INTRODUCTION

Throughout much of the Cenozoic Era, South America was home to a unique guild of macropredatory carnivores. Whereas most of the macropredatory niches on other landmasses were occupied by eutherian carnivores or creodonts, South America’s carnivore guild was largely composed of metatherian mammals (Goin, 1995; Forasiepi, 2009), sebecosuchian crocodyliformes (Pol et al., 2012), giant boine and madtsoiid snakes (Head et al., 2011), and several hypercarnivorous didelphid taxa (including Thylophorops, Thylassodon, Lutreolina, and Hyperdidelphys) represent an evolutionary response to the decline in small, predatory sparassodont taxa during the late Cenozoic. This study documents new morphological diversity among the Sparassodonta and highlights the value of fossils from traditionally undersampled parts of South America.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

A NEW SPECIES OF SMALL-BODIED SPARASSODONT (MAMMALIA, METATHERIA) FROM THE MIDDLE MIocene LOCALITY OF QUEBRADA Honda, BOLIVIA

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ABSTRACT—The Sparassodonta (Mammalia, Metatheria) are a group of carnivorous mammals that dominated the macro-predatory guild of South America during the Cenozoic. Here, we describe a new sparassodont based on a single specimen from the middle Miocene Quebrada Honda local fauna of southern Bolivia. This specimen (UF 27881) does not clearly correspond to any major sparassodont group (e.g., Hahliaconidae, Borhyaenidae, etc.) and represents a morphotype previously unknown among the Sparassodonta. UF 27881 is distinguished from other sparassodonts by its short, broad, borhyaenid-like rostrum and small size, among other features. However, we decline to coin a new name for UF 27881 due to the fragmentary nature of this specimen and the absence of most of its dentition. This specimen suggests that the appearance of the Sparassocynidae and several hypercarnivorous didelphid taxa (including Thylophorops, Thylassodon, Lutreolina, and Hyperdidelphys) represent an evolutionary response to the decline in small, predatory sparassodont taxa during the late Cenozoic. This study documents new morphological diversity among the Sparassodonta and highlights the value of fossils from traditionally undersampled parts of South America.

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the omnivorous basal sparassodont *Styloctenus*, the small hathliacynids *Notictis* and *Borhyaenidium* (Prevozi et al., 2013), and at least one indeterminate species of borhyaenid (Forasiepi et al., 2007).

In contrast to early and late Miocene taxa, middle Miocene sparassodonts are known from fewer localities and generally less complete specimens. Most well-preserved middle Miocene sparassodonts come from the locality of La Venta, Colombia, the best known of which is the basal borhyaenoid *Lycopsis* longirostrus, which is based on a nearly complete, articulated juvenile skeleton with preserved gut contents (Marshall, 1977a). The La Venta Fauna also includes the enigmatic basal sparassodont *Hondadelphys fieldsi* (Marshall, 1976b; Marshall et al., 1990; Goin, 1997), the large-bodied borhyaenid *Dukceyus magnus*, the thylacosmilid *Anachlysictis gracilis*, and poorly preserved remains that likely represent several additional species (Goin, 1997). Aside from the specimens from La Venta and the recently described *Patagosmilus goini* from the Collon Curá Formation of Argentina (Forasiepi and Carlino, 2010), well-preserved middle Miocene sparassodont remains have only been described from one other locality, Quebrada Honda, Bolivia.

Quebrada Honda is located in the Tarija Department of Bolivia, near the southernmost point of the country (Fig. 1). Fossils at this middle Miocene fossil site were first collected by Carlos Villarroel and Robert Hoffstetter in 1976, the latter of whom published the first formal report on this site’s fauna in the following year (Hoffstetter, 1977). Quebrada Honda was later visited by a team from the University of Florida in 1978, who discovered a second, coeval site, Río Rosario, some 5 km from the first locality (MacFadden and Wolff, 1981). Although it is not possible to directly correlate the stratigraphy of Quebrada Honda and Río Rosario, the same mammal species have been collected at both localities; therefore, these sites are considered to represent a single fauna (MacFadden et al., 1990; Croft and Anaya, 2006; Croft, 2007). The Quebrada Honda mammal fauna is diverse, including at least 30 species of metatherians, xenarthrans, rodents, and endemic ungulates (Croft, 2007, and references therein). Recent studies have described a new dwarf megatherioid (Pujo et al., 2011) and several species of caviomorph rodents (Croft et al., 2011) from this locality, and ongoing field studies have produced many new specimens including several new species that are currently under study (D. Croft, unpubl. data).

Until the present study, only one species of sparassodont had been identified at Quebrada Honda, *Acyon myctoderos* (Forasiepi et al., 2006). However, as detailed below, our examination of a previously undescribed specimen, UF 27881, indicates that this fossil represents an additional species of sparassodont at this locality. Although incompletely preserved, UF 27881 displays a unique combination of characters that suggest it represents a relatively basal sparassodont not closely related to *Acyon*. Moreover, UF 27881 clearly pertains to a species much smaller than *A. myctoderos*, comparable in size to some of the smallest known sparassodonts. In this paper, we describe this specimen as a small, hitherto unrecognized sparassodont and discuss its implications for the evolutionary history of South America’s small mammalian predator guild.

MATERIALS AND METHODS

Measurements of this specimen were taken with digital calipers to the nearest 0.01 mm unless otherwise noted. Additional data on sparassodonts and other groups of metatherians (pucadelphids, didelphoids, etc.) were taken from the published literature or direct observations by the authors. A complete list of specimens and references used for comparative analysis can be found in Supplementary Data, Appendix S1.

This paper follows the system of South American Land Mammal Ages (SALMAs) as defined by Flynn and Swisher (1995), as modified by Flynn et al. (2002), Cione and Tonni (2005), and Gelfo et al. (2009). Like Flynn et al. (2002), we consider the Frianian SALMA to represent a relatively short interval of time during the early middle Miocene, as opposed to the Frianian sensu lato of other authors (see discussion in Flynn and Swisher, 1995), which would include the Colloncuran, Laventan, and Mayoan SALMAs.

Anatomical Abbreviations—Upper and lower premolars are designated as P/p, whereas upper and lower molars are designated as M/m. Right and left are abbreviated R and L, respectively.

Institutional Abbreviations—CMNH, Cleveland Museum of Natural History, Cleveland, Ohio, U.S.A.; CORD-PZ, Museo de Paleontología, Facultad de Ciencias Exactas, Físicas y Naturales de la Universidad Nacional de Córdoba, Córdoba, Argentina; FMNH, The Field Museum, Chicago, Illinois, U.S.A.; IGM, Instituto Nacional de Investigaciones Geológico-Mineras, Bogotá, Colombia; MACN A, Ameghino collection, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; MACN Py, Vertebrate paleontology collection, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales de Mar del Plata, Mar del Plata, Argentina; MNHN-Bol, Museo Nacional de Historia Natural, La Paz, Bolivia; PVL, Paleontología Vertebrados Lillo, Tucumán, Argentina; UCMP, University of California Museum of Paleontology, Berkeley, California, U.S.A.; UF, University of Florida/Florida Museum of Natural History, Gainesville, Florida, U.S.A.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
METATHERIA Huxley, 1880
SPARASSODONTA Ameghino, 1894
gen. et sp. nov.

(Figs. 2–5; Tables 1, 2)

Specimen—UF 27881, a partial cranium preserving most of the rostrum, the anteriormost portion of the orbital region and braincase, and both M1s.
Locality—Unnamed formation of the Honda Group, Quebrada Honda local fauna, Bolivia. The exact horizon of UF 27881 is unknown as the specimen lacks additional stratigraphic data (R. Hulbert, pers. comm., February 2012).

