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PALEONEUROLOGIA DE *ANTIFER* (MAMMALIA: CERVIDAE), UM CERVÍDEO EXTINTO DA AMÉRICA DO SUL

Santa Maria, RS

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Emmanuelle Fontoura Machado

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Dissertação apresentada ao Curso de Mestrado do Programa de Pós-Graduação em Biodiversidade Animal, Área de Concentração em Sistemática e Biologia Evolutiva, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para obtenção do título de **Mestre em Biodiversidade Animal.**

Orientador: Prof. Dr. Leonardo Kerber

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Emmanuelle Fontoura Machado

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Santa Maria, RS
2021

DEDICATÓRIA

À ciência, que vem atualmente sendo descredibilizada, sofrendo ininterruptos cortes, contingenciamentos e redirecionamentos orçamentários; *à população brasileira* que fomenta a Universidade Pública; *à todas as mulheres cientistas* que foram silenciadas, subestimadas, impossibilitadas de acessarem o Ensino Superior, que receberam salários desiguais, que sofreram abusos das mais diversas formas.

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À minha família, ao meu namorado e aos meus amigos que me acompanharam nessa jornada: infelizmente, a pandemia do COVID-19 afastou muitos de vocês do meu cotidiano, porém, vocês conseguiram se fazer presentes e contribuíram muito para a realização desse projeto pessoal. Meu muito obrigada;

Aos coautores do estudo e trabalhos que compõem a dissertação, obrigada pela dedicação e pelas suas contribuições;

Aos colegas de laboratório, por todo apoio, conversas, risadas, discussões e aprendizados. Em especial, ao Prof. Dr. Flávio Pretto, ao Dr. Rodrigo Müller, ao Ms. José Darival Ferreira e a Dra. Jamile Bubadué, pelos conselhos, sugestões e trocas de experiências;

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Às Instituições de Ensino Público, que fizeram parte da minha trajetória e são essenciais para este país. Em 2017, registrou-se aproximadamente 35% da população como ingressantes nas Instituições de Ensino Superior, em um país que aponta atualmente mais de 210 milhões de habitantes segundo o Instituto Brasileiro de Geografia e Estatística. A desigualdade social é evidente, e reconheço meu privilégio em ocupar uma vaga dentro desta Universidade;

Ao Conselho Nacional de Desenvolvimento Científico pela bolsa de estudo (CNPq 130605/2019-0) e pelo financiamento para o desenvolvimento do projeto (CNPq 422568/2018-0). Muito obrigada.

Por fim, essa pesquisa só foi possível de executar-se devido à Universidade Federal de Santa Maria, ao Programa de Pós-Graduação em Biodiversidade Animal e ao Centro de Apoio à Pesquisa Paleontológica, agradeço pela infraestrutura disponibilizada e pela oportunidade.

“You cannot get through a single day without having an impact on the world around you. What you do makes a difference, and you have to decide what kind of difference you want to make.”

“Você não pode passar um único dia sem ter um impacto no mundo ao seu redor. O que você faz, faz a diferença, e você tem que decidir que tipo de diferença você quer fazer.”

Jane Goodall

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RESUMO

PALEONEUROLOGIA DE *ANTIFER* (MAMMALIA: CERVIDAE), UM CERVÍDEO EXTINTO DA AMÉRICA DO SUL

AUTORA: EMMANUELLE FONTOURA MACHADO

ORIENTADOR: LEONARDO KERBER

Os Cetartiodactyla terrestres surgiram na América do Norte e Europa durante o Eoceno inicial e irradiaram-se, dando origem, dentre outros, aos Ruminantia – onde está incluído o grupo Cervidae. O clado Cervidae atualmente divide-se em Cervinae, cervídeos europeus e asiáticos, e Capreolinae, os cervídeos americanos. A formação do Istmo do Panamá (Plioceno final) possibilitou a troca biótica entre os continentes da América do Norte e Central, e a América do Sul, onde os cervídeos capreolíneos Odocoileini irradiaram-se rapidamente após seu ingresso no continente. A paleoneurologia é um ramo da paleontologia que se dedica ao estudo da evolução neurológica através do tempo. Utilizando técnicas de tomografia computadorizada, é possível acessar a morfologia endocraniana de espécies extintas. Na presente dissertação, estudamos moldes endocranianos do encéfalo do cervídeo extinto *Antifer ensenadensis* (Pleistoceno final), uma das maiores formas que viveram neste continente. Para isso, espécimes provenientes da Formação Touro Passo (Pleistoceno Superior), oeste do Rio Grande do Sul, foram tomografados e modelos virtuais da cavidade endocraniana foram gerados. Como metodologia, foi utilizada morfologia comparada com outros cervídeos, morfometria geométrica e coeficiente de encefalização. Os moldes endocranianos analisados demonstram que *A. ensenadensis* possuiu um cérebro girencefálico, possuindo o seio sagital superior saliente na superfície do molde endocraniano, além de ser anteroposteriormente alongado e com formato romboide. A análise de morfometria geométrica sugeriu uma tendência alométrica linear entre o tamanho e a forma do molde endocraniano cerebral e destaca *A. ensenadensis* como uma forma extrema dentro dos cervídeos analisados, em relação à morfologia cerebral. O coeficiente de encefalização de *Antifer ensenadensis* (0.68, Jerison, 1973; 0.63, Eisenberg, 1981) está dentro da variação dos cervídeos atuais (0.64 – 1, Jerison, 1973; 0.60 – 1.06, Eisenberg, 1981) – sugerindo que o padrão de encefalização das formas sul-americanas já estava estabelecido pelo menos desde o final do Pleistoceno.

