

Chlorocyon phantasma, a Late Eocene Borhyaenoid (Mammalia: Metatheria: Sparassodonta) from the Los Helados Locality, Andean Main Range, Central Chile

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ABSTRACT

Sparassodont metatherians were the dominant terrestrial mammalian predators during South America's long Cenozoic isolation. This group's early fossil record is very poor, however, particularly for the late Eocene and early Oligocene. Here, we describe a new sparassodont, *Chlorocyon phantasma*, gen. et sp. nov., based on a specimen from Los Helados, a new locality within the Abanico Formation of the Andean Main Range of central Chile. New ⁴⁰Ar/³⁹Ar dates at Los Helados bracketing the fossil-bearing level constrain the age of this specimen to 37–36 Ma (late Eocene), indicating that this new taxon likely pertains to the Mustersan South American Land Mammal “Age.” *Chlorocyon* is the first Paleogene sparassodont reported from Chile and the first sparassodont described from the Abanico Formation. Distinctive features, including a p3 with an anterior edge that is more curved than the posterior edge and the lack of a hypoconulid on m4, suggest that *Chlorocyon* is a borhyaenoid closely related to *Pharsophorus* or *Plesiofelis*, although much smaller. *Chlorocyon* represents a welcome addition to the sparse record of late Eocene sparassodonts and indicates that the diversity of non-proborhyaenid borhyaenoids prior to the late Oligocene was greater than previously thought.

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INTRODUCTION

Sparassodonts, an extinct group of metatherians, were the predominant mammalian carnivores in South America from the Paleocene (Tiupampan or Peligran South American Land Mammal “Age,” or SALMA; Forasiepi and Rougier, 2009; Muizon et al., 2018) to the late early Pliocene (Chapadmalalan SALMA; Goin and Pascual, 1987; Prevosti et al., 2013). Sparassodont finds span the continent, from the La Guajira Peninsula of Colombia (Suarez et al., 2016) to the famous fossil beds of Santa Cruz Province, Argentina (Sinclair, 1906; Prevosti et al., 2012). The record of sparassodonts is heavily geographically biased, however, with most fossils coming from Argentina (Forasiepi, 2009) and a few localities in Bolivia (Villarroel and Marshall, 1982; Petter and Hoffstetter, 1983; Muizon, 1998; Forasiepi et al., 2006; Engelman and Croft, 2014; Engelman et al., 2015; Muizon et al., 2018) and Colombia (Marshall, 1977; Goin, 1997).

Of the small number of sparassodonts reported from Chile, most derive from the earliest middle Miocene Río Frías Formation at the locality of Alto Río Cisnes in the south ($\sim 44.5^\circ$ S). Marshall (1990) identified four sparassodont taxa from this locality, the hathliacynids *Sipalocyon gracilis* and *Cladosictis patagonica* and the borhyaenoids *Prothylacynus patagonicus* and *Borhyaena tuberata*. This sparassodont fauna is generally similar to slightly older sparassodont faunas from the Santa Cruz Formation (Marshall, 1990; Prevosti et al., 2012). More recently, Flynn et al. (2002) and Flynn et al. (2008) reported *Cladosictis* and cf. *Sipalocyon* in faunal lists of late early Miocene levels at Pampa Castillo in southern Chile ($\sim 47^\circ$ S) and Laguna del Laja in south-central Chile ($\sim 37.5^\circ$ S), respectively. Notably, all these occurrences span a relatively narrow temporal interval (late early Miocene–earliest middle Miocene; Flynn and Swisher, 1995; Flynn et al., 2002, 2008) and appear to represent taxa previously known from the Santa Cruz Formation of Argentina.

Here, we describe a new sparassodont from the Los Helados Locality of the Abanico Formation, near Estero Los Helados in the Tinguiririca River drainage in central Chile. Although the Abanico Formation is best known for producing early Oligocene mammal fossils (e.g., Flynn et al., 2003a; Hitz et al., 2006; Croft et al., 2008a; Bertrand et al., 2012; Bradham et al., 2015, and references therein), its assemblages span a wide age range, from Eocene to Miocene (Flynn et al., 2003b, 2012; Hitz et al., 2006; Croft et al., 2008b). The specimen described here is late Eocene in age, making it one of the few late Eocene sparassodonts known. It is also the first sparassodont from the Abanico Formation to be formally described (though another specimen is currently under study by our group; Engelman et al., 2017). The sparse representation of this group within the Abanico Formation is somewhat puzzling given the unit’s overall richness in mammal fossils (Croft, 2006). This is the first taxon to be described from what promises to be an intriguing, but as yet little-studied, Andean fossil mammal fauna.

MATERIALS AND METHODS

We follow the SALMA chronology formulated by Flynn and Swisher (1995), as modified by Flynn et al. (2003a), Ré et al. (2010), Woodburne et al. (2014), and Krause et al. (2017).

Three samples of pyroclastic flow and fall deposits (CH-130, CH-131, and CH132B) that stratigraphically bracket the horizon that produced the specimen described here (SGOPV

6200) were dated via argon geochronology. Purified ~30 mg separates of plagioclase were produced via standard density, magnetic separation, and hand-picking techniques. Samples were analyzed in the $^{40}\text{Ar}/^{39}\text{Ar}$ geochronology laboratory at the University of California, Santa Barbara, by incremental heating in a Staudacher-type resistance furnace. Isotopic analyses were obtained on a MAP 216 mass spectrometer, using the general procedures and system described by Gans (1997). The flux monitor used for all irradiations was Taylor Creek Rhyolite (Dalrymple and Duffield, 1988) with an assigned age of 28.27 Ma in order to make it compatible with an assumed age of 28.1 Ma on Fish Canyon Tuff Sanidine (another widely used standard). All errors given for our estimated (preferred) ages as reported throughout the text and in table 1 are $\pm 2\sigma$ (95% confidence).

ABBREVIATIONS

ANATOMICAL ABBREVIATIONS: Lower premolars and molars are designated by p and m.

INSTITUTIONAL ABBREVIATIONS: **AC**, Beneski Museum of Natural History, Amherst, Massachusetts; **AMNH**, American Museum of Natural History, New York; **MACN-A**, Ameghino collection, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina; **MCN.P**, Museu de Ciências Naturais, Setor de Ciências Biológicas, Universidade Federal do Paraná, Curitiba, Brazil; **MLP**, Museo de La Plata, La Plata, Argentina; **MPEF-PV**, vertebrate paleontology collections, Museo Paleontológico Edigio Ferugulio, Trelew, Argentina; **PVL**, Paleontología Vertebrados Lillo, Tucumán, Argentina; **SGOPV**, vertebrate paleontology collections, Museo Nacional de Historia Natural, Santiago, Chile; **UATF-V**, vertebrate paleontology collection, Universidad Autónoma “Tomás Frías,” Potosí, Bolivia; **UCMP**, University of California Museum of Paleontology, Berkeley, California.