Age—Late middle Miocene, Serravallian age, Laventan SALMA. MacFadden et al. (1990) estimate the age of the fossil-bearing layers at this locality to be between 13.0 and 12.7 Ma, based on a combination of paleomagnetic and radioisotopic (40K/40Ar age determination) data.

Comments—UF 27881 can be referred to the Metatheria based on the alveoli of its postcanine dentition, which indicate the presence of three premolars and four molars. More specifically, UF 27881 can be assigned to the Sparassodonta based on the combination of several features, including the presence of a lacrimal tubercle, a single lacrimal foramen positioned within the orbit, contact between the nasal and lacrimal bones, and the absence of the maxillopalatine fenestrae and a single, well-developed major palatine foramen (see below). Although some of these features are also present in certain didelphoids (e.g., Hyperdidelphys, Sparassocyon), these characteristics only occur together in members of the Sparassodonta. UF 27881 exhibits a combination of features (discussed below) that prevent it from being assigned to either the Heliacynidae or the Borhyaenoidae, the two major recognized subgroups of sparassodonts. This interpretation is supported by our phylogenetic analysis (discussed below), which also suggests that this specimen does not pertain to any currently recognized sparassodont clade. Although UF 27881 almost certainly represents a new species, we refrain from coining a new scientific name for this animal until more complete remains are discovered, because the two most phylogenetically informative regions of the cranium, the basicranium and dentition, are missing or poorly preserved.

DESCRIPTION

Rostrum

The rostrum of UF 27881 is triangular in dorsal view (Fig. 2) and is constricted at the level of P1. Anterior to P1, the snout bulges conspicuously around the enlarged canine alveoli, similar to but less strongly developed than the condition observed in some other sparassodonts, such as Cladosictis centralis and Prothylacynus patagonicus. The rostrum also broadens posterior to the level of P1, with the 'cheeks' of the maxilla (sensu Forasiepi, 2009) flaring laterally behind the level of the infraorbital foramen in ventral view. One of the more unusual features of UF 27881 is its short snout relative to the rest of the skull. In most sparassodonts for which the rostrum is known, the preorbital length accounts for one-third to one-half of the entire length of the cranium (Figs. 2–3; see also Forasiepi, 2009). The only clear exceptions to this pattern are several genera of derived, large-bodied borhyaenoids (e.g., Borhyaena, Arctodontis, Pharsophorus, and Prothylacynus), in which the rostrum constitutes less than one-third of the total length of the skull. UF 27881 resembles these large, derived borhyaenoids in having a very short rostrum, probably less than one-third of total skull length (Fig. 2; Table 1).

The anterior-most portion of the rostrum, including both premaxillae, is missing from UF 27881. However, enough of the snout is preserved in this specimen to show that the premaxillae did not possess a large ascending postdorsal process, unlike many other sparassodonts. In these taxa, such as Cladosictis, Borhyaena, Arctodontis, Acyon, and Callistoe, as well as some non-sparassodont marsupials such as the thylacine (Thylacinus cynocephalus) and Tasmanian devil (Sarcophilus harrisii), a portion of the premaxilla extends between the maxilla and nasal bones to form part of the dorsal surface of the rostrum (Fig. 2D–G), often extending posterior to the canine. In contrast, the nasal and maxilla of UF 27881 are in close contact with one another and extend to the preserved anterior end of the cranium (this contact cannot be seen in Fig. 2 because the anterior part of the nasomaxillary contact is obscured by matrix in dorsal view). The anterior edge of the right maxilla curves medially towards the midline of the skull and shows no evidence of an anterolateral process. In most marsupials other than sparassodonts, the paracanine fossa is formed by both the premaxillae and an anterolaterally extending process of the maxilla (Forasiepi, 2009). Therefore, as in most other sparassodonts, it is likely that the paracanine fossa in UF 27881 would have been formed solely by the premaxillae.

Most of the sutures of UF 27881 have been obscured by damage and postmortem deformation, particularly in the region of the nasofrontal suture. On the left side of the skull, two structures could represent the nasofrontal suture, of which the more anterior (see Fig. 2) is more likely the true nasofrontal suture, based on comparison with other sparassodonts. In either case, the nasals of UF 27881 extend posteriorly as far as the orbits. The nasals are relatively narrow and uniform in width anterior to the infraorbital foramen but widen considerably posterior to this structure, resembling the condition in Borhyaena, Cladosictis, Arctodontis, and Acyon.

Parts of the rostrum of UF 27881, particularly the surface of the enlarged canine alveolus, are covered in many small foramina (Fig. 3). These foramina are most closely packed together near the anterior end of the maxilla, giving this area a pockmarked, ‘spiny’ texture. Among sparassodonts, similar foramina have been reported in the thylacosmilids Thylocoenomys and Patagomys (Forasiepi and Carlini, 2010), as well as a specimen tentatively referred to the proborthyaeid Arminheringia (MLP 82-V-1-1; Forasiepi, pers. comm., August 2012). Small maxillary foramina surrounding the canine alveolus have also been observed in the non-mammalian cynodont Thrinaxodon (Estes, 1961) and therocephalian synapsids (Huttonlocker et al., 2011). Because such foramina are only present in sparassodonts with enlarged canines (Thylocoenomys, Patagomys, Arminheringia, and UF 27881; see below), it is possible that these structures represent an adaptation related to the large canines of these taxa (see Discussion).

Palate

The palate is the best-preserved region of UF 27881, with the sutures between the palatines and maxillae clearly visible in ventral view (Fig. 4). The palatines extend anteriorly to the anterior root of M2, reaching the level of the maxillary foramen, and extend posteriorly beyond M4. The posterior end of the palatines shows that the region underlying the choanae was concave posteriorly, as in other sparassodonts (Forasiepi, 2009).

Like other sparassodonts (Forasiepi, 2009; Fig. 4C, D) and some didelphoids (e.g., Sparassocyclus and caluromyids; see Reig and Simpson, 1972; Voss and Jansa, 2009), UF 27881 lacks any trace of the maxillopalatine fenestrae. Additionally, the palate of UF 27881 bears many tiny foramina instead of a single, large major palatine foramen. This condition has been noted in other sparassodonts (Forasiepi et al., 2006; Forasiepi, 2009) and contrasts with that seen in didelphoids and other marsupials. The largest of these foramina is located just medial to canine alveolus and opens anteriorly. This unnamed foramen is present in several other sparassodonts, including Arctodontis, Acyon, Cladosictis, Thylocoenomys, Borhyaena, and possibly Callistoe. Remnants of the minor palatine foramen are present on the left side of the palate of UF 27881, at the posterior border of the maxilla and palatine bones. This foramen is similar in size to that of living didelphoids and resembles the minor palatine foramina of most sparassodonts (except Arctodontis sinclairi; see Forasiepi, 2009). The posterior edges of the palate around the minor palatine foramen are not inflected inwards to form ‘corners’ as they are in didelphids and sparassocynids.
FIGURE 2. Dorsal views of the crania of UF 27881 and other sparassodonts. A–C, photograph (A), line drawing (B), and reconstruction (C) of UF 27881; D, Borhyaena tuberata, modified from Sinclair (1906); E, Arctodictis sinclairi, modified from Forasiepi (2009); F, Cladosictis patagonica, modified from Sinclair (1906); G, Acyon myctoderus, modified from Forasiepi et al. (2006). Gray regions in B represent areas in which the surface of the bone is missing. The small foramina on the canine alveolus are not represented in B. In C, missing areas of the cranium (highlighted in light gray) were modeled after Hondadelphys and Borhyaenidium. Scale bars equal 3 cm in A–C and 10 cm in D–G. Abbreviations: fr, frontal; iof, infraorbital foramen; lac, lacrimal; lat, lacrimal tubercle; mjs, maxillojugal suture; mx, maxilla; na, nasal; opl, orbital platform; tl, temporal line.
The palate of UF 27881 has three pairs of large, conspicuous palatal pits, located slightly lingual to the posterior roots of the first three pairs of molars. Although similar pits have been identified in several carnivorous marsupials, including many species of sparassodonts as well as the sparassocynid Hesperocynus, the presence of three palatal pits in UF 27881 is unusual. Most sparassodonts have only one or two pairs of palatal pits, the exact number of which is subject to ontogeny and individual variation. Further study has shown that in addition to UF 27881, three palatal pits are present in at least one specimen of Sipalocyon gracilis (MACN A 692) and Pseudonoticis pusillus (MLP 11-26). The only other carnivorous marsupial known to have a similar number of palatal pits is the sparassocynid Hesperocynus dolgopolaev, which has three palatal pits located lingual to the posterior roots of the first three molars, as well as a fourth pit between P3 and M1 (Forasiepi et al., 2009). Because three or more pairs of palatal pits have only been observed in small-bodied taxa, this feature may be a result of allometric scaling.

