



CLADOSICTIS PATAGONICA (METATHERIA, SPARASSODONTA) FROM THE COLLÓN CURA FORMATION (MIDDLE MIOCENE), RÍO NEGRO, ARGENTINA

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A major microbial development over an extensive area indicates stressful conditions in this part of Gondwana.

A BASAL AETOSAUR FROM THE UPPER TRIASSIC OF ARGENTINA

An incomplete skeleton from the Ischigualasto Formation is described, including novelties on appendicular armor and caudal ventral carapace.

SPARASSODONTA FROM THE MIOCENE OF PATAGONIA

Cladosictis patagonica from the Collón Cura Formation is reported and analyzed considering the intraspecific variability.

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Key words. *Cladosictis patagonica*. Collón Cura Formation. Middle Miocene. Intraspecific variability.

Palabras clave. *Cladosictis patagonica*. Formación Collón Cura. Mioceno Medio. Variabilidad intraespecífica.

SPARASSODONTA (METATHERIA) was the major mammalian predator group in terrestrial ecosystems of South America during most of the Cenozoic. Currently, nearly 60 species are valid. By the late early Miocene (Burdigalian, Santacrucian age), their richness had peaked at 11 species (Prevosti *et al.*, 2012a). Subsequently (Burdigalian–Langhian Friasian and Langhian Colloncuran ages), their richness curve steeply declined; however, this pattern is likely the result of sampling bias (Prevosti & Forasiepi, 2018).

One classical middle Miocene vertebrate association occurs in the Collón Cura Formation (CCF), exposed in north-western Patagonia (Río Negro, Neuquén, and Chubut provinces) (*e.g.*, Pascual *et al.*, 1984; Vucetich *et al.*, 1993; Bucher *et al.*, 2021; see Supplementary Online Information). Sparassodonts have rarely been encountered in the CCF, the two best known being the small sized hathliacynid *Pseudonotictis chubutensis* and the thylacosmilid *Patagosmilus goini*. Additional sparassodonts from the CCF are known, but only as entries in faunal lists: *Prothylacynus* sp. (Pascual *et al.*, 1984), an indeterminate borhyaenid (Pascual *et al.*, 1978), and a fragmentary maxilla assigned to cf. *Arctodictis* sp. (Pardiñas, 1991). However, the determinations were not accompanied by sufficient information to allow their taxonomic identification or in collections.

The objective of this contribution is to report the first discovery of the sparassodont *Cladosictis patagonica* in the CCF, based on MAPBAR-5150 and another specimen (MAPBAR-7798) tentatively referred to this species, both collected in the area of Comallo, Pilcaniyeu Department, Río Negro province, Patagonia, Argentina, from levels of the Collón Cura Formation (middle Miocene; Colloncuran age).

Institutional abbreviations. MAPBAR, Museo de la Asociación Paleontológica Bariloche, San Carlos de Bariloche, Río Negro, Argentina.

Anatomical abbreviations. M/m, upper/lower molar; P/p, upper/lower premolar.

MATERIALS AND METHODS

Comparative material. See Supplementary Online Information.

Traditional morphometrics. We used traditional morphometrics, based on nine linear measurements of the upper dentition (UD) and seven linear measurements of the dentary and lower dentition (= lower jaw; LJ) to compare MAPBAR-5150 with available specimens of the hathliacynids *Cladosictis patagonica* (N= 10 UD; N= 6 LJ), *Sipalocyon gracilis* (N= 4), *Sipalocyon obusta* (N= 1 LJ), in addition to one undetermined specimen of *Sipalocyon* sp. (UD) which contributes characterizing the morphospace of the genus, and the

borhyaenoid *Prothylacynus patagonicus* (N= 3). The living didelphids include *Didelphis albiventris* (N= 17) and *Lutreolina crassicaudata* (N= 20) (Tabs. S1 and S2). We could not include specimen MAPBAR-7798 in the analyses, which we tentatively refer to *C. patagonica*, because many measurements could not be taken due to its fragmentary condition. In order to mitigate errors caused by taphonomic deformation and reduce the amount of missing information, we standardized the fossil data using mean measurements (Tabs. S1, S2).

We performed a Principal Component Analysis (PCA) on the variance-covariance matrix, using common logarithm transformed measurements (Legendre & Legendre, 1998). To correct the data for the effect of size, we used geometric means (see Meachen-Samuels & Van Valkenburg, 2009).

