

4. Discussion
(a) Completeness of the fossil record
More than one-third of sparassodont character states could not be coded (257 of 697 states; electronic supplementary material, table S7). This reflects the rarity of sparassodont specimens in the fossil record [9,12,13,34] as well as their generally poor preservation (cf. [11,35,36]). The relative contributions of ecology, taphonomy, sampling and other factors to such scarcity remain unresolved, but the sparassodont record should be interpreted with caution, given the large amount of missing data. Hence, we focus our discussion on broad temporal patterns, a well-sampled fossil site (Santa Cruz) and taxa known from relatively complete remains.
from diffusion in morphospace or adaptive radiation [37]. The Early Oligocene (Tinguirirican) drop in diversity (figure 2) is almost certainly an artefact of the very limited fossil record for this interval, which is only sampled from a few sites [38,39] and has not yielded specimens complete enough to be analysed. Curiously, sparassodonts do not
appear to have decreased in diversity or disparity during the Middle Eocene, unlike North American carnivoramorphans, 'creodonts' and other groups [40–42]. This could indicate little significant climate/habitat change in Patagonia during this interval, as has been documented for the later Palaeogene [43], or be an artefact of comparatively poor sampling of earlier intervals.

The relatively high disparity recorded before the extinction of the sparassodonts (figure 2) corresponds most closely to Foote’s model G of clade decline in which ‘selection against morphological intermediates causes an increase in morphological variance, analogous to disruptive selection within populations’ [37]. In other words, sparassodonts remained broadly separated in morphospace despite decreasing Late Cenozoic diversity (electronic supplementary material, figure S1). Based on our analysis, Late Miocene sparassodont disparity was greater than Late Oligocene disparity, and we find no support for a protracted decline after the Deseadan interval (Late Oligocene), as postulated by Marshall [10]. A decrease in disparity may have commenced after the Early Miocene, but a post-Middle Miocene or even post-Miocene decline is more likely given sampling differences among intervals; the early Late Miocene represents a large gap in knowledge, with only one well-sampled site of Chasicoan age and no sparassodonts yet discovered from the few known extra-Patagonian localities [5]. Similarly, low-latitude species of the sparassodonts (figure 2) correspond most closely to Foote’s model G of clade decline in which ‘selection against morphological intermediates causes an increase in morphological variance, analogous to disruptive selection within populations’ [37]. In other words, sparassodonts remained broadly separated in morphospace despite decreasing Late Cenozoic diversity (electronic supplementary material, figure S1). Based on our analysis, Late Miocene sparassodont disparity was greater than Late Oligocene disparity, and we find no support for a protracted decline after the Deseadan interval (Late Oligocene), as postulated by Marshall [10]. A decrease in disparity may have commenced after the Early Miocene, but a post-Middle Miocene or even post-Miocene decline is more likely given sampling differences among intervals; the early Late Miocene represents a large gap in knowledge, with only one well-sampled site of Chasicoan age and no sparassodonts yet discovered from the few known

(c) Ecological communities

Comparing the terrestrial carnivore guild of Santa Cruz, Argentina to selected modern and fossil guilds from other continents yields two noteworthy observations (figure 4). First, diversity is low: the guild includes fewer mammal species than all three modern carnivore guilds and all but one fossil guild. Second, the distribution of species among trophic categories is unlike any other guild. If this accurately represents the Santa Cruz carnivore guild, it presents an ecological anomaly: why are there no mesocarnivores or hypocarnivores?

One potential explanation is sampling: sparassodonts filled these niches but simply were not preserved in the fossil record. This is a reasonable explanation for most fossil sites, but the Santa Cruz Fauna derives from what is probably South America’s most productive fossil mammal-producing formation and is considered to faithfully represent its ancient carnivore guild [9,23]. In fact, the abundance of Santa Cruz specimens, combined with the formation’s broad geographical extent and stratigraphic thickness, has resulted in the opposite problem for most mammal groups: a plethora of invalid junior synonyms and an overestimation of diversity [35,48,49]. Thus, it is unlikely that a significant portion of the Santa Cruz carnivore guild remains unsampled.

Alternatively, Santa Cruz may not represent a typical Cenozoic South American ecological community. This relatively high-latitude site (approx. 51°S) is characterized by an unexpectedly low diversity of arboreal and/or frugivorous mammals [14,50], potentially reflecting a scarcity of fruit owing to pronounced Patagonian seasonality [14,51]. Thus, Santa Cruz may be missing hypocarnivorous or mesocarnivorous species that would be present at a lower-latitude site of similar age. In this respect, it is worth noting that the two Neogene sparassodonts universally regarded as omnivorous, Hondadelphys and Stylocynus [11,20,52], come from extra-Patagonian localities [5].
of Lycopsis (L. longirostrus and L. padillai) have proportionally larger molar grinding areas than Patagonian L. torresi (R. Engleman 2017, personal observation), suggesting more omnivorous habits. Additional sampling of middle- and low-latitude sites may eventually make it possible to test for regional differences in guild structure in South America.