GEOGRAPHIC AND GEOLOGIC SETTING

The specimen described below was recovered from the Abanico Formation in the Estero Los Helados, a northern tributary of the Río Tinguiririca immediately west of Río Azufre (fig. 1), in the Andean Main Range of central Chile. The Río Azufre drainage produced the early-diverging interatheriid notoungulate *Antepithecus brachystephanus* (Hitz et al., 2006), which suggests an early late Eocene age (Barrancan subage of the Casamayoran SALMA sensu Cifelli, 1985) for at least one level of the >1.5 km thick, continuous section of the Abanico Formation exposed in that region. The formation exceeds ~3.6 km in composite thickness along the main trunk of the Tinguiririca drainage from roughly the longitude of Los Helados to Termas del Flaco (Mosolf, 2013; Mosolf et al., 2018), though its base is unexposed in the area. The oldest dated horizon in the Abanico Formation in the Río Tinguiririca drainage, or anywhere in the Andean Main Range, is roughly 75 Ma (i.e., Late Cretaceous; Mosolf, 2013; Mosolf et al., 2018), but the age of the oldest fossiliferous level in the unit has yet to be securely established. The lower portion of what is generally regarded as the Abanico Formation in the Tinguiririca drainage (an interval evidently devoid of fossils) has recently been reassigned to the Plan de los Yeuques Formation (Muñoz et al., 2018). This more restricted view of the Abanico Formation

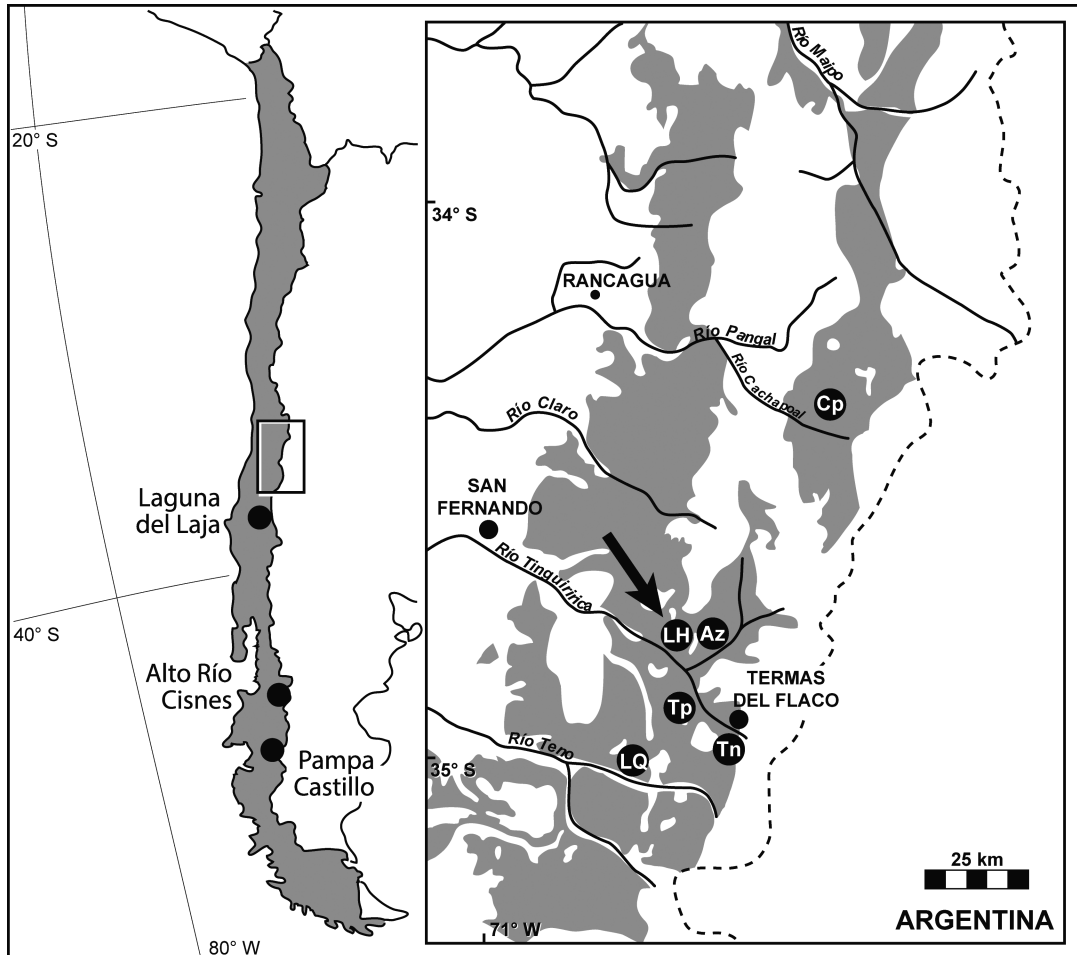


FIG. 1. Map of Chile (left) and central Chile (inset box) showing the location of Los Helados (LH, at arrow) and other selected Paleogene Chilean fossil mammal localities of the Abanico Formation. Gray area in inset box represents Abanico Formation outcrops. Abbreviations: Az, Azufre (middle Eocene?); Cp, Cachapoal (early Oligocene); LQ, Los Queñes (late Eocene? and late Oligocene?); Tn, Tinguiririca (early Oligocene); Tp, Tapado (middle Eocene?).

influences notions of its thickness and the age of its base, as the Los Lunes, Guanaco, and Guzmaná members of the Abanico Formation (*sensu* Mosolf et al., 2018) would shift to the Plan de los Yeuques Formation. This debate has no bearing on the age or stratigraphic provenance of SGOPV 6200, however, as the specimen was collected from stratigraphically higher levels of the Abanico Formation.

The stratigraphic succession of the Abanico Formation in the Los Helados drainage consists of a thick succession of ignimbrites, reworked pyroclastic flows, debris flows, ash and lapilli fall deposits, and fluvial sandstone and conglomerate (fig. 2). All sedimentary units are composed entirely of volcanoclastic detritus—including an abundance of pumice, vitric ash, and well-formed volcanic crystals—suggesting a local source of juvenile tephra and pyroclastic deposits. Units dip moderately westward or northwestward, and the exposed section exceeds