Palavras chaves: alometria, molde endocraniano, endocrânio, Pleistoceno final, Odocoileini

ABSTRACT

VIRTUAL BRAIN ENDOCAST OF *ANTIFER* (MAMMALIA: CERVIDAE), AN EXTINCT LARGE CERVID FROM SOUTH AMERICA

AUTHOR: EMMANUELLE FONTOURA MACHADO

ADVISOR: LEONARDO KERBER

Terrestrial Cetartiodactyla arose in North America and Europe during the early Eocene and diversified, giving rise, among others, to the clade Ruminantia, which includes Cervidae. Cervidae is divided into Cervinae, European and Asian deer, and Capreolinae, the American deer. The formation of the Isthmus of Panama (late Pliocene) enabled the biotic interchange between the continents of North and Central Americas, and South America (Great American Biotic Interchange), where the Cervidae radiated quickly after their arrival. Paleoneurology is a branch of paleontology that is dedicated to the study of neurological evolution through time. Using computed tomography techniques, it is possible to access the endocranial morphology of extinct species. Here, we studied the brain endocast of the extinct late Pleistocene cervid *Antifer ensenadensis* from southern Brazil, one of the largest forms that lived on this continent. Comparative morphology, geometric morphometrics, and encephalization quotients were employed to compare this extinct species with other American and Eurasian forms. For this purpose, specimens from the Touro Passo Formation (Upper Pleistocene), southern Brazil, were scanned, and virtual models of the endocranial cavity were generated. The analyzed endocasts demonstrate that *A. ensenadensis* had a gyrencephalic brain, showing a prominent longitudinal sinus (=sagittal superior sinus), which is also observed in the large South American cervid *Blastocerus dichotomus*. Also, the endocast is anteroposteriorly elongated and rhomboid in shape. The geometric morphometric analysis suggested a clear and linear allometric trend between brain endocast size and shape and highlights *A. ensenadensis* as an extreme form within the analyzed cervids regarding brain morphology. The encephalization coefficient of *A. ensenadensis* (0.68, Jerison, 1973; 0.63, Eisenberg, 1981) is within the range of extant cervids (0.64 - 1, Jerison, 1973; 0.60 - 1.06, Eisenberg, 1981) - suggesting that the pattern of encephalization of South American forms was already established at least since the end of the Pleistocene.

Keywords: allometry, endocast, endocranium, late Pleistocene, Odocoileini

APRESENTAÇÃO DA ESTRUTURA DA DISSERTAÇÃO

A dissertação a seguir se encontra estruturada segundo as normas do Manual de Dissertações e Teses (MDT) da Universidade Federal de Santa Maria e possui os requisitos necessários para obtenção do título de Mestre em Ciências Biológicas – área Biodiversidade Animal, pelo Programa de Pós-Graduação em Biodiversidade Animal da Universidade Federal de Santa Maria.

O primeiro capítulo (**Capítulo 1**) apresenta uma introdução ao tema, contextualizando-o e trazendo os objetivos da presente dissertação.

O segundo capítulo (**Capítulo 2**) é composto pelos artigos científicos que foram produzidos a partir deste estudo. O Artigo 1 (**Capítulo 2.1**) intitula-se "*Virtual brain endocast of Antifer (Mammalia: Cervidae), na extint large cervid from South America*", sendo este o corpo principal desta dissertação. Este trabalho traz uma análise comparativa do encéfalo de *Antifer ensenadensis*, um grande cervídeo extinto do Pleistoceno da América do Sul, e espécimes atuais sul-americanos e euroasiáticos – utilizando morfologia, morfometria geométrica e coeficiente de encefalização. Este trabalho encontra-se publicado no periódico *Journal of Morphology* (Qualis B2 em Biodiversidade). Adicionalmente, o **Capítulo 2.2,** contém uma publicação dos modelos tridimensionais gerados no artigo do capítulo 2.1.

Os materiais e métodos utilizados neste estudo estão presentes no corpo do artigo científico e, por questões de brevidade, não serão descritos neste manuscrito.