The morphological disparity of *Cladosictis patagonica* compared to other species was evaluated using the trace of variance-covariance matrix, as in Echarri and Prevosti (2015) with the effect of size included (see Prevosti *et al.*, 2012b; Echarri & Prevosti, 2015). In a second analysis, we excluded *Prothylacynus patagonicus* because available specimens (three) are few to explore species variability.

SYSTEMATIC PALEONTOLOGY

Subclass METATHERIA Huxley, 1880

Order SPARASSODONTA Ameghino, 1894

Family HATHLIACYNIDAE Ameghino, 1894

Genus *Cladosictis* Ameghino, 1887

Type species. *Cladosictis patagonica* Ameghino, 1887.

Temporal and geographical distribution. Early to middle Miocene (Colhuehuapian, Santacrucian, Friasian, Colloncuran), Argentina and Chile.

Diagnosis. See Marshall (1981).

Cladosictis patagonica Ameghino, 1887

Figure 1, Tables S1–S2

Referred specimen. MAPBAR-5150, partial cranium with dentition (Figs. S2–S4).

Tentatively referred specimen. MAPBAR-7798, fragment of right maxilla with M2–M3 (Fig. S5).

Geographic and stratigraphic provenance. MAPBAR-5150 is from the vicinity of Puesto Familia González; MAPBAR-7798 is from the vicinity of Puesto La Alemana, Estancia Paso Limay, Pilcaniyeu Department, Río Negro province, Patagonia, Argentina. Collón Cura Formation, middle Miocene (Langhian), Colloncuran age (Supplementary Online Information).

Description. See Supplementary Online Information.

Comparisons and taxonomic considerations. MAPBAR-5150 and MAPBAR-7798 are medium sized hathliacynids within the range of other specimens assigned to *Cladosictis patagonica* (Santacrucian and Friasian ages) (Tabs. S1 and S2; see also Marshall, 1981). *Cladosictis centralis* Ameghino, 1902 (Colhuehuapian age) is slightly smaller than *C. patagonica* (Marshall, 1981; Goin *et al.*, 2007), and both species are smaller than the phylogenetically close *Acyon* Ameghino, 1887 (Forasiepi *et al.*, 2006; Engelman *et al.*, 2015). Other known early to middle Miocene hathliacynids, *i.e.*, *Perathereutes pungens* Ameghino, 1891, *Pseudonotictis pusillus* (Ameghino, 1891) and *P. chubutensis* Martin & Tejedor, 2007, *Sipalocyon gracilis* Ameghino, 1887 and *S. obusta* (Ameghino, 1891) are noticeably smaller in size (Marshall, 1981; Martin & Tejedor, 2007). In common with *Cladosictis* spp. and *Acyon* spp., MAPBAR-5150 has a narrow postorbital constriction, prominent postorbital processes, and maximum skull width at the level of the postorbital process equivalent to the maximum width of the cranial vault at the level of the squamosal (differing from *Sipalocyon* spp. in which the cranial vault is wider; Forasiepi, 2009). MAPBAR-5150 is similar to other hathliacynids in having flaring cheeks behind the infraorbital foramen (as seen in ventral view), while this area of the maxilla is flat in *Acyon myctoderos* Forasiepi, Sánchez-Villagra, Goin, Takai, Shigehara, & Kay, 2006 (condition unknown in the other species of the genus; Forasiepi *et al.*, 2006; Engelman *et al.*, 2015). Cranial features of MAPBAR-5150 permit assignment of this specimen to *Cladosictis*.

The upper molars of MAPBAR-5150 and MAPBAR-7798 exhibit a narrow styler shelf on M3, as in *C. patagonica*. In *Acyon myctoderos*, the styler shelf is broader on M3 (Forasiepi *et al.*, 2006; Engelman *et al.*, 2015). Morphological details of M2–M3 are more evident on MAPBAR-7798 because the wear stage of MAPBAR-5150 is very advanced and some elements are broken. The protocone is narrow, with a shallow