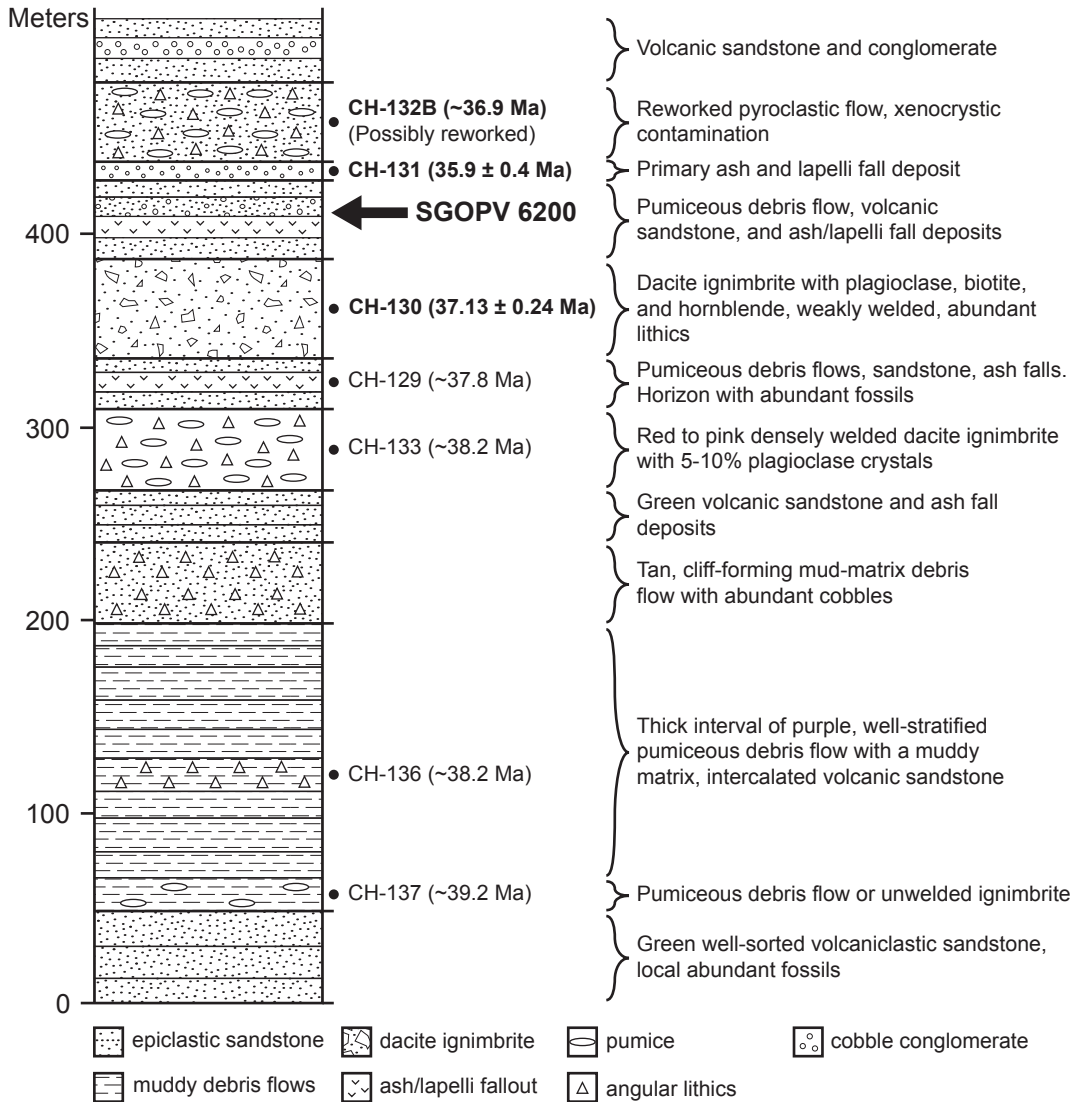


FIG. 2. Simplified stratigraphic column for the Los Helados area. Radioisotopic ($^{40}\text{Ar}/^{39}\text{Ar}$) dates discussed in the text are denoted in bold. Approximate U-Pb zircon ages for older samples are also illustrated but should be considered very preliminary.

500 m in thickness. The detailed stratigraphy and U-Pb and $^{40}\text{Ar}/^{39}\text{Ar}$ geochronology of the entire section will be reported elsewhere (Gans et al., in prep.). Here, we describe briefly the geologic context and geochronologic constraints on the fossil-bearing horizon from which SGOPV 6200 was obtained.

This fossil was collected from a bench far up the southeastern side of the drainage from a pumiceous debris flow within a ~50 m thick sequence of sandstone, conglomerate, and lapilli fall deposits. Excellent age brackets exist for SGOPV 6200, as the specimen was recovered from a level approximately midway between two primary volcanic deposits for which we have

TABLE 1. Summary data for $^{40}\text{Ar}/^{39}\text{Ar}$ analyses.

Sample ID	CH-130	CH-131	CH-132B
Irrad #	SB67-77	SB67-80	SB67-84
Mineral	plagioclase	plagioclase	plagioclase
Geological context	tan crystal-rich ignimbrite, with abundant, fresh crystals of plagioclase, biotite, hornblende, and minor quartz	green primary lapelli and ashfall deposit, crystals of plagioclase and pyroxene	reworked pyroclastic flow deposit with abundant lithics, rounded pumice
Experiment	6 step heat	6 step heat	6 step heat
WMPA (Ma)	37.13	35.86	36.95
$\pm 2\sigma$ (Ma)	0.24	0.38	0.28
TFA	37.00	35.64	36.78
Steps used (%39)	880°–1080° (58%)	880°–1030° (49%)	880°–1030° (55%)
Isochron age (Ma)	36.64 ± 2.4	36.1 ± 2.7	37.04 ± 0.40
Iso age temp steps (% 39)	same	same	all (100%)
MSWD	0.38	1.35	1.76
K/Ca	0.18–0.22	0.065–0.082	0.11–0.12
Radiogenic yield (%)	87–97	82–96	84–95
Comments	flat spectrum with excellent central plateau	slightly disturbed but fairly flat spectrum with decent central plateau	fairly flat spectrum with good central plateau

obtained reliable ages. A dacite ignimbrite (sample CH-130) approximately 15 m stratigraphically below the fossil yielded an $^{40}\text{Ar}/^{39}\text{Ar}$ plateau age on plagioclase of 37.13 ± 0.24 Ma (table 1). This ignimbrite is a pumiceous crystal-rich, weakly welded tuff with abundant fresh crystals of plagioclase, biotite, and hornblende and trace amounts of quartz. A lapilli and ashfall tuff approximately 20 m stratigraphically above the fossil (sample CH-131) yielded a reasonably flat $^{40}\text{Ar}/^{39}\text{Ar}$ age spectrum on plagioclase with an interpreted age of 35.86 ± 0.38 Ma (table 1). This deposit contains pristine glass shards and pumice lapilli with fresh crystals of plagioclase and minor pyroxene, indicating it is a primary fall deposit that has not been reworked. A slightly higher pyroclastic flow deposit (sample CH-132B) that displays some evidence for sedimentary reworking (abundant somewhat rounded andesitic cobbles, highly rounded pumice) yielded a slightly older plagioclase plateau age of 36.95 ± 0.28 , suggesting it may have incorporated some older detritus. The simplest interpretation is that SGOPV 6200 is between 37 and 36 Ma, with maximum and minimum allowable age ranges of 37.4–35.5 Ma and 36.9–36.24 Ma, respectively. This inferred age partly overlaps the ~38–37 Ma range estimated for Mustersan SALMA faunas at Gran Barranca in Argentina, based on isotopic dating of the El Rosado and Bed 10 tuffs (Bond and Deschamps, 2010; Madden et al., 2010; Ré et al., 2010; Dunn et al., 2013). Referral to the Mustersan SALMA is supported by preliminary identifications of the associated fauna, which includes polydolopid metatherians, dasypodid xenarthrans, the archaeohyracid notoungulate *Pseudhyrax*, early-diverging interatheriids (“notopithecines”),

and toxodontian notoungulates that are less hypsodont than those typical of early Oligocene (Tinguirirican SALMA) sites. Therefore, the stratigraphic level at Los Helados that produced SGOPV 6200 appears to pertain to the Mustersan SALMA, congruent with previous interpretations (Croft et al., 2008b; Flynn et al., 2012).