O último capítulo (**Capítulo 3**) apresenta as considerações finais, relacionando os objetivos com os resultados obtidos, e as referências bibliográficas referentes ao primeiro e terceiro capítulos.

CAPÍTULO 1 – *ASPECTOS INTRODUTÓRIOS*

1.1 INTRODUÇÃO

1.1.1 Os Cetartiodactyla terrestres e os Cervidae

O clado Cetartiodactyla inclui mamíferos eutérios terrestres e semiaquáticos – camelídeos, suídeos, hipopotamídeos (além de outros grupos extintos), e aquáticos – cetáceos. A sua origem e suas relações filogenéticas têm sido discutidas por diversos autores (GRAUR e HIGGINS, 1994; LUCKETT e HONG, 1998; THEODOR e FOSS, 2005; AGNARSSON e MAY-COLLADO, 2008; SPAULDING et al., 2009; ZHOU et al., 2011; HASSANIN et al., 2012; ZURANO et al., 2018; RODRIGUES et al., 2020). Os táxons terrestres incluem formas morfologicamente e taxonomicamente diversas, caracterizadas pela presença de dígitos pares recobertos por cascos, condição paraxônica dos membros, presença de astrágalo com “dupla tróclea” e pelo quarto pré-molar decíduo possuir seis cúspides (PAULA-COUTO, 1979; EISENBERG e REDFORD, 1999; THEODOR et al., 2005; CASSINI et al., 2016).

Cetartiodáctilos terrestres surgiram na América do Norte e Europa durante o Eoceno inicial, irradiaram-se, e deram origem a três clados: os Suiformes JAECKEL, 1911, os Tylopoda ILLIGER, 1811 e os Ruminantia SCOPOLI, 1777 – onde está incluso o grupo Cervidae, que são encontrados em todos os continentes, com exceção da Antártida (HASSANIN et al., 2012). Do Oligoceno a metade do Plioceno, o clima, a vegetação e a geografia global sofreram mudanças significativas, dando a oportunidade para estes grupos irradiarem e se diversificarem, principalmente a partir do surgimento de novas rotas migratórias na Europa, Ásia e África (HERNÁNDEZ-FERNÁNDEZ e VRBA, 2005; HECKEBERG, 2020). A Ásia e a África, ao final do Mioceno, apresentavam o clima mais árido e frio, ocasionando a troca de vegetação: das florestas para campos de pastagem abertos. Sucessivamente, a vegetação dominante passa a ser composta por gramíneas C3 e, logo após, pelas C4. Tais condições favoreceram a origem, dispersão e diversificação de cervídeos e outros ruminantes, fato que tem sido apontado como um fator de extrema importância para a evolução desses animais (GILBERT et al., 2006; HECKEBERG, 2020).

Ao final do Plioceno, houve a formação do Istmo do Panamá (2.5 ma; O’DEA et al., 2016), o que permitiu uma troca biótica entre os continentes da América do Norte e Central, e a América do Sul. Esse evento biogeográfico é conhecido como Grande Intercâmbio Biótico Americano (MARSHALL et al., 1984; EISENBERG e

REDFORD, 1999; TONNI e PASQUALI, 1999; WILSON e MITTERMEIER, 2011; O'DEA et al., 2016; Figura 1), e foi através dele que houve o ingresso de cetertiodáctilos terrestres (*i.e.* Tayassuidae, Camelidae e Cervidae) em nosso continente.

Figura 1. Representação do Grande Intercâmbio Biótico Americano. Acima, estão os cervídeos que ingressaram à América do Sul e abaixo, os mamíferos que habitavam a América do Sul, como marsupiais, xernartros e ungulados nativos (entre outras linhagens).

Dentre os Cetartiodactyla terrestres, o clado Cervidae é o mais diversificado (GROVES, 2007; Figura 2). Esses ruminantes são caracterizados pela presença dos dígitos III e IV como principais eixos de sustentação dos membros, e redução dos dígitos II e V, presença de dentição selenodonte, ausência de incisivos superiores, crânio apresentando dois forames lacrimais, uma fossa lacrimal, uma vacuidade pré-orbital e apresentado de galhadas, sua característica mais emblemática (REIS et al., 2011; HECKEBERG, 2020; Figura 3).