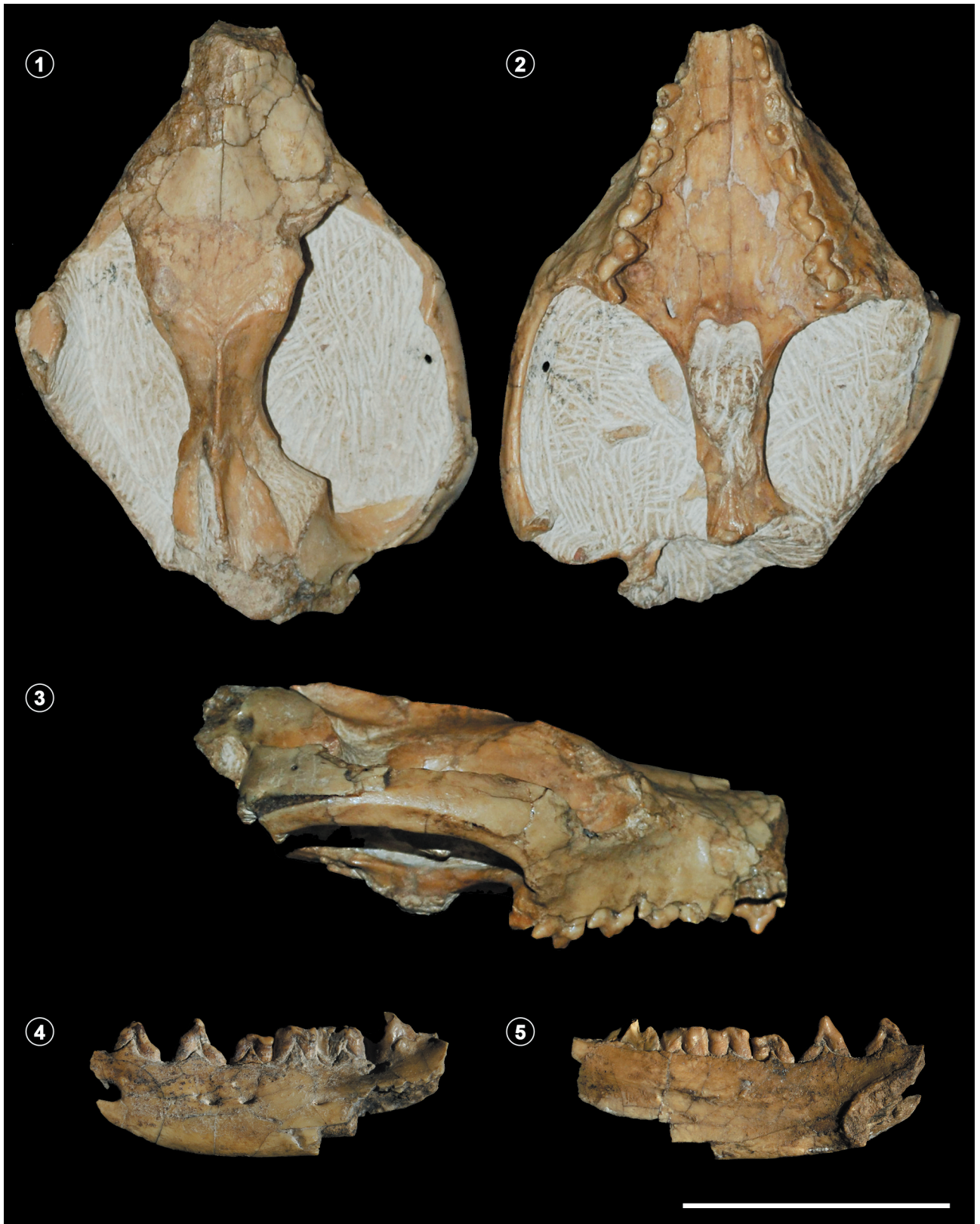


Figure 1. 1–5, *Cladosictis patagonica*, MAPBAR-5150; 1, in dorsal; 2, ventral; 3, lateral; 4, left dentary in lateral; 5, medial view. Scale bar equals 50 mm.

basin as seen in *C. patagonica* (e.g., holotype MLP 11-103), and differing from *Acyon myctoderos*, *Sipalocyon* spp. (Marshall, 1981; Forasiepi *et al.*, 2006; Engelman *et al.*, 2015), and the congeneric species *C. centralis* (Goin *et al.*, 2007) which have broader and distinctly basined protocones. The M4 preserved of MAPBAR-5150 is double rooted and labiolingually narrow, similar to *Cladosictis* spp. and *Acyon myctoderos*, and differing from *Sipalocyon gracilis* which has three roots and wider M4.