SGOPV 6200 is thus late Eocene in age, predating the earliest Oligocene Tinguiririca Fauna, which was recovered from deposits north and south of the Río Tinguiririca near the town of Termas del Flaco (~22 km to the SSE) and is the basis for the Tinguirirican SALMA (Flynn et al., 2003a). Isotopic dates indicate that the Tinguirirican is early Oligocene in age; horizons bearing Tinguirirican fossils and those immediately bracketing them are no younger than ~31.5 Ma (Flynn et al., 2003a), and correlative faunas have been determined to be no older than ~33.5 Ma (Ré et al., 2010; Dunn et al., 2013). SGOPV 6200 likely postdates the Tapado Fauna from the main drainage of the Río Tinguiririca, which is geographically interposed between Estero Los Helados and Termas del Flaco. Although the stratigraphic section producing the Tapado Fauna has now been dated isotopically (Mosolf et al., 2018), the fossil localities and geochronologic results have yet to be fully integrated. Nevertheless, the composition of the Tapado Fauna suggests a middle Eocene age, similar to that inferred for the level producing *Antepithecus* at Azufre (Flynn et al., 2005, 2012; Croft et al., 2008b). SGOPV 6200 appears to be roughly equivalent in age to lower levels of Los Queñes, located ~30 km to the southwest in the western reaches of the Río Teno. Preliminary assessments of the mammals recovered from these levels suggest they also correspond to the late Eocene Mustersan SALMA (Flynn et al., 2012).

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758

METATHERIA Huxley, 1880

SPARASSODONTA Ameghino, 1894

BORHYAENOIDEA Simpson, 1930

Chlorocyon phantasma, gen. et sp. nov.

Figures 3–5; tables 2, 3

HOLOTYPE: SGOPV 6200, associated left and right dentaries preserving fragments of the symphyseal region, the left and right lower canines and roots of right p1–3, along with natural molds of the lingual face of the dentaries and the crowns of p1–m4 on both sides.

DIAGNOSIS: A borhyaenoid (based on the presence of a heellike m4 talonid lacking a distinct hypoconulid) that differs from all other sparassodonts (at least those for which the dentary and lower dentition are known) in the following combination of features: straight posteroventral border of the mandible in lateral view, p1–3 that increase gradually in size, absence of a precingulid or precingulid cusp on p2, diastemata between the lower canine and p1 and p1–2, p3 with convex anterior face and nonbulbous roots, and metaconid present on

m2–4. Differs from *Lycopsis* spp. in a straight posteroventral border of the mandible in lateral view, absence of a precingulid on p2, presence of a metaconid on m2–4, and a mandibular condyle dorsoventrally aligned with the toothrow. Differs from *Prothylacynus patagonicus* and *Pseudothylacynus rectus* in having a p3 with a convex anterior face, diastemata between lower canine and p1–2, and metaconids on m2–4. Further differs from *Prothylacynus patagonicus* in having p1–3 that increase gradually in size and in the absence of a precingulid on p2. Differs from *Pharsophorus* spp. and *Plesiofelis schlosseri* in having p1–3 that increase gradually in size, presence of diastemata between lower canine and p1–2, smaller size (length of m1–4 <70% that of the smallest species of *Pharsophorus*), and a shallower dentary (depth at m4 is 66% m1–4 length versus >72% in other species).

TYPE LOCALITY: Los Helados, central Chile. SGOPV 6200 derives from volcanoclastic sediments of the Abanico (= Coya-Machali) Formation in the greater Río Tinguiririca drainage (~35° S), in the Andean Main Range of central Chile, roughly 20 km west of the border with Argentina. It was recovered from ~20° west-dipping strata near the crest of the divide between the Azufre and Los Helados drainages.

AGE: Late Eocene, Mustersan SALMA.

DISTRIBUTION: Known only from the Los Helados type locality.

ETYMOLOGY: The genus combines the Greek root for “green” (*chloro-*), in reference to the color of the sediments in which the holotype was found, and “dog” (*cyon*), a common suffix for sparassodont genera. The specific epithet (a noun in apposition), is from the Greek/Latin word for an “apparition” or “phantom” and alludes to the preservation of the holotype, which consists primarily of an almost complete natural mold of both dentaries and lower dentitions.

DESCRIPTION AND COMMENTS: The right dentary measures approximately 11.0 cm in anteroposterior length (the posterior edge cannot be identified on the left side). The two dentaries are separated at the symphysis and splayed apart, with the concave natural molds of the lingual surfaces of the dentaries and teeth projecting into the slab (i.e., the now missing labial surfaces would have faced the observer) (fig. 3). The symphysis apparently was not fused in *Chlorocyon* (as it is in *Prothylacynus* and proborhyaenids), as the two halves of the mandible became disarticulated prior to burial. The lingual faces of the two dentaries are directed into the slab, obscuring the extent of the mandibular symphysis and whether its surface is smooth or rugose. Nevertheless, judging from the smooth surfaces of the casts (fig. 4E, F), the symphysis did not reach the p3/m1 embrasure and probably extended only slightly posterior to p2 (contrary to the condition in proborhyaenids and some borhyaenids). Possible remnants of the mandibular canal and anterior mental foramen are preserved on the right dentary (figs. 4E, 5A), suggesting the anteriormost mental foramen opened at or anterior to the level of p2.

The ventral border of the dentary posterior to m4 is noteworthy for being nearly straight in lateral view. This feature can be observed in both dentaries (though only fragments of bone are preserved on the left side; see fig. 4B). This is an uncommon feature in sparassodonts, documented previously only in *Pharsophorus lacerans*, *Prothylacynus patagonicus*, *Proborhyaena gigantea*, and *Thylacosmilus atrox*. By contrast, the ventral mandibular border is strongly curved in lateral view in most other sparassodonts, including *Pharsophorus tenax*. The condition of the



FIG. 3. Photo of the holotype of *Chlorocyon phantasma* (SGOPV 6200) showing orientation of dentaries as they were discovered. Scale = 5 cm.

mandible in *Plesiofelis*, which has been considered to be closely related to *Pharsophorus* (Cabrera, 1927; Simpson, 1948; Marshall, 1978), deserves special mention. At first glance, the posteroventral border of the best-preserved dentary of *Plesiofelis*, MLP 11-114, appears to be curved in lateral view. However, the presence of many complementary fractures separated by wax and plaster suggests that the dentary has been reconstructed improperly. Eliminating these artificial spaces among the bone fragments would result in a much shallower dentary with a flat posteroventral border that bears a striking resemblance to that of *Prothylacynus* and the holotype of *Pharsophorus lacerans*. The ventral border of the dentary is straight in the holotype of *Pharsophorus lacerans* (MACN-A 52-391) but curved posterior to m4 in a second specimen tentatively referred to this taxon, MPEF-PV 4190 (Goin et al., 2010), calling into question the latter specimen's identification. This finding, along with the reinterpretation of "*Pharsophorus*" *antiquus* (now *Australohyaena antiquua*; Forasiepi et al., 2015) as a borhyaenid (rather than a basal borhyaenoid), highlights the need for a phylogenetic and taxonomic revision of *Pharsophorus* and other non-proborhyaenid borhyaenoids (i.e., *Plesiofelis*).