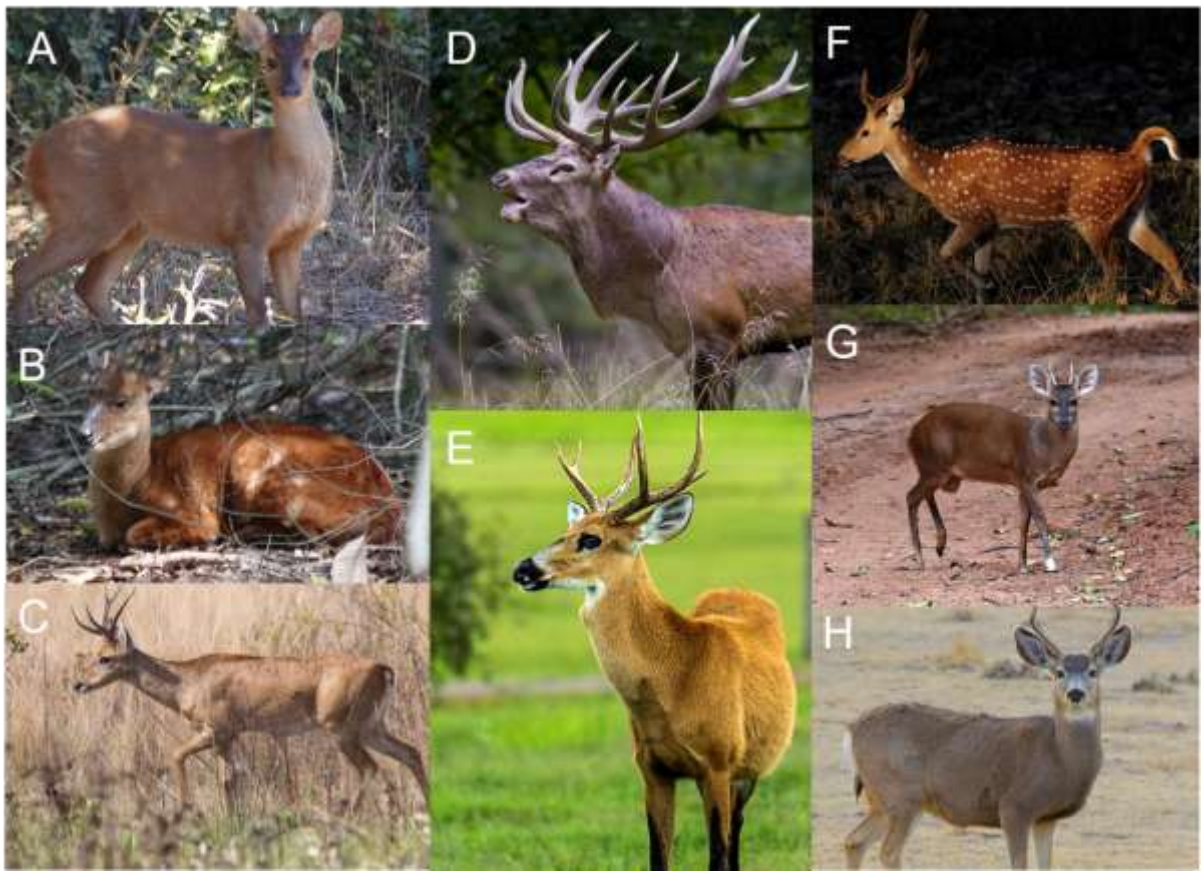

Figura 2. Diversidade de Cervidae. **A.** *Mazama americana* (Autor: Bernard Dupont: https://commons.wikimedia.org/wiki/File:Red_Brocket_(Mazama_americana)_male_(28091090800).jpg); **B.** *Mazama nana* (Autor: Luiz Carlos Marques Rocha: https://commons.wikimedia.org/wiki/File:Mazama_nana_2.jpg); **C.** *Ozotoceros bezoarticus* (Autor: Fabio Rage: https://commons.wikimedia.org/wiki/File:O._bezoarticus_buck.jpg); **D.** *Cervus elaphus* (Autor: Bill Ebbesen: https://commons.wikimedia.org/wiki/File:Red_deer_stag_2009_denmark.jpg); **E.** *Blastocerus dichotomus* (Autor: Jonathan Wilkins: commons.wikimedia.org/wiki/File:Cervo_do_pantano.jpg); **F.** *Axis axis* (Autor: Yathin S Krishnappa: https://commons.wikimedia.org/wiki/File:2010-kabini-chital-portrait.jpg); **G.** *Mazama gouazoubira* (Autor: Miguel Rangel Jr.: https://commons.wikimedia.org/wiki/File:Brocket_deer_Mazama_gouazoubira_Santa_fe_do_Sul_1.jpg); **H.** *Odocoileus hemionus* (Autor: Yathin S Krishnappa: https://commons.wikimedia.org/wiki/File:2012-mule-deer-male.jpg);

Uma das primeiras classificações de Cervidae foi feita por naturalista anglo-irlandês Victor Brooke em 1878, a partir de caracteres morfológicos, em que dividiam o clado em Plesiometacarpi – cervídeos europeus e asiáticos (“Velho Mundo”), que incluem os elementos mais proximais dos metacarpais II e V; e Telemetacarpi –

cervídeos americanos (“Novo Mundo”), onde são incluídos aqueles que possuem apenas o elemento mais distal dos metacarpais II e V (BROOKE, 1878; GOSS, 1983; HECKEBERG, 2020; Figura 3).