Table 1. Selected cranial measurements of UF 27881 (in mm).

| Measurement                                      | Value  |
|-------------------------------------------------|--------|
| Greatest length of specimen                     | 33.6   |
| Estimated total skull length (based on Prothyacynus) | 70.6   |
| Greatest width of specimen                      | 27.4   |
| Estimated greatest width of skull               | 37.1   |
| Width of snout at level of infraorbital foramen | 18.5   |
| Greatest length of palate                       | 31.7   |
| Width of the palate at the level of the canines (from the lingual edge of alveolus to the midline) | 2.3    |
| Estimated width of palate at the level of the canines | 4.6    |
| Width of palate at the level of M1 (between the protocones) | 10.5   |
| Width of palate at the level of M3 (from the protocone to the midline) | 8.2    |
| Estimated greatest width of the palate at the level of M3 | 16.4   |
| Greatest diameter of palatal pits between M1 and M2 | 2.0    |
| Greatest diameter of palatal pits between M2 and M3 | 2.4    |
| Width of braincase at the level of the postorbital processes | 12.7   |
| Preserved preorbital length                     | 15.4   |

Orbital Region and Anterior Braincase

The lacrimal of UF 27881 clearly identifies this specimen as a member of the Sparassodonta, because it possesses several features considered characteristic of this group (Fig. 2). Part of the lacrimal extends onto the rostrum to the level of M1, contacting the nasals on the dorsal surface of the snout and preventing contact between the maxilla and frontal bones. Previous studies have considered this feature to be characteristic of sparassodonts (e.g., Marshall, 1978; Goin, 1997), although this feature also occurs in other taxa (such as deltatheroideans; Rougier et al., 1998). In contrast, strongly developed nasolacrimal contact has only been reported in one species of didelphoid, Hyperdidelphys dimartinoi (Goin and Pardiñas, 1996; Voss and Jansa, 2009). Like other members of the Sparassodonta, UF 27881 has a single lacrimal foramen that opens inside the orbit. The lateral margin of the lacrimal bears a large lacrimal tubercle that obscures the lacrimal foramen in lateral view. These features have been considered characteristic of the Sparassodonta (Marshall, 1976a, 1978, 1981), although they also occur in other marsupial groups (Forasiepi, 2009). The only other Neogene marsupial to have both a lacrimal tubercle and a single lacrimal foramen positioned inside the orbit is the sparassocynid Sparassocynus.

The anterior margin of the orbit of UF 27881 is formed by the frontal, lacrimal, and maxilla. Although the jugal is not preserved in this specimen, the shape of the maxilla-jugal suture suggests that this bone would have also contributed to the orbital rim. The ventral-most point of the maxillojugal suture in UF 27881 is very low, almost extending to the level of the palate. Compared with other sparassodonts (e.g., Prothyacynus; see Sinclair, 1906), UF 27881 has a broad orbital platform, extending posteriorly to the level of the postorbital constriction. Much of this platform is composed of the orbital process of the maxilla, but at least some of the orbital platform is also composed of the palatine, as indicated by the sphenopalatine foramen visible on the orbital floor. The sphenobital foramen appears to open near the palatomaxillary suture and is extremely small. This contrasts with the large maxillary foramen in this specimen, which is positioned near the floor of the orbit. The orbits appear relatively large compared with the rest of skull, but whether the large orbits of UF 27881 are
FIGURE 4. Ventral view of the crania of UF 27881 and other sparassodonts. A, photograph and B, line drawing of UF 27881; C, Borhyaena tuberata, modified from Sinclair (1906); D, Arctodictis sinclairi, modified from Forasiepi (2009); E, Cladosictis patagonica, modified from Sinclair (1906); F, Acyon myctoderos, modified from Forasiepi et al. (2006). Gray regions in B represent areas in which the surface of the bone is missing. Scale bars equal 3 cm in A and B and 10 cm in C–F. Abbreviations: iof, infraorbital foramen; mch, ‘cheek’ of maxilla (sensu Forasiepi, 2009); mpf, major palatine foramen; mx, maxilla; pa, palatine; pp, palatal pit; uaf, unnamed anterior foramen.
abnormally large (possibly indicative of nocturnal or crepuscular behavior) or are simply the result of allometric scaling is a question that is beyond the scope of this study, particularly due to the incomplete nature of the specimen.

The infraorbital foramen of UF 27881 is large (Table 2) and positioned dorsal to P3. On the right side of the cranium, which is better preserved, the infraorbital foramen is positioned above the anterior root of the P3, whereas on left side of the skull, the infraorbital foramen is positioned dorsal to the posterior root of P3. Compared with living didelphoids, UF 27881 has a proportionally larger infraorbital foramen (Table 2), but is most similar in terms of relative size to the hypercarnivorous *Lutreolina crassicaudata* and the semiaquatic *Chironectes minimus*. Among sparassodonts, UF 27881 could only be directly compared with two juvenile specimens assigned to *Lycopsis* *longirostris* and *Prothylacynus patagonicus*. The infraorbital foramen of UF 27881 is relatively larger than that of *L. longirostris*, but was found to be either relatively larger or smaller than the foramen of *P. patagonicus* depending on what scaling metric was used. The infraorbital foramen of UF 27881 is nearly circular, in contrast to *L. longirostris*, which is incompletely developed and fully formed, indicating that this tooth was also in place before being lost to postmortem damage. In most sparassodonts, the sagittal crest is quite pronounced and extends onto the frontal bone in many species (e.g., *Acyon* and *Cladosictis*).

### Dentition

Unfortunately, most of the dentition is not preserved in UF 27881. The only teeth that are present in this specimen are the left and right M1, both of which are broken and/or worn (Figs. 4, 5). However, the right canine alveolus and most of the post-canine alveoli are preserved in this specimen, except for LM4 (which is incomplete), RM3, and RM4. Thus, UF 27881 clearly had three upper premolars and four molars, which is plesiomorphic for metatherians and characteristic of most sparassodonts and didelphoids (Forasiepi, 2009; Voss and Jansa, 2009).

Despite its small size, several features of the dentition of UF 27881 indicate that this individual is most likely an adult. There is no sign of a replacement tooth below the alveolus of P3, indicating that the permanent adult premolar had already erupted by the time this animal had died. Additionally, the alveoli of M4, which are partially preserved on the left side of the skull, are well developed and fully formed, indicating that this tooth was also in place before being lost to postmortem damage. In most sparassodonts, the sagittal crest is quite pronounced and extends onto the frontal bone in many species (e.g., *Acyon* and *Cladosictis*).