Both dentaries of SGOPV 6200 preserve the base of the coronoid process, which is separated from m4 by a space of ~4 mm, but neither element preserves enough of the coronoid process to confidently determine the angle between its anterior border and the toothrow. The opening of the mandibular canal is filled with matrix on the right dentary, indicating that the mandibular foramen was positioned near the anteroposterior midpoint of the coronoid process. A small portion of the coronoid notch is preserved on the left dentary, which suggests that the mandibular condyle was probably dorsoventrally aligned with the toothrow but slightly dorsal to the alveolar border. In most sparassodonts, including *Australohyaena*,

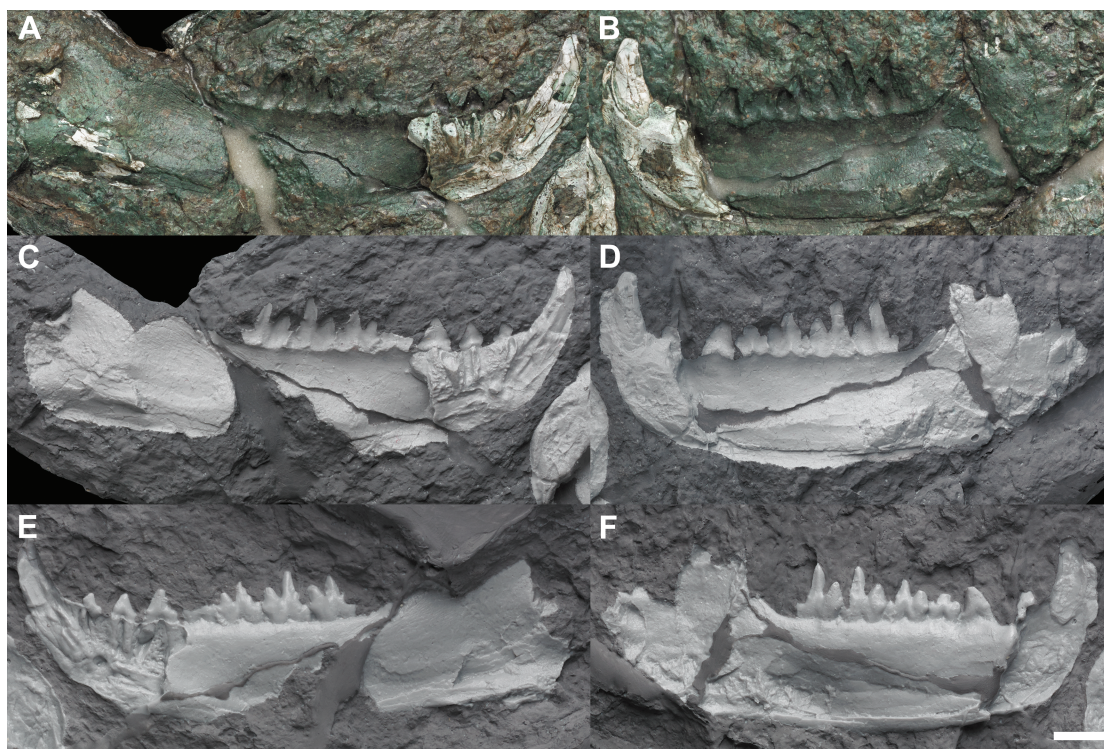


FIG 4. Right (A, C, E) and left (B, D, F) dentaries of the holotype of *Chlorocyon phantasma* (SGOPV 6200) in lingual view. A–B, Original specimen; C–D, replica of original specimen with the natural molds and areas of preserved bone and teeth painted light gray for enhanced contrast; E–F, “negative” cast made by infilling the natural molds preserved in the original specimen, with areas representing teeth and bone painted light gray. Scale = 1 cm.

Arctodictis, *Borhyaena*, *Prothylacynus*, *Plesiofelis* (when accounting for restoration), *Callistoe*, *Proborhyaena*, *Anachlysictis*, and *Thylacosmilus*, the mandibular condyle is level with the alveolar border of the molar row. In *Cladosictis*, *Acyon*, *Dukecynus*, and the specimen of *Pharsophorus* from La Cantera (MPEF-PV 4190), the condyle is dorsal to the alveolar border of the molars but not dorsal to the crowns of the molars, similar to the condition in *Chlorocyon*. The mandibular condyle is positioned completely dorsal to the lower dentition in *Allqokirus australis*, *Sipalocyon gracilis*, *Lycopsis longirostris*, an unnamed sparassodont from the early Miocene Gaiman Formation of Argentina (MPEF-PV 4770), and possibly *Borhyaenidium musteloides*, *?Perathereutes* (Prevosti et al., 2012), and *Hondadelphys fieldsi* (the condyle is not preserved in the holotype but the posterior border ventral to the condyle is preserved to a point almost above the trigonid). The mandibular condyle may be dorsal to the tooththrow in *Lycopsis torresi*, given that the coronoid notch of the left dentary of the holotype (MLP 11-113) is dorsal to the tooth crowns, but restoration of this specimen makes this point uncertain.

The only observable remnant of the anterior dentition in SGOPV 6200 is a small fragment of a left lower incisor (fig. 4B, 5C). This tooth is appressed to the base of the left canine, suggest-