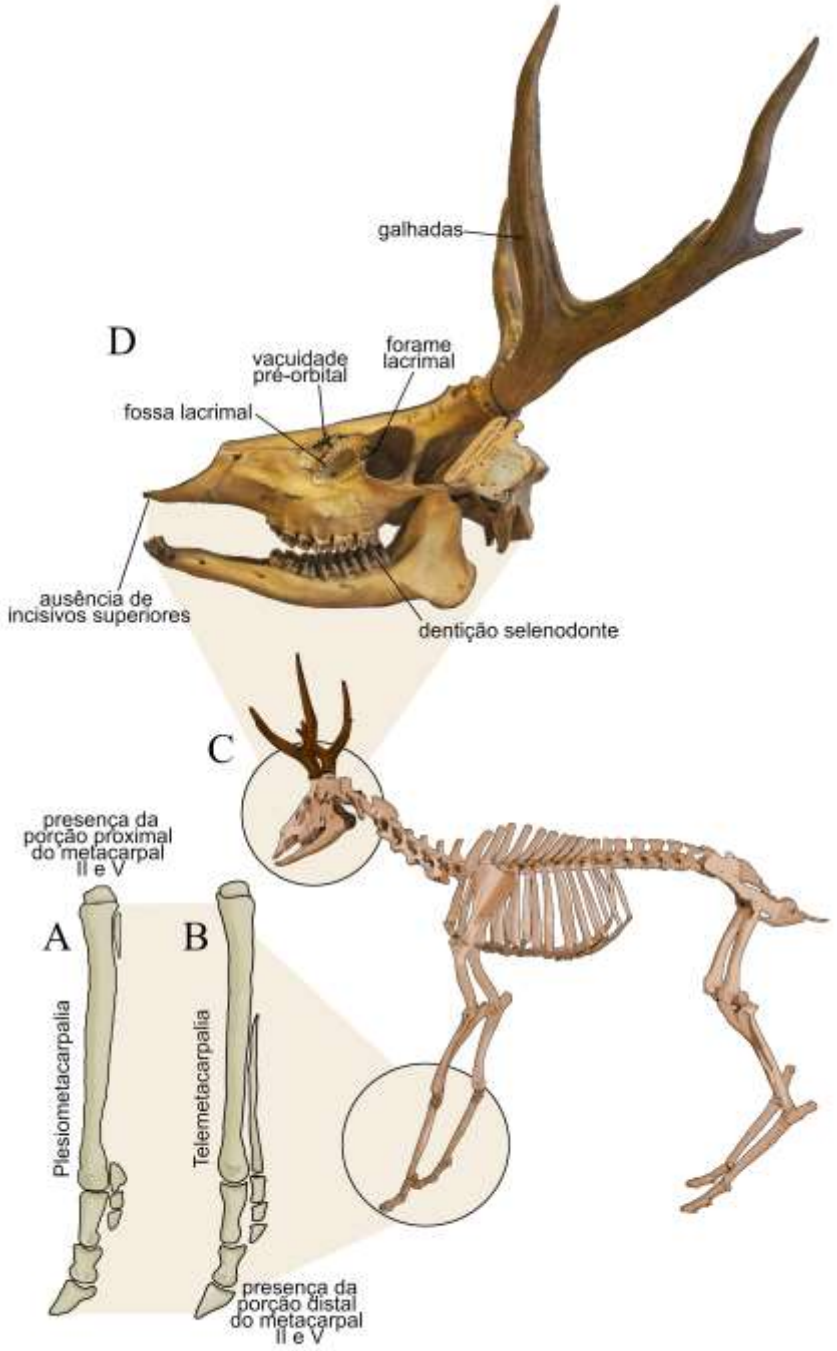

Figura 3. Principais características osteológicas de Cervidae. **A**. Membro anterior de Plesiometarcapalia; **B**. Membro anterior de Telemetarcapalia; **C**. Esqueleto do Cervo-do-Pantanal (*Blastocerus dichotomus*); **D**. Crânio de *B. dichotomus* apresentando algumas das características anatômicas do clado.