### Table 2. Relative size of the infraorbital foramen (IOF) in UF 27881, didelphoids, and two sparassodonts.

| Species                        | Specimen | IOF area (mm²) | PL (mm) | M1 length (mm) | R1 | R2 | Average ratio | Diet          |
|-------------------------------|----------|----------------|---------|----------------|-----|-----|---------------|---------------|
| Sparassodonta gen. et sp. nov. | UF 27881 | 5.39           | 30.07   | 4.40           | 0.28 | 0.21 | 0.44          | ?             |
| *Caluromys derbianus*          | FMNH 69327 | 1.36         | 25.15   | 2.60           | 0.20 | 0.21 | 0.42          | FR            |
| *Caluromys lanatus*            | FMNH 114649 | 1.23         | 22.73   | 2.62           | 0.18 | 0.21 | 0.49          | FR            |
| *Caluromys philander*          | FMNH 92037 | 1.16         | 23.24   | 2.52           | 0.18 | 0.20 | 0.44          | FR            |
| *Chironectes minimus*          | FMNH 19349 | 3.52         | 33.16   | 3.94           | 0.23 | 0.27 | 0.44          | HY/OM/IN      |
| *Lutreolina crassicaudata*     | FMNH 53944 | 3.61         | 35.30   | 4.02           | 0.22 | 0.26 | 0.49          | HY/OM/IN      |
| *Metachirus nudicaudatus*      | CMNH 1889 | 2.03          | 24.71   | 2.99           | 0.23 | 0.28 | 0.52          | HY/OM/IN      |
| *Marmosa deramareae*           | CMNH 18894 | 0.78         | 20.75   | 2.44           | 0.13 | 0.16 | 0.29          | OM/IN         |
| *Marmosa murina*               | CMNH 18878 | 1.04         | 17.73   | 2.24           | 0.21 | 0.27 | 0.32          | OM/IN         |
| *Prothylacynus patagonicus*    | MACN Pv 14453 | 31.81     | 90.00   | 9.85           | 0.33 | 0.36 | 0.40          | ?             |
| *Lycopsis* *longirostris*      | UCMP 38061 | 36.13        | 98.18   | 13.10          | 0.21 | 0.29 | 0.44          | ?             |

Raw data and methods for calculating infraorbital foramen and palatal measurements can be found in Supplementary Data, Table S2. Measurements of *Prothylacynus patagonicus* and *Lycopsis* *longirostris* were taken from Marshall (1979) and Marshall (1977a), respectively. Dietary information for living didelphoids is from Vieira and Astúa Moraes (2003). **Abbreviations:** DU, durophagous; FR, frugivorous; HY, hypercarnivorous; IN, insectivorous; IOF, infraorbital foramen; OM, omnivorous; PL, palatal length (from the posterior edge of the canine to the posterior end of the palate); R1, ratio calculated from palatal length; R2, ratio calculated from M1 length.
Table 3. Comparison of upper canine proportions in sparassodonts, the thylacinid *Thylacinus cynocephalus*, and the dasyurid *Sarcophilus harrisii*.

| Taxon                                | Specimen               | Group                     | L/W ratio | Canine size |
|--------------------------------------|------------------------|---------------------------|-----------|-------------|
| Sparassodontota gen. et sp. nov.     | UF 27881               | Basal Sparassodontota     | 1.24      | 0.63        |
| *Hondadelphys fieldsi*               | UCMP 37960             | Basal Sparassodontota     | 1.81      | 0.80        |
| Acyon mycteros                       | MNHN-Bol-V-003668 (left) | Hattilucyphidae      | 1.40      | 0.28        |
| Acyon mycteros                       | MNHN-Bol-V-003668 (right) | Hattilucyphidae     | 1.44      | 0.29        |
| Borhyaeniodus riggsi                 | FMNH 14409             | Basal Borhyaenoid         | 1.43      | 0.17        |
| Cladocits centralis                  | MACN A 11639           | Hattilucyphidae          | 1.64      | 0.55        |
| Cladocits patagonica                 | MACN A 5927            | Hattilucyphidae          | 1.49      | 0.65        |
| Sipalocyn externa                    | MACN A 52-383          | Hattilucyphidae          | 1.44      | 0.41        |
| ‘Lycopsis’ longirostrus (juvenile)   | UCMP 38061             | Basal Borhyaenoid         | 1.27      | 0.20        |
| Prothylacynus patagonicus (juvenile) | MACN A 5931            | Basal Borhyaenoid         | 1.26      | 0.35        |
| Prothylacynus patagonicus (juvenile) | MACN P 11453 (left)    | Basal Borhyaenoid         | 1.41      | 0.45        |
| Prothylacynus patagonicus (juvenile) | MACN P 11453 (right)   | Basal Borhyaenoid         | 1.48      | 0.44        |
| Pharsophorus antiquus                | MACN A 52-532          | Basal Borhyaenoid         | 1.47      | N/A         |
| Acrocyon riggsi                      | FMNH P13433            | Borhyaenidae              | 1.36      | 0.79        |
| Arctodictis munizi                  | CORD-PZ 1210-1/5       | Borhyaenidae              | 1.42      | 1.61        |
| Arctodictis sinclair                 | MLP 85-VII-3-1 (left)  | Borhyaenidae              | 1.32      | 1.10        |
| Arctodictis sinclair                 | MLP 85-VII-3-1 (right) | Borhyaenidae              | 1.27      | 1.03        |
| Borhyaena tubera                     | MACN A 6203-6265 (left) | Borhyaenidae            | 1.46      | 0.58        |
| Borhyaena tubera                     | MACN A 6203-6265 (right) | Borhyaenidae          | 1.47      | 0.57        |
| Borhyaena tubera                     | MACN A 5780            | Borhyaenidae              | 1.52      | N/A         |
| Callistoe vincei                    | PVL 4187               | Proboborhyaenida         | 1.38      | 1.29        |
| Arminderingua auceta                 | MACN A 10972           | Proboborhyaenida         | 1.48      | 0.85        |
| Proboborhyaena gigantea             | MLP 79-XII-18-1        | Proboborhyaenida         | 1.75      | N/A         |
| Thylacosimus atrox                   | MLP 35-X-4-1           | Thylacosimilidae          | 2.45      | N/A         |
| Thylacosimus atrox                   | FMNH P14531            | Thylacosimilidae          | 2.50      | 0.96        |
| Thylacosimus atrox                   | FMNH P14474            | Thylacosimilidae          | 2.55      | 0.94        |
| Thylacosimus atrox                   | MMP 1470               | Thylacosimilidae          | 2.63      | N/A         |
| Thylacosimus cynocephalus (left)     | CMNH 18916             | Thylacinidae             | 1.41      | 0.35        |
| Thylacosimus cynocephalus (right)    | CMNH 18916             | Thylacinidae             | 1.34      | 0.38        |
| Sarcophilus harrisii (left)          | CMNH 18915             | Dasyuridae                | 1.12      | 0.50        |
| Sarcophilus harrisii (right)         | CMNH 18915             | Dasyuridae                | 1.13      | 0.53        |

Canine length/width ratio is calculated by dividing maximum anteroposterior length at the base of the canine by maximum mediolateral width at the same point. In *Arctodictis munizi*, the greatest length and greatest width of the canine are used instead of anteroposterior length and mediolateral width, respectively, because this taxon has canines that are oriented obliquely to the tooth row. Relative size of the canines was calculated by scaling the cross-sectional area of the canine by the length of M3 squared. Additional information about the measurements in this table can be found in Supplementary Data, Table S1.

The canine alveolus of UF 27881 is relatively large and deep (Table 3), indicating a hypertrophied upper canine. Additionally, the orientation of this alveolus suggests that the canines were slightly procumbent in life. These features, along with the short snout of UF 27881, would have caused the skull of this animal to resemble a borhyaenid or proborhyaenid sparassodont. The canine alveolus of UF 27881 is nearly circular in cross-section (Fig. 3), and based on data from Christiansen (2008:fig. 3c) and Van Valkenburgh and Ruff (1987:fig. 3), the inferred canine proportions of UF 27881 most closely resemble those of several extant species of conical-toothed cats.