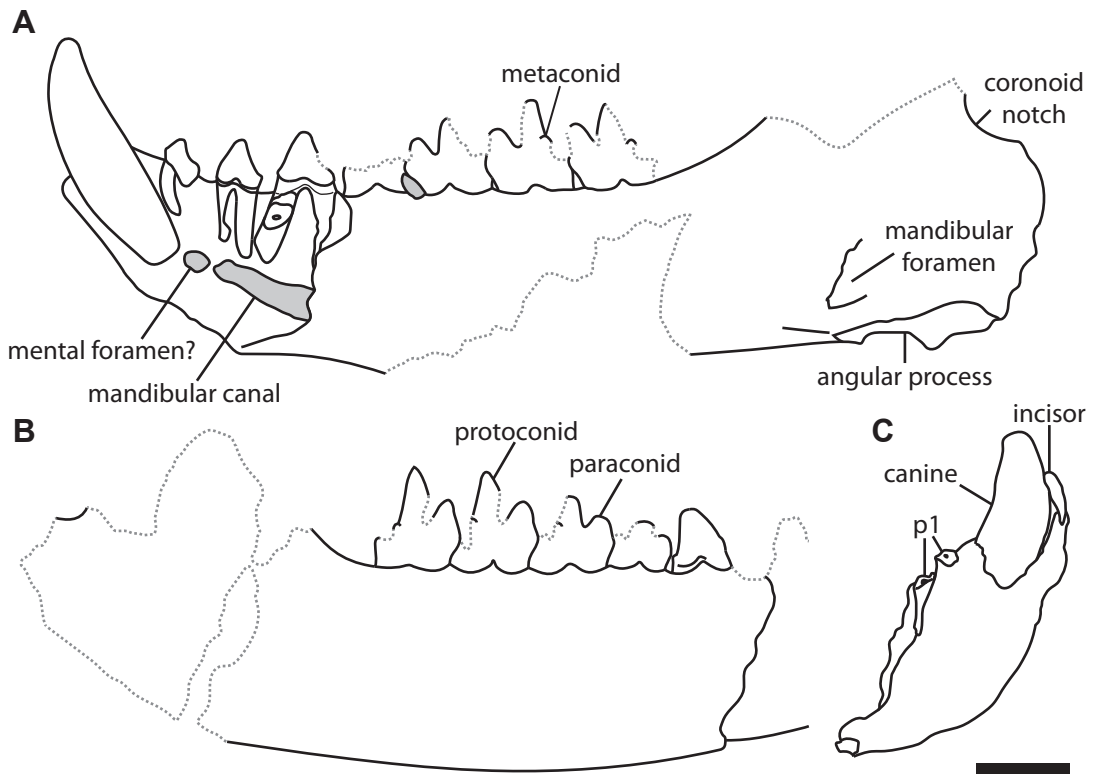


FIG 5. Holotype of *Chlorocyon phantasma* (SOGO-PV 6200): line drawings of “negative” casts made by infilling the natural molds of the original specimen (A, B) and the original specimen (C). A, right dentary in lingual view; B, left dentary in lingual view (with anterior region omitted); C, left dentary in labial view (reversed to match B). Areas where the border of the specimen is uncertain due to poor contrast between the cast and the matrix are denoted by dashed gray lines; areas where matrix has infilled the bone are denoted in gray. Scale = 1 cm.

ing it represents either i2 or i3 (both of which contact the lower canine in many sparassodonts). The lower canines are large and single rooted. The root of the right lower canine is closed.

Small diastemata separate the canine from p1, p1 from p2, and possibly p2 from p3. The three premolars, best seen in casts of the right p1–3 (fig. 4E, F), are simple, triangular in profile, and similar in shape, gradually increasing in size posteriorly (table 2). Small posterobasal heels are present on p1–3; since these structures are only preserved as partial molds it is difficult to compare them in detail to those of other sparassodonts. Whether p1 is oriented obliquely to the toothrow, as in most borhyaenoids, cannot be determined with certainty. The posterior root appears to be more lingual than the anterior one, similar to the condition in borhyaenoids in which p1 is obliquely oriented, but this may be an illusion based on the angle at which the slab is preserved. The well-defined anterior border of p2 bears no evidence of a precingulid or anterior cusp. Precingulids are present on p2 in most sparassodonts (see appendix 1) but are absent in the borhyaenid *Borhyaena*, the basal borhyaenoids *Pseudothylacynus* and *Plesiofelis*, the basal sparassodonts *Stylocynus* and *Allqokirus*, an unidentified sparassodont from the early Miocene Gaiman Formation of Argentina (MPEF-PV 4770), and a specimen (MCN.P.1259)

TABLE 2. Mesiodistal lengths (in mm) of the lower dentition of the holotype of *Chlorocyon phantasma* (SGOPV 6200). * = estimated measurement.

Side	p1	p2	p3	m1	m2	m3	m4	p1-3	m1-4
Left	—	—	7.60	6.22	8.33	9.29	9.51	15.24*	32.15
Right	4.45	4.84	6.54	—	8.59	9.25	9.67	19.17	33.36

assigned to *Nemolestes* by Sedor et al. (2017). The presence of a precingulid on p2 is uncertain in *Pharsophorus*; the crown of p2 is broken in the holotype of *P. lacerans*, and the presence or absence of a precingulid in the specimen from La Cantera, Argentina (MPEF-PV 4170) is uncertain due to poor preservation. A juvenile sparassodont from Salla, Bolivia, which may pertain to *Pharsophorus* (UATF-V-000131), appears to lack a precingulid on p2.

The main cusp of p3 is strongly curved posteriorly and asymmetric in lateral view; its anterior face is convex, whereas its posterior face is less curved and only slightly concave. A small protrusion may represent a tiny anterobasal cuspule or shelf. The roots of p3 are much larger, more massive, and more divergent than those of p1–2, but they are less bulbous than in species with presumed bone-cracking habits such as borhyaenids and proborhyaenids. The premolars of SGOPV 6200 are notably more gracile and much less robust than those in *Pharsophorus*, *Plesiofelis*, and borhyaenids. The left p3 is strongly canted posteriorly (the angle between the base of the crown and the alveolar border of m1–4 is $\sim 22^\circ$); this is less evident in the right p3 (the same angle is $\sim 10^\circ$), indicating that some or all of this inclination may be a taphonomic artifact due to plastic deformation (as opposed to breakage, for which evidence is lacking). A posteriorly canted p3 occurs in several other borhyaenoids, including the basal borhyaenoids *Plesiofelis schlosseri* and *Pharsophorus lacerans* and the borhyaenids *Australohyaena antiquua*, *Arctodictis sinclairi*, and *Borhyaena macrodonta* (Marshall, 1978; Forasiepi et al., 2015).

Like the premolars, the molars of SGOPV 6200 are preserved solely as partial natural molds, limiting us to a lingual view (best seen from the “positive” cast created by infilling the molds: figs. 4E, F; 5A, B). As in nearly all sparassodonts, the paraconid and protoconid are the largest and tallest cusps of the molars; both cusps progressively increase in height from m1 to m4. An antero-lingual ventral keel is present on the paraconid, a feature typical of most sparassodonts except proborhyaenids and possibly *Thylacosmilus*. Well-developed crests occur on the anterior and posterior edges of the protoconid. Casts of the lower molars show a small metaconid on m2–4 that is best observed on the right m3 (fig. 4E, 5A). The metaconid of m4 is smaller than the metaconids of m2–3. Metaconids on m2–4 are variably present among borhyaenoids; they are absent in *Lycopsis*, *Pseudothylacynus*, *Prothylacynus*, *Angelocabrerus*, proborhyaenids, and thylacosmilids, but present in borhyaenids and the Eocene-Oligocene borhyaenoids *Plesiofelis* and *Pharsophorus*. The metaconid of m4 is absent in *Arctodictis* and variably present in *Borhyaena* (Forasiepi et al., 2015). Metaconids on m2–4 also occur in *Patene*, *Hondadelphys*, *Nemolestes*, *Stylacynus*, and several Paleogene sparassodont specimens that have yet to be securely identified. The left m1 of SGOPV 6200 shows no evidence of a metaconid (the natural mold of the right m1 does not include an impression of the crown), suggesting that this cusp was absent on m1 in *Chlorocyon*, as in all borhyaenoid and hathliacynid sparassodonts. The natural molds of the molar

talonids are poorly preserved, limiting what can be said about their morphology. The proportions of the posterior ends of m1–3 suggest that these teeth bore relatively large talonids (i.e., more closely resembling hathliacynids and *Lycopsis* spp. than borhyaenids or proborhyaenids). A lingual cusp (likely an entoconid) seems to be present at the midpoint of the talonid (likely an entoconid), but this is not entirely certain. The cast of left m4 suggests that its talonid consisted of a simple, nonbasined “heel.” The m4 talonid appears to be proportionally larger than its counterparts in *Plesiofelis* and *Pharsophorus*, smaller than in *Pseudothylicynus*, and roughly similar to the condition in *Lycopsis* spp. A heellike m4 talonid, a derived attribute of borhyaenoids among sparassodonts, suggests that *Chlorocyon* is a member of this clade.