Brooke ainda indicou a existência de uma correlação entre a presença da condição morfológica Telemetacarpalia e a presença de uma divisão completa da cavidade nasal pelo vômer (BROOKE, 1878; CROITOR, 2018). Entretanto, de acordo com GROVES e GRUBB (1987), tais grupos, como definidos por Brooke, não representam linhagens monofiléticas. Logo, Plesiometacarpi e Telemetacarpi não são válidos de acordo com as normas do Código Internacional de Nomenclatura Zoológica (ICZN; GILBERT et al., 2006; CROITOR, 2018). Atualmente, aceita-se que o clado Cervidae divide-se em Cervinae, cervídeos europeus e asiáticos, e Capreolinae, os cervídeos americanos, de maneira similar a divisão entre Pleisiometacarpi e Telemetacarpi, entretanto definidos como clados monofiléticos (GILBERT et al., 2006; CROITOR, 2018; HECKEBERG, 2020; Figura 3). O primeiro possui dois clados menos inclusivos (Cervini e Muntiacini) que contém oito gêneros, e o segundo, mais diverso, inclui quatro clados (Capreolini, Odocoileini, Rangiferini e Alceini) contendo 11 gêneros (HECKEBERG, 2020).

1.1.2 Cervídeos Sul-Americanos e o gênero *Antifer*

Os cervídeos foram os únicos ruminantes a distribuírem-se nos biomas tropicais e subtropicais da América do Sul durante o Grande Intercâmbio Biótico Americano (MARSHALL et al., 1984; EISENBERG e REDFORD, 1999; TONNI e PASQUAL, 1999; GILBERT et al., 2006; WILSON e MITTERMEIER, 2011; O'DEA et al., 2016). Após sua chegada no continente, esses animais sofreram uma irradiação adaptativa, o que pode ser observado a partir da diversidade morfológica das espécies extintas e viventes, bem como da variabilidade de habitats em que eles estão inseridos atualmente (GILBERT et al., 2006). Esse processo se deu principalmente a partir do Pleistoceno Médio, quando o registro fossilífero se torna mais abundante (MENEGÁZ e ORTIZ-JAUREGUEZAR, 1995; ALCARAZ e CARLINI, 2003; OLIVEIRA et al., 2014).

Os cervídeos viventes da América do Sul, pertencentes ao clado Odocoileini (Capreolinae), incluem os gêneros *Mazama* RAFINESQUE, 1817, *Pudu* GRAY, 1852, *Hippocamelus* LEUCKART, 1816, *Blastocerus* ILLIGER, 1815, *Ozotoceros* LINNAEUS, 1758 e *Odocoileus* RAFINESQUE, 1832 (OLIVEIRA et al., 2014; ROTTI et al., 2018; HECKEBERG e WORHEIDE, 2019) (Figura 3). Entretanto, é importante mencionar que pode haver uma diversidade genérica ainda maior, uma vez que

Mazama tem sido reconhecido como polifilético e suas espécies estão posicionadas filogeneticamente em dois clados de Odocoileini – Blastocerina e Odocoileina, o que sugere houveram duas colonizações sul-americanas, sendo a primeira pelo ancestral de Blastocerina (Plioceno inicial – 4.9-3.4 ma) e a segunda pelo ancestral de *Mazama americana* e *Odocoileus virginianus* (Plio-Pleistoceno; HECKEBERG, 2020).