The alveoli of P1 and P2 indicate that these teeth were double-rooted and roughly subequal in size (Fig. 4). In contrast, the alveolus of P3 is larger than that of either P1 or P2, and the anterior root is larger than the posterior one. The right P3 is double-rooted, but the alveolus of LP3 suggests that the anterior root may have been partially subdivided in this tooth. The premolar alveoli, especially P1 and P2, are much smaller than those of the molars, in contrast to *Acyon, Cladocits, ‘Lycopsis’ longirostrus, Prothylacynus* (though this species has a small P1), and *Hondadelphys*. UF 27881 is unusual among short-snouted sparassodonts in that P1 is oriented parallel to the tooth row. In contrast, all other short-snouted sparassodonts (which are all members of the Borhyaenoidae) have a P1 that is obliquely or even transversely oriented to the tooth row (Goin, 1997; Foraisipi, 2009). Another unusual feature of this specimen is the lack of gaps between the premolar alveoli. Most sparassodonts typically have prominent diastemata between their premolars, whereas closed dentitions are otherwise found only in large-bodied, short-snouted borhyaenoids such as borhyaenids and proborhyaenids (Foraisipi, 2009).

The left M1 is slightly more complete than the right M1, which is missing most of the paracone (Fig. 5). These teeth lack any sign of a cingulum or additional cusps or ridges, with each tooth apparently composed solely of the metacone, protocone, and paracone. The paracone and metacone are absent and there is no preprotocrista or postprotocrista, a feature shared with derived borhyaenoids (*Prothylacynus, Borhyaena, Arctodictis, Thylacosimus*), and the hihalciynid *Notogale*. Compared with most other sparassodonts, the protocone of UF 27881 is relatively large and is not reduced to a swelling or absent as in many other short-snouted taxa (proboryhaenids, borhyaenids, thylacosimids, and *Pharsophorus*). The apex of this cusp is deflected labially towards the metacone and paracone. Most marsupials have an extensive stylar shelf that displaces the metacone and paracone towards the midline of the tooth (Ungar, 2010). This condition is also present in many sparassodonts, including *Patene, Hondadelphys, Sipalocyon, ‘Lycopsis’ longirostrus*, and *Lycopsis torresi*. However, in UF 27881, the preserved bases of the metacone and paracone on M1 are positioned labially, almost to the edge of the maxilla, suggesting that the stylar shelf was not extensive on this tooth. Despite being relatively poorly preserved, it is apparent that the stylar shelf on M1 of UF 27881 is reduced compared with that of *Sipalocyon or Patene*. The first three molars of this specimen have three roots (Fig. 4), whereas M4 has at least two roots, possibly three. The alveoli of M1–3 are subequal in size.
TABLE 4. Selected dental measurements of UF 27881 (in mm).

| Tooth      | Measurement | Left    | Right   |
|------------|-------------|---------|---------|
| Canine     | Length      | —       | 4.4*    |
|            | Width       | —       | 3.6*    |
| P1–2       | Length      | 1.8*    | 1.8*    |
|            | Width       | 0.9*    | 0.8*    |
| P2–3       | Length      | 2.4*    | 2.4*    |
|            | Width       | 1.0*    | 1.0*    |
| P3–4       | Length      | 2.7*    | 2.9*    |
|            | Width       | 1.8*    | 1.5*    |
| M1–2       | Length      | 4.4*    | 4.4*    |
|            | Width       | 3.1     | 3.1     |
| M2–3       | Length      | 4.4*    | 4.4*    |
|            | Width       | 3.2*    | 3.1*    |
| M3–4       | Length      | 4.4*    | —       |
|            | Width       | 3.25*   | —       |
| P1–3       | Length      | 7.6*    | 7.7*    |
| P1–M3      | Length      | 22.9*   | —       |
| M1–3       | Length      | 14.2*   | —       |
| M1–4       | Length      | 16.2*   | —       |

Alveolar measurements are indicated by an asterisk (*). and indicate that the molars were much larger than the premolars (Table 4).

PHYLLOGENETIC ANALYSIS

In order to determine the position of UF 27881 within the Sparassodonta, we performed a maximum parsimony analysis in PAUP* version 4.0b10 (Swofford, 2002) based on a matrix of 39 ingroup taxa and 307 characters (Supplementary Data, file ECMatrix.nex and Appendix S2) compiled in Mesquite (Madison and Maddison, 2011). Characters and codings in this analysis were taken from Forasiepi (2009), with some modifications based on recent studies and personal observations. All characters were weighted equally. In addition to UF 27881, the early Eocene proborhyaeid Callistoe vincei and the early middle Miocene thylacosmilid Patagosmilus gorni were also added to this analysis. The dasyuromorphian Thylacinus cynocephalus was excluded from this study due to its high degree of morphological convergence with sparassodonts (see Forasiepi, 2009, for more information). A complete list of changes from Forasiepi (2009) can be found in Supplementary Data, Appendix S2.

Our analysis recovered eight most parsimonious trees (MPTs), each with a length of 994 steps. These trees had a consistency index (CI) of 0.379, retention index (RI) of 0.651, rescaled consistency index (RC) of 0.247, and homoplasy index (HI) of 0.621. Support measures for the consensus tree (Bremer support and bootstrap values via an analysis of 100 heuristic search bootstrap replicates) were computed in TNT (Goloboff et al., 2008). A combined version of the eight MPTs is presented in Figure 6.

In all eight MPTs, UF 27881 is positioned as a basal sparassodont, sister to the clade formed by Hathliacyiidae + Borhyaenidae. The MPTs only differ in the position of a few taxa such as the hathliacynid Sallacyon hoffstetteri (Fig. 6). In some trees, Sallacyon hoffstetteri and Notogale mitis form a ‘Salla clade’ that sister to Sipalocyon, whereas in others Sallacyon groups with the hathliacynids Cladosictis and Acyon. Regardless of the position of Sallacyon, Cladosictis and Acyon were found to be more closely related to one another than either was to Notogale or Sipalocyon, and vice versa (see presentation of Hathliacyiidae in Fig. 6). Another unstable taxon in this analysis was the borhyaenoid Pharsophorus, which was either recovered as the sister taxon of Prothylacos (or as sister to the clade formed by the Proboryaeidae, Borhyaenidae, and Thylacosmilidae. Like Forasiepi (2009), we did not recover a close relationship between Pharsophorus and borhyaenoids (Borhyaena and Arctodictis), contrary to traditional conception of the family Borhyaenidae (Marshall, 1978; Goin et al., 2010).

Both Patagosmilus gorni and Callistoe vincei grouped with their assumed closest relatives in this analysis, Thylacosmilus atrox and Paraborhyaeana boliviana, respectively. However, unlike some studies, we did not recover a monophyletic clade of Proboryaeidae + Thylacosmilidae (Babot et al., 2002), nor a paraphyletic Proboryaeidae (Babot, 2005, in Argot and Babot, 2011). Rather, in contrast to Forasiepi (2009), we recovered thylacosmilids as the sister group to borhyaenids. This suggests that the relationships among these three clades of derived borhyaenoids are still unclear, and that more complete remains of this group are needed to clarify their interrelationships.

The Stagodontidae, represented by Didelphodon and Eodelphis, were recovered as the sister taxon to the Sparassodonta in this analysis. Stagodontids have previously been considered to be closely related to sparassodonts (e.g., Marshall et al., 1990), but this idea has been strongly criticized as based on homoplasic features related to a carnivorous diet (Fox and Naylor, 1995; Rougier et al., 1998). The topology recovered here may be due to such homoplasic features, but would support a hypothesized Cretaceous origin of the Sparassodonta (Forasiepi, 2009).