Comparing with *C. patagonica*, the Colhuehuapian *C. centralis* is (1) slightly smaller in size and with more generalized molars, depicted by (2) upper molars with better developed protocones, and (3) m4 with distinctly basined talonids (Marshall, 1981; Goin *et al.*, 2007). In the first two features, MAPBAR-5150 and MAPBAR-7798 are similar morphologically to the Santacrucian *C. patagonica*. Unfortunately, because of the condition of the m4 in MAPBAR-5150, we could not evaluate the diagnostic feature in the lower molar. Regarding MAPBAR-7798, the size and morphology of its M2-M3 are congruent with those of *C. patagonica*, to which we tentatively refer it in the absence of other cranial features that might support this determination.

QUANTITATIVE ANALYSIS

The PCAs of the upper dentition (Fig. 2.1, 2.2) and lower jaw (Fig. 2.3, 2.4) were performed excluding (Fig. 2.1, 2.3) and including (Fig. 2.2, 2.4) the effect of size. We present PC 1 and PC 2 because these two components explain more than 80% of the total variation in all analyses (Tab. S3). Although other axes group the species in a similar manner as the first two components, the groupings overlap. The contribution of each variable to the different axes is detailed in Table S3.

The PCA of upper dentition measurements, excluding the effect of size (Fig. 2.1), shows a “logical” separation among groups corresponding to different species in our sample pool. The marsupial *Didelphis albiventris* and *Lutreolina crassicaudata* separate clearly from other taxa on PC 1, and both species separate from each other on PC 2. A less obvious but still evident separation occurs among sparassodont species, with *Sipalocyon* placing in more positive areas of PC 2, while *Cladosictis* and *Prothylacynus* cluster in the remaining area of PC 2, but are separated in PC 1. When size is included in the analysis (Fig. 2.2), the re-

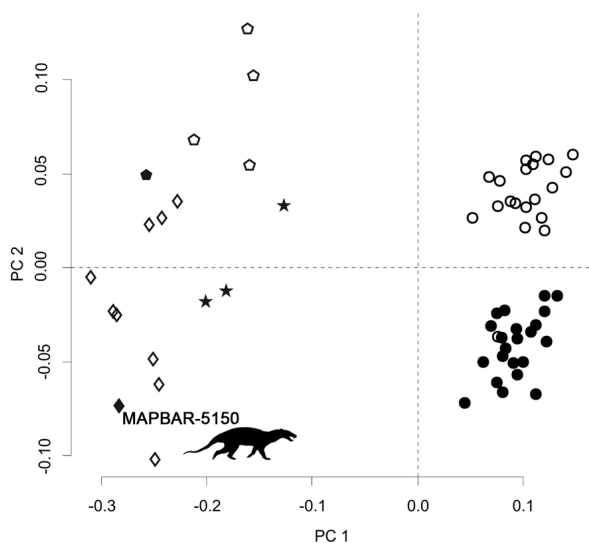
sulting topology is similar but with a much more restricted dispersion of individuals within the morphospace and a better separation between most taxa. This is more evident in the representatives of Sparassodonta. *Prothylacynus patagonicus* (the largest taxon in our sample) clearly separates from specimens of *Cladosictis* and *Sipalocyon* in PC 2. The two genera of hathliacynids are less discriminated in PC 1. In both analyses of the upper dentition, MAPBAR-5150 lies within the morphospace of the Santacrucian specimens of *Cladosictis patagonica*.

The separation between these groups is less evident in the PCA of the lower jaw, excluding or including the effect of size (Fig. 2.3, 2.4). However, the pattern of dispersion in the morphospace of each species is roughly similar, especially in the PCA including size. The position of MAPBAR-5150 in both PCAs of the lower jaw varies in relation to other species: when size is included, this specimen is situated among the Santacrucian specimens of *Cladosictis patagonica*, but when size is excluded, it lies closer to *Sipalocyon gracilis* than to *Cladosictis patagonica*. In the latter analysis (Fig. 2.3), specimens of the living marsupials *L. crassicaudata* and *D. albiventris* largely overlap in the morphospace. Some specimens are closer to the other living species than the one to which they actually belong. Also, the sparassodont *P. patagonicus* lies in the same area of the morphospace as specimens of *D. albiventris*.