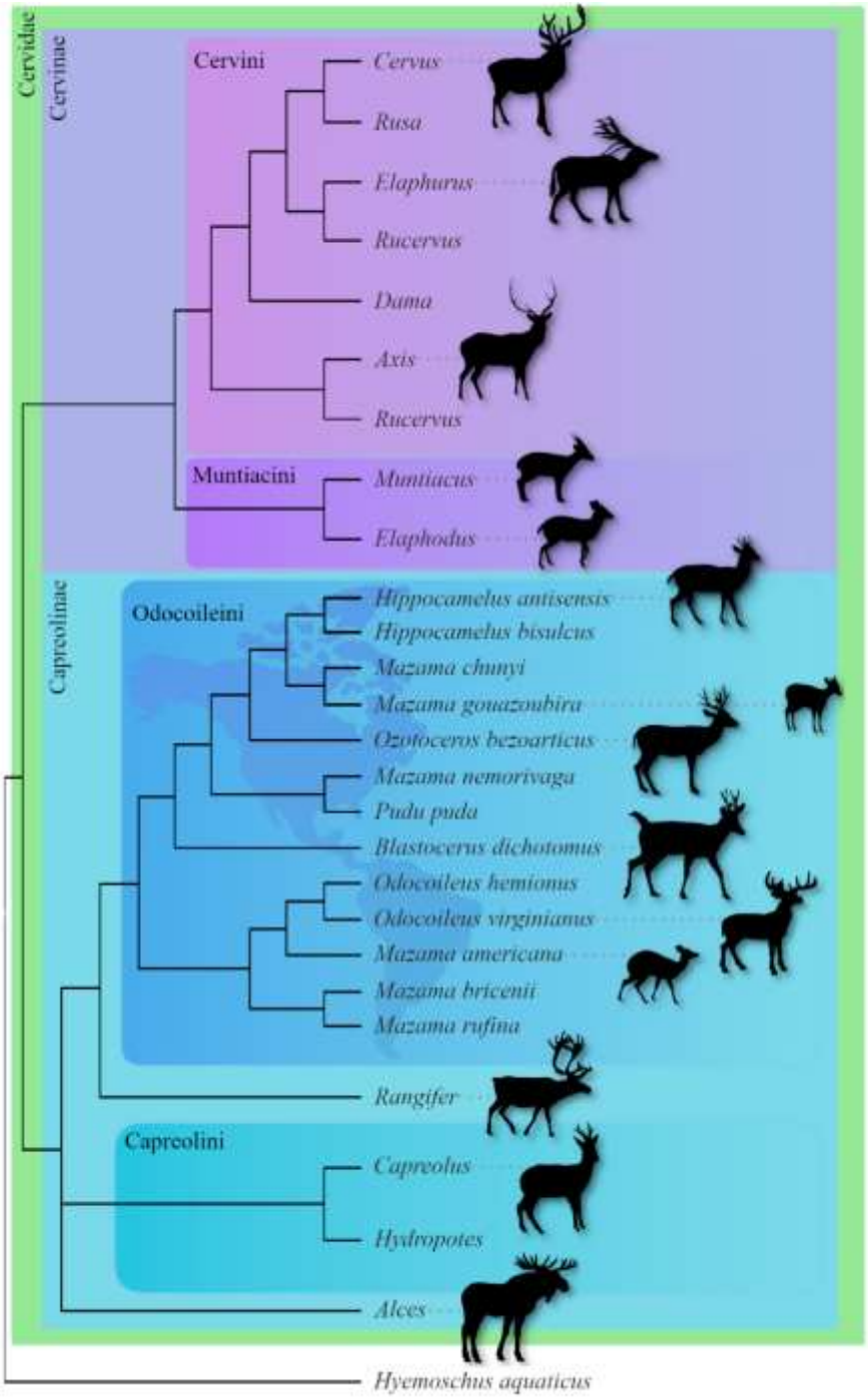

Figura 3. Relações filogenéticas de Cervidae. O clado Odocoileini (de maior interesse aqui) está detalhado em nível de espécie e o restante está em nível de gênero (Modificado de HECKEBERG, 2020; Fig. 12.).

Por sua vez, o registro paleontológico sul-americano inclui diversos táxons extintos, como *Antifer* AMEGHINO, 1889 (1.2 ma), *Charitoceros* HOFFSTETTER, 1963 (1.8 ma), *Morenelaphus* CARETTE, 1922 (0.5 ma), *Epieuryceros* AMEGHINO, 1889 (1.2 ma), *Agalmaceros* HOFFSTETTER, 1952 (1.8-0.8 ma) e *Paraceros* AMEGHINO, 1889 (0.5 – 0.2 ma; OLIVEIRA et al., 2014; ROTTI et al., 2018; HECKEBERG e WORHEIDE, 2019). *Antifer* representa, juntamente com *Epieuryceros*, um dos cervídeos mais antigos do continente (MENEGÁZ e ORTIZ-JAUREGUIZAR, 1995). Esses táxons extintos têm sido incluídos em Odocoileini (MENEGÁZ e ORTIZ-JAUREGUIZAR, 1995). Contudo, cabe-se ressaltar a que as relações filogenéticas dos cervídeos extintos sul-americanos com as formas viventes ainda não foram estudadas utilizando metodologia cladistica.

Antifer é caracterizado por possuir galhadas robustas e largas, com sulcos longitudinais ao longo da superfície e com ramificações dicotômicas e irregulares, alcançando até 90 cm de comprimento (CASTELLANOS, 1945; FORASIEPI et al., 2007; ALCARAZ, 2010). É considerado um cervo de grande porte, assemelhando-se ao Cervo-do-Pantanal (*Blastocerus dichotomus*; FORASIEPI et al., 2007). Três espécies foram incluídas no gênero: *A. ultra* AMEGHINO, 1888 (Pleistoceno Médio e Superior do Uruguai, Argentina, Chile e Brasil; ALCARAZ e ZURITA, 2004; UBILLA et al., 2004; KERBER e OLIVEIRA, 2008; AIRES e LOPES, 2012; PEREIRA et al., 2012; VALLI, 2018), *A. ensenadensis* AMEGHINO, 1888 (Pleistoceno Inferior à Superior da Argentina; ALCARAZ e CARLINI, 2003; ALCARAZ, 2010; VALLI, 2018) e *A. niemeyeri* CASAMIQUELA, 1984 (Pleistoceno Superior do Chile; CASAMIQUELA, 1984). Essa última foi identificada com sinônimo júnior de *A. ultra* por LABARCA e ALCARAZ (2011; VALLI, 2018).