With regard to crown-group Marsupialia, the topology recovered here is similar to that of Forasiepi (2009). However, Herpetotherium was recovered within crown-group Marsupialia, basal to the Australidelphia, rather than as a sister taxon to the group. This contrasts with the results of several other studies of marsupial phylogenetics (Sánchez-Villagra et al., 2007; Forasiepi, 2009; Horovitz et al., 2009), but agrees with that of Beck (2012). In contrast to Horovitz et al. (2009), we did not recover a close association between the Peradectidae and the Didelphoidea. Instead, the Peradectidae were recovered as the sister taxon to either crown-group Marsupialia or the Pucadelphidae.

The association of Mayulestes with Andinodelphis and Pucadelphus was one of the most stable arrangements in this analysis, appearing in nearly every experimental tree examined. This arrangement is similar to the results obtained in other phylogenetic studies of marsupials, such as Horovitz and Sánchez-Villagra (2003), Sánchez-Villagra et al. (2007), Horovitz et al. (2009), and Beck (2012). However, in this study Mayulestes was recovered within the Pucadelphidae rather than as the sister taxon to this group. Like Forasiepi (2009), we did not recover a close relationship between Mayulestes and the Sparassodonta. However, in contrast to this study, we found the Tiupampa taxa to occupy a more crownward position than sparassodonts, near crown-group marsupials. In this respect the cladogram resembles the analysis of Rougier et al. (1998), which recovered the Tiupampa taxa and Sparassodonta as successive sister groups to crown-group Marsupialia. Constraining Mayulestes as a member of the Sparassodonta added 13 steps to the MPT. Our analysis does not support the idea that Mayulestes belongs to the Sparassodonta, as proposed by Muizon (1994, 1998), indicating that the similarities between this taxon and sparassodonts most likely represent convergent specializations towards carnivory. This, in turn, suggests that Mayulestes should not be used to represent Sparassodonta in phylogenetic analyses. Rather, Patene or another definitive sparassodont should be used, although many basal members of this group are known from much less complete remains.

DISCUSSION

Sparassodont Canine Morphology

Based on the shape of the canine alveolus, UF 27881 has canines that are more circular in cross-section than most other sparassodonts (see Table 3). The proportions of the canines in this specimen are comparable to several living pantherine
Felids (Van Valkenburgh and Ruff 1987; Christiansen, 2008) and the extant cougar, *Puma concolor* (Van Valkenburgh and Ruff, 1987). The canine alveoli of UF 27881 are also relatively large for a non-borhyaenoid sparassodont, second only to a specimen of *Cladosictis patagonica* (MACN A 5927). Aside from MACN A 5927 and a specimen of *Acrocyon riggsi* (FMNH P13433), all sparassodonts with proportionally larger canines than UF 27881 (i.e., proborhyaenids and *Arctodictis*) are species that have been noted to possess abnormally large canines relative to the rest of the group (Marshall, 1978; Babot et al., 2002).

Interestingly, the specimens with the next most circular canine cross-sections among the Sparassodonta, MACN A 5931...
and UCMP 38061 (corresponding to the basal borhyaenoids *Prothylacynus patagonicus* and *Lycopsis* longirostris, respectively), are both juveniles (Marshall, 1976c; Forasiepi, 2009). This suggests that the relatively round canines of these specimens could be related to their immature status, especially because the canine proportions of adult specimens of *Prothylacynus* resemble other sparassodonts.

Aside from these juvenile specimens, the sparassodont with most similar canine length/width ratios to UF 27881 is the early Miocene (Colhuehuapian SALMA) *Arctodictis sinclarii*, which has canine proportions comparable to that of a modern lion (*Panthera leo*; see Christiansen, 2008). Several other features of *Arctodictis sinclarii* suggest that this sparassodont may have been a general ecological analogue of big cats such as the lion (*Panthera leo*) or jaguar (*Panthera onca*). These features include its proportionally large infraorbital foramen (see below), fused mandibular symphyses (in contrast to *Borhyaena*, in which it is sutured but unfused; Marshall, 1978), and several features of the postcranium. Forasiepi (2009) considered *Arctodictis sinclarii* to be a generalized carnivore in terms of its postcranium, intermediate in morphology between *Borhyaena* and *Prothylacynus*. A later study by Ercoli et al. (2012) found A. sinclarii to group with both scansorial and terrestrial taxa but did not recover a clear association with either group. Other studies of carnivoran mammals have noted that features seemingly indicative of a scansorial or arboreal mode of life may in fact be adaptations for grappling prey, and vice versa (Meachen-Samuels, 2012). In particular, *Arctodictis sinclarii* has been noted to possess a relatively flexible wrist joint and restricted range of motion at the elbow (Forasiepi, 2009; Ercoli et al., 2012). Such a combination of features would be consistent with a predominantly terrestrial animal that occasionally climbed trees and hunted by grappling prey with its forelimbs, like modern big cats. It is not certain if the other species of *Arctodictis*, *A. munizi*, may have exhibited a similar lifestyle, because this taxon has canine proportions within the normal range of sparassodonts.

Compared with the taxa mentioned above, most sparassodonts included in this analysis had narrower, somewhat mediolaterally compressed canines (i.e., canine length/width ratios $>$1.35). These proportions are similar to basal machairodontine felids such as *Promeganteron* and morphopredatory canids (Van Valkenburgh and Ruff, 1987). Indeed, some sparassodonts, such as *Borhyaena, Arminierhina*, and *Cladosictis*, have canine length/width ratios that are more similar to some saber-toothed carnivores or morphopredatory dogs than any modern conical-toothed cat. In contrast, most postcranial studies of sparassodonts have suggested that these animals were more similar to conical-toothed cats than canids or saber-toothed predators in their habits (i.e., they were ambush predators that, with the exception of thylacosmilids, did not kill their prey with a specialized canine bite; Argot, 2004a, 2004b). Conical canines are highly advantageous for ambush predators, because they can more easily withstand the highly erratic bending and torsional forces created by struggling prey (Meachen-Samuels and Van Valkenburgh, 2009). Predators with mediolaterally compressed canines, on the other hand, tend to favor hunting strategies that involve a minimal amount of contact between the prey and canine teeth, such as a series of shallow, slashing bites while chasing down prey (like macropredatory hyenas and dogs; see Van Valkenburgh and Ruff, 1987) or a single, highly precise throat bite (like saber-tooth taxa; see Akersten, 1985; Anderson et al., 2011; Wheeler, 2011).

Lacking both the conical canines of modern ambush predators and the cursorial limbs of pursuit-hunting taxa, sparassodonts may have killed their prey in a different manner than any living carnivoran. The recently extinct thylacine (*Thylacinus cynocephalus*) might provide a more suitable analogue for sparassodont hunting behavior, because it possessed forelimbs adapted for grappling prey (Figueirido and Janis, 2011) as well as mediolaterally compressed canines (Jones, 1995). Anecdotal evidence suggests that thylacines killed their prey by crippling it with an initial bite and then ripping open the abdominal cavity and eating the wounded animal alive (Jones, 1995). This hunting style is partially reminiscent of both living felids and macropredatory dog-like predators, which may reflect the mix of dog-like and cat-like traits in thylacines (Jones and Stoddart, 1998; Figueirido and Janis, 2011). However, sparassodonts differ from *T. cynocephalus* in their larger and more frequently damaged canines (Table 3; Jones and Stoddart, 1998), implying that there may still have been differences in the behavior of these two groups of predatory mammals.