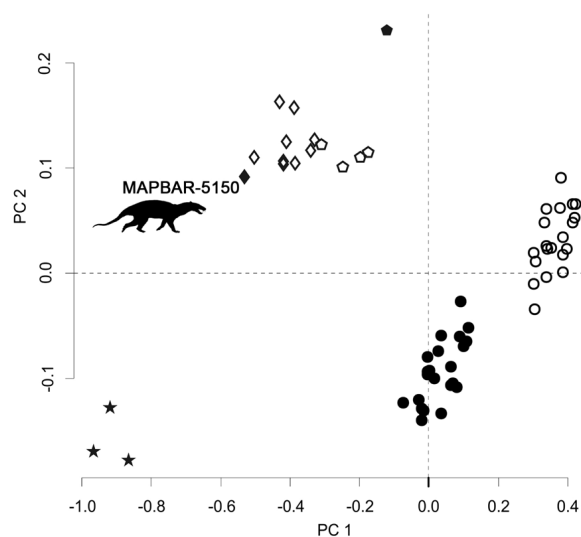
Variability. When size is included in the PCA of the upper dentition, the morphospace dispersion of our sampled specimens of *Cladosictis patagonica* is fairly similar to that of the living marsupials *Didelphis albiventris* and *Lutreolina crassicaudata* (Fig. 2.2). For the other sparassodonts, the number of sampled individuals is few, which means that drawing conclusions on the basis of our sample is more uncertain. In the case of the PCA of the lower jaw with size considered (Fig. 2.4), morphospace dispersion of *C. patagonica* is similar to that of *L. crassicaudata* but more restricted than that of *D. albiventris*, likely because our sampled data is more variable for the latter species (CV values for several measurements are higher; Tab. S2). Both PCAs seem to indicate that the variability of *Cladosictis patagonica* is fairly similar to that of the extant species.

In comparing between-species variability using the trace of the variance-covariance matrix, as in Echarri & Prevosti (2015), we found that the upper dentition of *Cladosictis*

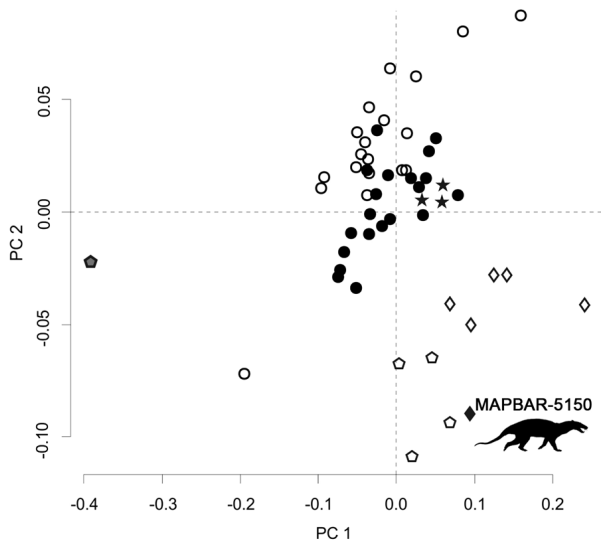
1 PCA upper dentition without size



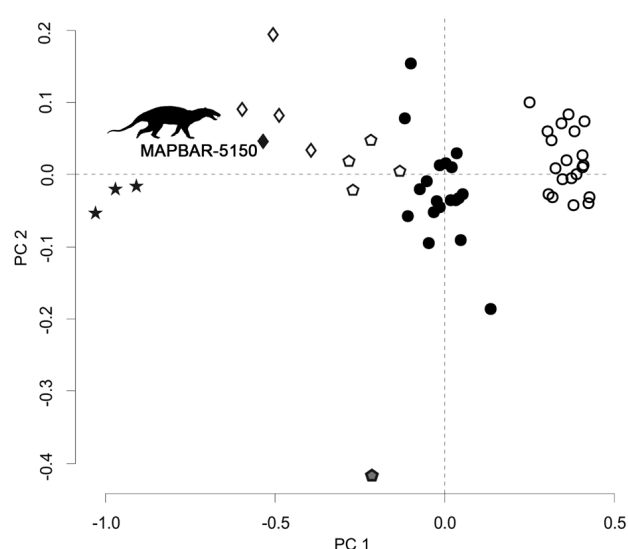
2 PCA upper dentition with size included



3 PCA dentary and lower dentition without size



4 PCA dentary and lower dentition with size included



SPARASSODONTA

◇ *Cladosictis patagonica*

◆ *C. patagonica* (MAPBAR-5150)

★ *Prothylacynus patagonicus*

○ *Sivalocyon gracilis*

◆ *Sivalocyon* sp.