DISCUSSION

Chlorocyon cannot be referred to the Proborhyaenidae or Thylacosmilidae based on its closed-rooted canines, lack of a symphyseal flange, and presence of a metaconid on m2–4, among other features. *Chlorocyon* resembles borhyaenids in the presence of metaconids on m2–4, but it differs from all members of this group in lacking bulbous roots on its premolars, possessing diastemata among the premolars, and having a straight posteroventral margin of the dentary in lateral view. It is unlikely that *Chlorocyon* pertains to the Hathliacynidae, despite its relatively small size (see below). Although the early history of hathliacynids is poorly understood, all currently known hathliacynids lack metaconids on m2–4, have a hypoconulid on m4, and have a curved posteroventral margin of the dentary in lateral view. Hathliacynids other than *Pseudonotictis pusillus* and *Borhyaenidium altiplanicus* are also characterized by a p3 in which the anterior edge is less curved than the posterior one (as opposed to a more curved anterior edge, as in *Chlorocyon*). The only potential hathliacynid synapomorphy of *Chlorocyon* is a diastema between the lower canine and p1, a feature present in *Acyon* spp., *Borhyaenidium* spp., *Cladosictis* spp., *Notogale mitis*, and *Sipalocyon gracilis*, but absent in *Perathereutes*, *Pseudonotictis*, and *Notocynus*. A diastema between the lower canine and p1 is absent in other sparassodonts with gracile rostra, including *Allqokirus australis*, the *Patene* specimen from the Quebrada de Los Colorados Formation, *Hondadelphys fieldsi*, *Stylocynus paranensis*, *Lycopsis viverensis*, and possibly *L. longirostris* (the holotype of this last taxon is of an immature individual and the anterior end of the dentary is not complete).

Among remaining sparassodonts, *Chlorocyon* most closely resembles the late Eocene basal borhyaenoid *Plesiofelis schlosseri* and the Oligocene borhyaenoid *Pharsophorus* spp. in having a p3 with an anterior edge that is more curved than the posterior edge, absence of the precingulid on p2 (the precingulid also is absent in a few other taxa such as *Pseudothylicynus*, but the condition is ambiguous in *Pharsophorus* spp.), presence of a metaconid on m2–4, and a straight posteroventral margin of the dentary in lateral view (shared with *Pharsophorus lacerans* and *Plesiofelis* but possibly absent in *Pharsophorus tenax*). However, *Chlorocyon* also differs from *Plesiofelis* and *Pharsophorus* in several respects. First, *Chlorocyon* is much smaller: both *Plesiofelis* and *Pharsophorus* are large-bodied taxa, the smallest species of which (*Pharsophorus tenax*) is estimated to have weighed about 21 kg (table 3). By con-

TABLE 3. Lower molar row mesiodistal length (Lm1–4), estimated body mass, and dentary depth at m4 (Dm4) of *Chlorocyon phantasma* and species of *Pharsophorus* and *Plesiofelis*. All measurements in mm and all body mass estimates (in kg) were determined using m1–4 length and the regression equation of Myers (2001) for dasyuromorphians. Body mass and dentary depth for *Chlorocyon* was estimated using the left dentary, as the ventral border of the dentary and lengths of m1–4 are better preserved on this side. Dentary depth for *Plesiofelis schlosseri* was measured in such a way as to compensate for the likely inaccurate restoration of the jaw (see text). The body masses of *Pharsophorus lacerans* and *Plesiofelis schlosseri* represent extrapolations from the modern dasyuromorphian comparative dataset used by Myers (2001), but the estimated masses for SGOPV 6200 and *Pharsophorus tenax* are within the range of variation of the sample used to generate the equation and thus likely to be more accurate.

Specimen	Taxon	Lm1–4	Body mass (kg)	Dm4	Dm4/Lm1–4
SGOPV 6200 (left)	<i>Chlorocyon phantasma</i>	32.2	5.9	21.3	0.66
MACN-A 52-391	<i>Pharsophorus lacerans</i>	56.0	35.3	42.5	0.76
MACN-A 11653	<i>Pharsophorus lacerans</i>	53.0	29.6	—	—
MPEF-PV 4190	<i>Pharsophorus</i> cf. <i>P. lacerans</i>	56.8	37.0	42.9	0.75
AC 3004	<i>Pharsophorus tenax</i>	48.0	21.5	34.6	0.72
MLP 11-114	<i>Plesiofelis schlosseri</i>	58.6	40.8	45.7	0.78

trast, *Chlorocyon*, with a molar row length ~55%–65% that of *Plesiofelis* and *Pharsophorus lacerans* and ~70% that of *Pharsophorus tenax*, is much smaller, with an estimated body mass of 5.9 kg (table 3), roughly the size of the hathliacynid *Cladosictis patagonica* (Ercoli and Prevosti, 2011). In addition, the dentary of *Chlorocyon* is much shallower—in both absolute and relative terms—than that of *Plesiofelis* or *Pharsophorus* (table 3). *Chlorocyon* further differs from these taxa in having diastemata among the lower premolars, and is distinct from *Pharsophorus lacerans* in having p1–3 that increase gradually in size, rather than p1 being significantly smaller than p2–3 (the condition is unknown in *Plesiofelis* and *Pharsophorus tenax*). *Chlorocyon* is comparable in size to the late Eocene *Procladosictis anomala* (see Croft et al., 2018), but the latter taxon is known only from a highly unusual upper dentition, thereby precluding direct comparison of dental morphology. Nonetheless, *P. anomala* is considered a hathliacynid or basal sparassodont rather than a borhyaenoid (Marshall, 1981; Forasiepi, 2009), thus distinguishing it from *Chlorocyon*, which is most likely a borhyaenoid. The talonids of *Chlorocyon* also are slightly shorter mesiodistally than would be expected for *P. anomala*, judging from the mesiodistal length of the protocones of the holotype of *P. anomala* (the talonid of m2 is ~2.2 mm long in *Chlorocyon*, while the protocone of M2 is 3.2 mm long in *P. anomala*). In summary, *Chlorocyon* likely represents a borhyaenoid most closely related to *Plesiofelis schlosseri* and *Pharsophorus* spp., but differs sufficiently from these taxa (smaller size, shallower dentary, diastema among the premolars, premolar size differences, etc.) to warrant recognition as a new genus and species.

In addition to representing a new taxon, SGOPV 6200 is noteworthy for its late Eocene (Mustersan SALMA) age. Only a handful of Mustersan sparassodont specimens have been described previously, all from localities in Argentina: the holotype of *Procladosictis anomala* from Gran Barranca (Marshall, 1981); three specimens from the locality of Cerro del Humo (including

the holotype of the borhyaenoid *Plesiofelis schlosseri*; Simpson, 1948; Marshall, 1978); four undescribed specimens from Gran Hondonada (Ruigómez, personal commun.) that have been referred to *Procladosictis* and *Plesiofelis* (Cladera et al., 2004: table 1); and an isolated lower molar of the proborhyaenid *Callistoe* sp. from Antofagasta de la Sierra (Goin et al., 1998; Powell et al., 2011).