Surprisingly, the other basal sparassodont included in this analysis, *Hondadelphys fieldisi*, had a canine length/width ratio of 1.8, comparable to several species of nimravids and intermediate to the proportions seen in basal saber-toothed cats such as *Promeganteron* and more derived species such as *Smilodon* (Van Valkenburgh and Ruff, 1987; Christiansen, 2008). This suggests that, despite its plesiomorphic didelphid-like cheek tooth morphology, *Hondadelphys* may not have resembled similar-sized living didelphoids in its habits.

**Paleobiology of UF 27881**

Sparassodonts generally fall into one of two major morphotypes, a paraphyletic stem group composed of taxa with dolichocephalic skulls (including hathiacycids, some basal borhyaenoids such as *Lycopsis* longirostris, and basal sparassodonts), and a monophyletic group with short snouts and deep skulls (Borhyaenidae, Proboryhaenidae, Thylacosmilidae, and closely related genera of basal borhyaenoids such as *Prothylacynus* and *Pharsophorus*). These two morphotypes can be distinguished from one another by several features (Table 5), and features of one morphotype are generally not present in members of the other group. In this regard, UF 27881 is unusual, because it combines characters of both borhyaenid-like and hathiacynid-like sparassodonts, such as a short snout and P1/p1 oriented parallel to

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**TABLE 5. Comparison of craniodental features between hathiacynid-like sparassodonts (hathiacycids, basal sparassodonts, and basal borhyaenoids such as *Lycopsis* longirostris) and borhyaenid-like sparassodonts (borhyaenids, proboryhaenids, thylacosmilids, and basal borhyaenoids such as *Prothylacynus* and *Pharsophorus*).**

| Character                      | Hathiacynid-like sparassodonts | Borhyaenid-like sparassodonts | UF 27881 |
|-------------------------------|--------------------------------|-------------------------------|----------|
| Orientation of P1/p1          | Parallel to tooth row (except in *Patene, Noticis, and Lycopsis*) | Oblique or perpendicular to tooth row | Parallel to tooth row |
| Diastema anterior to P1        | Present (except in *Lycopsis*) | Absent | Absent |
| Diastema posterior to P1       | Present | | |
| Preorbital length              | $\geq$1/3 total skull length | $<1/3$ total skull length | $<1/3$ total skull length |
| Size of protocone              | Not vestigial | Vestigial to absent | Not vestigial |
| Metaconule and paraconule      | Present (except in *Notogale*) | Absent | Absent |

See text for discussion.
the tooth row. Other features typical of borhyaenid-like sparassodonts cannot be identified in UF 27881, because these regions are missing from this specimen.

Perhaps the most distinctive features of UF 27881 are the suite of characteristics associated with its short snout and hypertrophied canines. Short, broad snouts are a common feature of both hypocarnivorous placental (Van Valkenburgh, 2007; Meachen-Samuels and Van Valkenburgh, 2009; Figueirido et al., 2011) and marsupial (Wroe and Milne, 2007) taxa, because this arrangement helps to increase bite force, resist torsional forces from struggling prey (Goswami et al., 2011), and compensate for the trade-off between bite force and gape in taxa with long canines (Slater and Van Valkenburgh, 2009).

Other morphological features of UF 27881 may be related to the large canines of this taxon. For example, the small formamina covering the surface of the canine alveolus might be evidence of an extensive mucoperiosteum and enlarged gingivae, similar to what has been proposed for nimravids (Wheeler, 2011) and the machairodontine felid Smilodon (Riviere and Wheeler, 2005). This interpretation is supported by the presence of small maxillary foramina in the sparassodonts Thylacosmilus, Patagosmilus, and Armintheringia, which also have hypertrophied canines (see above). Some authors have argued that the presence of these foramina in other synapsids (such as the cynodont Thrinaxodon) indicates that these taxa possessed enlarged vibrissae (see discussion in Estes, 1961). However, vibrissae do not leave osteological traces on the surface of the cranium in living mammals, even in taxa with highly developed vibrissae such as pinnips (Marshall et al., 2006; Muchlinski, 2010). Additionally, similar foramina are present in animals that lack vibrissae (such as the modern tegu Tupinambis), suggesting that these pits are more likely transmitted arteries and/or nerves (Estes, 1961).

The inference of well-developed gingivae in sparassodonts is based on different osteological correlates than in eutherian carnivores (Smilodon and the Nimravidae), but this might result from differences in ontogeny. In contrast to eutherians, sparassodont canines are either open-rooted (e.g., proboryhaenids and thylacosmilids; Babot et al., 2002) or form roots late in life (e.g., hithiacynids and borhyaenids; Marshall, 1976c). Riviere and Wheeler (2005) suggested that the presence of enlarged gum tissue in Smilodon represents an adaptation towards greater precision when biting, which would be essential for a mammal with hypertrophied canines that would be vulnerable to torsion forces when biting, which would be essential for a mammal with the infraorbital nerve, which innervates the vibrissae (Muchlinski, 2010) found that cat-like ambush carnivores (such as the fossa Cryptoprocta ferox, the marten Martes flavigula, and the felids Puma concolor, Panthera leo, and Panthera tigris) have relatively large infraorbital foramina, even compared with other terrestrial, short-snouted hypocarnivores (e.g., hyaenids).

In terms of general cranial morphology, UF 27881 is most similar to certain species of mustelids (e.g., Martes), dasyurids (e.g., Dasyurus maculatus), and, to a lesser extent, felids. Members of the genus Martes are small-bodied (mean total skull length of 75 mm according to Elbroch, 2006) mesocarnivorous to hypocarnivorous mustelids (Ben-David et al., 1997; Hickey et al., 1999; Cumberland et al., 2001) that, like felids, have been reported to kill their prey via a precise bite to the neck (Clark et al., 1987). Much of the caloric content of the diet in some members of this genus, such as M. americana, is composed of larger prey items (Cumberland et al., 2001), such as grousse (Bonasa umbellus and Canachites canadensis) and snowshoe hares (Lepus americanus). Similar hunting behaviors have also been reported in some preda- tors marsupials. The spotted-tailed quoll (Dasyurus maculatus), which has the least mediolaterally compressed canines of any living large-bodied dasyurid (aside from the highly specialized Tasmanian devil, Sarcophilus harrisii), has also been observed to kill prey with a precise neck bite and is known to take large prey relative to its body size (Jones, 1995; Jones and Stoddart, 1998).

Based on the similarities between these carnivorous mammals and UF 27881, it seems plausible that this marsupial killed prey in a similar method to the living Dasyurus maculatus and Martes spp. Other features of UF 27881 such as its short, broad snout (see above) support this interpretation, because this type of rostral morphology is common in predatory mammals that tend to kill prey about the same size or larger than themselves (Meachen-Samuels and Van Valkenburgh, 2009). Therefore, the majority of the diet of UF 27881 probably consisted of similar-sized birds, mammals, and reptiles, such as the caviid Guiomys unica (Croft et al., 2011).

The Smallest Sparassodonts

Although there has been some discussion of the size of the largest sparassodonts (Babot et al., 2002; Ercoli and Prevosti, 2011), few studies have investigated the lower size limit of this group (Marshall, 1981; Ercoli and Prevosti, 2011; Prevosti et al., 2012). In his review of the then-known species of small-bodied sparassodonts, Marshall (1981) considered the late early Miocene (Santarucranian) hithiacynid Pseudonoticctes pusillus to be the smallest known member of this group. More recently, Martín and Tejedor (2007) described a second species of this genus, Pseudonoticctes chubutensis, from the middle Miocene (Colloncuran SALMA) of Argentina, which appears to have been even smaller than P. pusillus. Some species, such as Patene campbelli from the Paleogene Santa Rosa local fauna of Peru (Goin and Candela, 2004) or Allqokirus australis from the early Paleocene of Bolivia (Marshall and Muizon, 1988), have also been suggested to be the smallest known sparassodonts, but these species are only known from fragmentary teeth and the identification of the latter taxon (Allqokirus) as a sparassodont is still questionable.