◐ *Sivalocyon obusta*

DIDELPHIMORPHIA

○ *Lutreolina crassicaudata*

● *Didelphis albiventris*

Figure 2. 1–4, Analysis of principal components (PCA) for 1–2, the upper dentition and 3–4, the lower jaw; 1, 3, excluding or 3, 4 including the effect of size.

patagonica varies significantly more than that of *D. albiventris* (significant difference at 10%) or *L. crassicaudata* (5%) (Tab. 1). In the case of the lower jaw, variability of *Cladosictis patagonica* is not significant compared with other species;

significant differences were detected between *D. albiventris* and *L. crassicaudata* only at the 10% level (Tab. 1). Other comparisons of variability yielded no additional significant differences among the species analyzed.

TABLE 1. Results in comparing between-species variability.

	P value	
	Upper dentition	Dentary and lower dentition
<i>C. patagonica</i> vs. <i>D. albiventris</i>	0.0754 *	0.4466
<i>C. patagonica</i> vs. <i>L. crassicaudata</i>	0.0302 **	0.1490
<i>C. patagonica</i> vs. <i>S. gracilis</i>	0.3037	0.2821
<i>D. albiventris</i> vs. <i>L. crassicaudata</i>	0.8030	0.0972 *

* significant differences at 10%; **, significant differences at 5%.

DISCUSSION AND CONCLUSION

Cladosictis patagonica is the most abundant sparassodont collected within the Santa Cruz Formation, Santacrucian age (e.g., Marshall, 1981; Prevosti *et al.*, 2012a). This species is also present in the mammal assemblages from the Río Frías Formation, Friasian (Marshall, 1990) and the CCF, Colloncuran (this contribution). A likely temporal overlap between these faunal associations has been suggested in the past in view of their taxonomic resemblance (e.g., Vucetich *et al.*, 1993; Madden *et al.*, 1997; Kramarz *et al.*, 2019). The taxonomic interpretation we present here (MAPBAR-5150 and MAPBAR-7798, assigned and tentatively referred to *Cladosictis patagonica*, respectively) adds another shared faunal element.

The CCF includes distinct mammal assemblages from the early middle Miocene (Colloncuran; Langhian) and younger (Mayoan; Serravallian) ages (Bucher *et al.*, 2021). Considering the geological and biochronological context recently proposed for outcrops of the CCF (Bucher *et al.*, 2021), sparassodonts from the CCF from higher latitudes (*Pseudonotictis chubutensis* from Cerro Zeballos in northern Chubut and *Patagosmilus goini* from Río Chico in southern Río Negro; Martin & Tejedor, 2007; Forasiepi & Carlini, 2010) may likely belong to younger associations than the specimens of *Cladosictis patagonica* considered here. In fact, the thylacosmilid *Patagosmilus goini* has been recently recognized at the Quebrada Honda fossil site, Serravallian in age, Bolivia (Suarez, 2019).

Morphological comparisons among specimens of *Cladosictis patagonica* suggest that there is a notable degree of variability within the species. This is reflected in certain morphological features, such as different relative

development of cranial crests, small differences in suture outlines (e.g., nasofrontal and palatomaxillary sutures), depth of mandible, presence and length of diastemata (with dentition more crowded in some specimens than others), small differences in the architecture of some teeth (mostly on M4/m4), and size (Prevosti *et al.*, 2012a, 2012b; see also Supplementary Online Information). This is important because variability has previously been largely ignored, resulting in a plethora of names for the same entity, as Marshall (1981) originally noted.

The quantitative features analyzed here (measurements from the upper dentition and lower jaw) show that the dispersion of the specimens of *Cladosictis patagonica* (including Santacrucian and Colloncuran material) in morphospace is comparable to what we see for the living marsupials *Didelphis albiventris* and *Lutreolina crassicaudata*. Size may be a valuable character for distinguishing species from one another, but only after within-species variability is controlled for (as also discussed for living marsupials of different orders by Martin, 2005, 2013, 2018).

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