The pre-late Oligocene record of Sparassodonta is remarkably poor, with most occurrences representing basal sparassodonts (e.g., *Patene*) or proborhyaenids, a grouping of exclusively Paleogene sparassodonts only distantly related to most Miocene forms (except possibly thylacosmilids; see Babot, 2005; Forasiepi et al., 2015; Engelman et al., 2017). If proborhyaenids are deeply nested within Borhyaenoidea, as is consistently recovered by many studies (Muizon, 1999; Babot et al., 2002; Forasiepi, 2009; Engelman and Croft, 2014; Forasiepi et al., 2015; Suarez et al., 2016; Muizon et al., 2018), then the major lineages of late Cenozoic sparassodonts (e.g., hathliacynids, borhyaenids) must have originated by the middle Eocene (Vacan subage of the Casamayoran SALMA), based on the earliest widely accepted occurrence of a proborhyaenid (Babot et al., 2002; Powell et al., 2011), or potentially even the early Eocene, based on possible proborhyaenid remains from the Las Violetas Fauna (Gelfo et al., 2010; Krause et al., 2017). An early or middle Eocene divergence of major sparassodont clades is supported by a recent report of a possible borhyaenid from the middle Eocene locality of La Barda, Argentina (Lorente et al., 2016). *Chlorocyon* indicates that the morphological diversity of Eocene sparassodonts was greater than previously thought, and that non-proborhyaenid borhyaenoids were far more diverse and morphologically disparate during the Eocene than currently reflected in the fossil record. This observation is compatible with the long ghost lineages inferred for many Neogene taxa and further highlights the need for additional sampling of Eocene localities from Chile and throughout South America. No less importantly, SGOPV 6200 provides a tantalizing preview of the paleontological novelty that will emerge from the Abanico Formation at Estero Los Helados as its fauna(s) become more completely studied.

ACKNOWLEDGMENTS

Our work has had the strong backing of the Museo Nacional de Historia Natural and the Consejo de Monumentos Nacionales, Santiago, Chile, and would not have been possible without the steadfast support of our colleague and friend, Reynaldo Charrier. We thank N. Wong for photographs of SGOPV 6200; A. Balcarcel for preparation, molding, and casting; C. Kammerer for etymological advice; M.J. Babot for comparative photos of *Patene*; F. Goin for facilitating access to specimens in their care; E. Ruigómez for information on the sparassodont specimens from Gran Hondonada; and R. Beck and F. Goin for insightful comments that improved this manuscript. This research was completed as part of a master's thesis in biology by R. Engelman at Case Western Reserve University. This research was supported by funding from the National Science Foundation (DEB-9317943, DEB-0317014, and DEB-0513476 to J.J.F.; DEB-9020213 and DEB-9318126 to A.R.W.) and the Frick Fund, Division of Paleontology, AMNH.

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APPENDIX 1

LIST OF SPARASSODONT MATERIAL EXAMINED IN THE STUDY OF SGOPV 6200

“Specimens” are specimens or casts examined firsthand, whereas “References” refers to observations made in part or solely on the primary literature. * = species in which a precingulid is observed to be present on p2.

Taxon	Specimens	References
<i>Acyon myctoderos</i> *	UATF-V-000926	Forasiepi et al. (2006)
<i>Allqokirus australis</i>	—	Muizon et al. (2018)
<i>Anachlysictis gracilis</i>	—	Goin (1997)
<i>Arctodictis munizi</i> *	—	Marshall (1978); Forasiepi et al. (2004)
<i>Arctodictis sinclairi</i> *	MLP 85-VII-3-1	Forasiepi (2009); Forasiepi et al. (2015)
<i>Australogale leptognathus</i> *	UATF-V-001984	Engelman et al. (In press)
<i>Australohyaena antiquua</i> *	—	Forasiepi et al. (2015)
<i>Borhyaena macrodonta</i>	MACN-A 52-390, MLP 77-VI-13-1	Forasiepi et al. (2015)
<i>Borhyaena tuberculata</i>	—	Sinclair (1906)
<i>Borhyaenidium musteloides</i> *	MLP 57-X-10-153	—
<i>Borhyaenidium altiplanicus</i> *	—	Villarroel and Marshall (1983)
<i>Callistoe vincei</i>	—	Babot et al. (2002)
<i>Chlorocyon phantasma</i> gen. et sp. nov.	SGOPV 6200	—
<i>Contrerascynus borhyaenoides</i> *	—	Contreras (1990)
<i>Cladosictis centralis</i> *	—	Marshall (1981)
<i>Cladosictis patagonica</i> *	MACN-A 5927	Sinclair (1906); Marshall (1981)
<i>Dukecynus magnus</i>	—	Goin (1997)
<i>Hondadelphys fieldsi</i> *	UCMP 39251	—
<i>Lycopsis longirostris</i> *	UCMP 38061	—
<i>Lycopsis torresi</i> *	MLP 11-113	—
<i>Lycopsis viverensis</i> *	—	Forasiepi et al. (2003)
<i>Nemolestes spalacotherinus</i>	MACN-A 10330	—
“ <i>Nemolestes</i> ” sp.	—	Sedor et al. (2017)
<i>Notocynus hermosicus</i>	MLP 11-91	—
<i>Notogale mitis</i> *	—	Patterson and Marshall (1978); Marshall (1981)
<i>Patene “simpsoni”</i> (Quebrada de los Colorados Formation)	PVL 2618	—
<i>Pharsophorus</i> cf. <i>P. lacerans</i>	MPEF-PV 4170	Goin et al. (2010)
<i>Pharsophorus lacerans</i>	MACN-A 52-391	Marshall (1978); Patterson and Marshall (1978)
<i>Pharsophorus tenax</i>	AC 3004	Marshall (1978); Patterson and Marshall (1978)
? <i>Pharsophorus</i> sp.	UATF-V-000131	—
<i>Plesiofelis schlosseri</i>	MLP 11-114	—

Taxon	Specimens	References
<i>Proborhyaena gigantea</i>	AMNH 29576	Mones and Ubilla (1978)
<i>Procladosictis anomala</i>	MACN-A 10327	—
cf. ? <i>Procladosictis</i> / <i>Nemolestes</i> sp.	AMNH 29433	Forasiepi et al. (2015)
<i>Prothylacynus patagonicus</i> *	MACN-A 706	Sinclair (1906)
<i>Pseudonotictis pusillus</i> *	MACN-A 666, MLP 11-26	—
<i>Pseudothylacynus rectus</i>	MACN-A 52-369	—
<i>Sipalocyon gracilis</i> *	MACN-A 691, MACN-A 5938, YPM-VPPU 15373	Sinclair (1906); Marshall (1981)
<i>Sparassodonta incertae sedis</i>	MPEF-PV 4770	—
<i>Stylocynus paranensis</i>	MLP 41-XII-13-1112	Cabrera (1927)
<i>Thylacosmilus atrox</i>	FMNH P14344	—

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