Another possibility is that mesocarnivore and hypocarnivore niches at Santa Cruz were filled by mammals other than sparassodonts. The palaeanodont metatherian Aceldis may have included some vertebrate prey in its diet [53], perhaps warranting consideration as a small (approx. 350 g [54]) hypocarnivore. Other possible hypocarnivores include armadillos, particularly euphractines, which are more omnivorous than other extant armadillos and are known to catch and eat vertebrates [55]. Euphractines were the predominant armadillos during much of the Cenozoic [56], and some were apparently specialized for preying on vertebrates [57]. Armadillos may even have prevented sparassodonts from entering more omnivorous niches owing to ecological incursion [58]. However, only a single Santa Cruz armadillo, Prozaedyus, may have had omnivorous habits like those of modern euphractines [59]. All other Santa Cruz mammals were primarily insectivorous, frugivorous and/or herbivorous [14,54,60]. Didelphids are not recorded at Santa Cruz or many other fossil sites outside equatorial latitudes prior to the Late Miocene, and those that are known are small (less than 500 g) and non-carnivorous [52,61]. In summary, one or two non-sparassodont mammals could potentially be considered broadly hypocarnivorous, but the Santa Cruz carnivore guild would still be anomalous in its proportion of hypocarnivores and lack of mesocarnivores.

A fourth possible explanation is that current palaeodietary reconstructions of sparassodonts are inaccurate, and that not all Santa Cruz species were hypercarnivorous. This hypothesis cannot presently be tested, though it may be possible in the future using stable isotopes, dental wear or another ‘taxon-independent’ method of dietary inference [62,63]. Caution is warranted when interpreting the palaeobiology of any extinct clade based on extant representatives of other groups, as there is no unequivocal way to ‘calibrate’ boundaries of ecological categories (e.g. dietary categories) along a morphological continuum (e.g. relative grinding area). This phenomenon is well illustrated by South American notoungulates; most notoungulates have long been interpreted as grazers or open-habitat feeders based on their very high-crowned (hypsodont) teeth (e.g. [64]), but recent studies using stable isotopes and dental wear have demonstrated that a simple relationship between hypsodonty and diet does not hold for this group [65,66], despite its use for many other clades. Studies of mandible shape in sparassodonts have interpreted some species as more omnivorous (mesocarnivorous or hypocarnivorous) than suggested by their dentition [20,67], and this could reflect inaccuracies in interpreting sparassodont dentofacial ecomorphology based on metrics derived from modern carnivores. Interestingly, Marshall’s [10] qualitative analysis of sparassodonts envisaged much greater dietary breadth in the group, with three Santa Cruz genera classified as large carnivores (Acrocanth, Arctictis, Borhyaena), two as large omnivores (Lycopsis, Prothylacynus), and the remainder as small to medium carnivores or omnivores similar to modern mustelids, mephitids, canids and didelphids (see his fig. 1). Marshall [10] had little objective basis for this classification, but the resulting carnivore guild has a trophic structure similar to those of other continents (figure 4).

If most sparassodonts truly were hypercarnivorous, certain trophic niches in South America were apparently unoccupied by mammals during much of the Cenozoic. Sparassodonts appear to have become hypercarnivorous early in their evolutionary history [5], and this may have precluded them from later exploiting meso- and hypocarnivorous niches despite ecological opportunity. Such a scenario is compatible with the concept of a macroevolutionary ratchet that favours hypercarnivory and selects against omnivory, as has been described for many other groups of carnivorous mammals [68–70].

Our palaeoecological analyses suggest that carnivore guilds of ancient South America were not analogous to modern carnivore guilds or fossil guilds from other continents. This seems to be partly or principally owing to the particular clade (sparassodonts) that dominated mammalian carnivore niches there for most of the Cenozoic. Although no analyses of fossil carnivore guilds on other continents that lack carnivoramorphans have yet been published, platypus ‘creodonts’ apparently displayed significant dietary breadth in Africa [71], and the same may also have been true of marsupials in Australia [72]. How sparassodonts were able to coexist with one another despite low trophic diversity is unclear. There is no strong evidence for character displacement in body size [23], and although some species clearly differed in postcranial morphology, locomotor habits can only currently be assessed for about half of Santa Cruz species. More precise characterization of the terrestrial predator guild of Santa Cruz and other localities in South America will require more complete specimens and additional analytical techniques. Our analyses highlight that the Santa Cruz carnivore guild, and probably the entire mammal community, was structured very differently from modern mammal communities. This presents a challenge for accurately characterizing the palaeoecology of this and other such faunas but also an opportunity to document ecological configurations of mammalian communities that extend beyond those that exist today.

**Data accessibility.** Supporting data necessary to replicate this study are available in the electronic supplementary material, tables S1–12, or in cited publications. All codings are based on published specimens or ones housed in publicly accessible collections.

**Authors’ contributions.** D.A.C. conceived of the project. D.A.C., R.K.E. and T.D. collected and coded the metatherian data. R.K.E. recoded the euarchontan Dentition Collection; A. Friscia, A. Jellema, A. Jones and D.A.C. recoded the eutherian data collected by G.W. D.A.C. analysed the data, compiled the figures and wrote the initial manuscript draft. All the authors contributed to interpretation of the results and compilation of the final manuscript.

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