Based on dental measurements, UF 27881 is clearly among the smallest sparassodonts, comparable in size to Pseudonoticctes pusillus, Patene simpsoni, and Notictis ortizii (Fig. 7). However, one specimen referred to these taxa stands out. PVL 2618 from the middle Eocene Lumberra Formation (Goin et al., 1986) has been referred to Patene simpsoni, but is more than 20% smaller than the other specimens assigned to this species (Supplementary Data, Table S3). This size discrepancy and the fact that PVL 2618 is much younger than the other specimens assigned to this species (Marshall, 1981) suggest that it may pertain to a species distinct from P. simpsoni. If eventually substantiated, this species would represent the smallest definitive sparassodont.

The Evolution of South America’s Predator Guild

UF 27881 was originally referred to the genus Sparassocynus (see Croft, 2007), which would have constituted the oldest known occurrence of the Sparassocynidae. However, with the reidentifi- cation of this specimen as a sparassodont, the pre-late Miocene...
fossil record of the Didelphoidea is almost entirely composed of small-bodied non-hypercarnivorous species, including the largely frugivorous caluromyids (Goin et al., 2007), the omnivorous *Marmosops* (Marshall, 1976b; Vieira and Astúa de Moraes, 2003), and the small, insectivorous *Thylamys* (Goin, 1997; Palma, 1997). The only possible occurrence of a pre-late Miocene hypercarnivorous didelphid is an unnamed species from La Venta, Colombia, represented by three lower molars, several mandibular fragments, and possibly a partial cranium (Goin, 1997).

There are two possible explanations for the absence or near absence of hypercarnivorous didelphids prior to the late Miocene (Huayquerian SALMA). One possibility is that didelphids were unable to move into hypercarnivorous niches prior to the late Miocene because these niches were occupied by similar-sized sparassodonts. This hypothesis is supported by UF 27881, which expands the known diversity of small sparassodonts in the middle Miocene. It is also supported by the observation that many species of hypercarnivorous didelphid taxa first appear in the fossil record only when the diversity of small sparassodonts begins to wane (Reig and Simpson, 1972; Goin and Paridinas, 1996).

The relationship between the rise of large, predatory didelphids and the decline of small sparassodonts can be examined by comparing the fossil record of these two groups during the late Cenozoic (Fig. 8). The general pattern supports the idea that these two phenomena are related. Didelphids are limited to small forms during the Laventan and Chasian SALMAs, with large didelphids first appearing during the Huayquerian SALMA. Even then, hypercarnivorous didelphids remain smaller than sparassodonts, only increasing in size as the small hithiacypnids *Borhyaenidium, Noticitis, and Notocynus* disappear. Didelphids reach their maximum size in the Chapalmalania SALMA when the only sparassodont was the large-bodied *Thylacosmilus atrox* (jaguar to female lion-sized; Ercoli and Prevosti, 2011). They may have become even larger in the subsequent Marpaltan SALMA after sparassodonts went extinct (Goin et al., 2009). The fact that didelphids and sparassodonts coexisted for at least 11 million years prior to the emergence of hypercarnivorous didelphids suggests that the decline in sparassodont diversity is not due to competitive exclusion (Goin et al., 2007; Prevosti et al., 2013). However, the possibility that predatory didelphids were better adapted to changing environmental conditions of the latest Cenozoic than sparassodonts cannot be discounted. A second faunal turnover may have occurred among hypercarnivorous members of the Didelphoidea in the early/middle Pleistocene (Ensenadan SALMA), as evidenced by the extinction of the sparassocynids, *Thylatheridium*, and *Thylatheriops* and the first appearance of the cold-adapted thylampin *Lestodelphys* (Marshall, 1977b; Goin, 1995; Goin et al., 2009).

A similar case of opportunistic replacement may have also occurred between the basal, omnivorous basal sparassodont *Stylocynus* and the South American procyonids *Cyonasua* and *Chapalmalania*. Although *Cyonasua* and *Stylocynus* coexisted in the late Miocene (Huayquerian SALMA), the earliest species of *Cyonasua* are also the species with strongest adaptations towards an omnivorous/hypocarnivorous mode of life (based on RGA values; see Prevosti et al., 2013). Soibelzon (2011) also noted that the species of *Cyonasua* that coexisted with *Stylocynus* were only about one-fourth of its size; therefore, the two animals were unlikely to be in competition. Only after the extinction of *Stylocynus* do larger procyonids (*Chapalmalania* spp.) and species of procyonids with relatively more pronounced adaptations for carnivory (*Cyonasua lataria* and *Chapalmalania* spp.) appear in the fossil record (Soibelzon, 2011; Prevosti et al., 2013).

The other possible explanation for the rarity or absence of hypercarnivorous didelphids prior to the late Miocene is that these animals were present in South America for much of the Cenozoic, but their remains have just not been found yet. This explanation seems plausible, because didelphid remains in general are rare prior to the late Miocene, and no didelphid fossils have been found in otherwise productive South American localities such as the Santa Cruz Formation (Marshall et al., 1983; Abello et al., 2012a). Furthermore, a long, unrecorded history of didelphids is supported by molecular studies, which suggest that most didelphid genera originated prior to the late Miocene (Steiner et al., 2005).

A long ghost lineage prior to the late Miocene has often been inferred for at least one group of hypercarnivorous didelphids, the sparassocynids. These marsupials are usually considered to be a sister group to the two remaining families of didelphids, the caluromyids and didelphids (Goin, 1995), suggesting that sparassocynids had diverged from other didelphids by the...
FIGURE 8. Relative sizes of sparassodonts and didelphoids from the Laventan (late middle Miocene) to Marplatan (late Pliocene–early Pleistocene) SALMAs based on the m2 length. Laventan (late middle Miocene) and Chasicoan (early late Miocene) SALMAs are combined because Chasicoan marsupials are known from fewer remains and span a relatively narrow range of sizes. Taxa for which m2 length has been estimated (e.g., UF 27881, Pseudolycopsis cabrerai, Thylystomys minutus, Thylyphorops lorentzinii) are shown in gray. Borhyaenidium riggsi from the Corral Quemado Formation has been regarded as either Chapadmalalan (Prevosti et al., 2013) or Montehermosan (Goin and Pardiñas, 1996; Reguero and Candela 2011) in age; this uncertainty is denoted by error bars. Details are available in Supplementary Data, Table S4.

earliest Miocene (the age of the earliest caluromyids and didelphids; Goin et al., 2007). Some authors have even suggested that sparassocynids diverged from other didelphoids by the early or middle Eocene (Marshall, 1987), roughly congruent with the results of molecular studies (Steiner et al., 2005). However, of this writing, the geologically oldest sparassocynid remains come from the late Miocene (Huayquerian SALMA) Cerro Azul, Andalhualá, and Maimará formations of Argentina (Abello et al., 2002, 2012b; Forasiepi et al., 2009), implying a ghost lineage of at least 11 million years if sparassocynids are sister to the other didelphoids. Additionally, some features of sparassocynids, including a canine alveolus spanning the premaxillary-maxillary suture and the presence of ventrally directed posterolateral corners of the palate, suggest that sparassocynids may be more closely related to or even within the Didelphidae (Reig and Simpson, 1972; Voss and Jansa, 2003, 2009). Similar conclusions were independently reached by another study whose details have not yet been published (Beck and Voss, 2012). This is more consistent with the known fossil record of the group.

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High resolution color images of UF 27881 are available online in Morphobank.

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