1.1.3 Paleoneurologia e Tomografia Computadorizada

A paleoneurologia é o ramo da paleontologia dedicada ao estudo da evolução neurológica através do tempo. Os tecidos do sistema nervoso não são preservados, pois rapidamente se decompõe após a morte do animal. Portanto, a paleoneurologia não trabalha diretamente com estes tecidos, mas através de impressões/contornos internos que foram deixadas nos ossos (possibilitando a confecção de moldes endocranianos “artificiais”), ou, mais raramente, com a sedimentação que preenche

as cavidades (moldes endocranianos “naturais”). Tais moldes são a simulação mais próxima de como esses elementos do sistema nervoso seriam morfologicamente (HOPSON, 1979). A forma que os moldes endocranianos possuem, refletem, principalmente, a anatomia da dura-máter – camada mais espessa e fibrosa das meninges que envolvem o sistema nervoso (HOPSON, 1979; KONIG et al., 2016).

Os primeiros estudos paleoneurológicos ocorreram ainda no final do século XIX (*e.g*. OWEN, 1875; MARSH, 1884). Entretanto, a paleoneurologia, como área do conhecimento científico ganhou força a partir das primeiras décadas do século XX, com o memorável trabalho realizado paleontóloga Tilly Edinger (1897-1967; Figura 4; vide BUCHHOLTZ e SEYFARTH, 1999). Essa cientista investigou dados neurológicos de forma sistemática e comparativa, diferenciando-se dos estudos realizados até o momento (que eram majoritariamente descritivos), documentando tendências entre representantes de grande e pequeno porte de arcossauros não-avianos, lepidossauros (*e.g.* EDINGER, 1955a), aves (*e.g.* EDINGER, 1951) e principalmente mamíferos (*e.g.* EDINGER, 1933, 1939, 1940, 1942, 1948, 1950, 1955b, 1966a, 1966b). Seus estudos baseados em equídeos se tornaram a base para futuros estudos sobre evolução dos sulcos cerebrais, relações de tamanho encefálico e tamanho corporal, e de mudanças nas estruturas do encéfalo e corporais (EDINGER, 1929; 1948; 1950; BUCHHOLTZ e SEYFARTH, 1999). Por exemplo, Edinger estabeleceu um princípio de não-correlação entre mudanças encefálicas e corporais, a partir da observação da expansão do neocórtex de equídeos durante o Eoceno, antes do aumento corporal típico do clado, que ocorreu a partir do Oligoceno (EDINGER, 1958; BUCHHOLTZ e SEYFARTH, 1999).

Figura 4. Tilly Edinger em Frankfurt, na década de 1920. Retirado de BUCHHOLTZ e SEYFARTH, 1999.

O encéfalo dos vertebrados, principal órgão do sistema nervoso central, possui uma organização uniforme e segmentada, sendo repartido em três regiões bem definidas: o *prosencéfalo* – que se divide em telencéfalo (bulbos olfatórios e córtex) e diencéfalo (onde se localiza o epitálamo, tálamo e hipotálamo), *mesencéfalo* (localizado a região ístima) e *rombencéfalo* – que divide-se em metencéfalo (localiza-se o cerebelo e a ponte) e mielencéfalo (medula oblongata; ROTH e DICKE, 2013; Figura 5). Durante a evolução do encéfalo de grande parte dos mamíferos, é evidenciado que o encéfalo aumenta em tamanho relativo (entretanto, é importante mencionar que existem diversas exceções), com exceção do sistema olfatório, que parece ser mais plástico. Além disso, existem regiões (neocórtex e cerebelo) em que o crescimento ocorre mais rápido em relação às outras partes, resultando em uma alometria (=relação entre tamanho e forma) positiva (ROTH e DICKE, 2013). Nas formas atuais, é observado que o neocórtex ocupa uma grande parte do encéfalo (KAAS, 2013). Por outro, a condição plesiomórfica evidencia a presença de um neocórtex reduzido em relação ao tamanho total do encéfalo, e os bulbos olfatórios e lobo piriforme ocupando maior parte do prosencéfalo. Tais características da evolução do encéfalo, como suas principais divisões e variações de tamanho relativo ao longo

do tempo, podem ser estudadas através do uso de moldes endocranianos (ORLIAC e GILISSEN, 2012). Em suma, é possível analisar características que estão representadas na morfologia externa do encéfalo. Esses estudos possibilitam reconstruções anatômicas em busca por caracteres de relevância filogenética, estudos morfométricos, interpretações sobre a evolução dos sistemas neurossensoriais e cognitivos de animais extintos, entre outros (e.g. ROWE et al., 2011; ROTH e DICKE, 2013; AHRENS, 2014; NAPOLI et al., 2017; PIERCE et al., 2017; BERTRAND et al., 2018; RODRIGUES et al., 2018). Por outro lado, a informação morfológica das regiões internas do encéfalo não é acessível na maioria dos casos para a paleoneurologia.

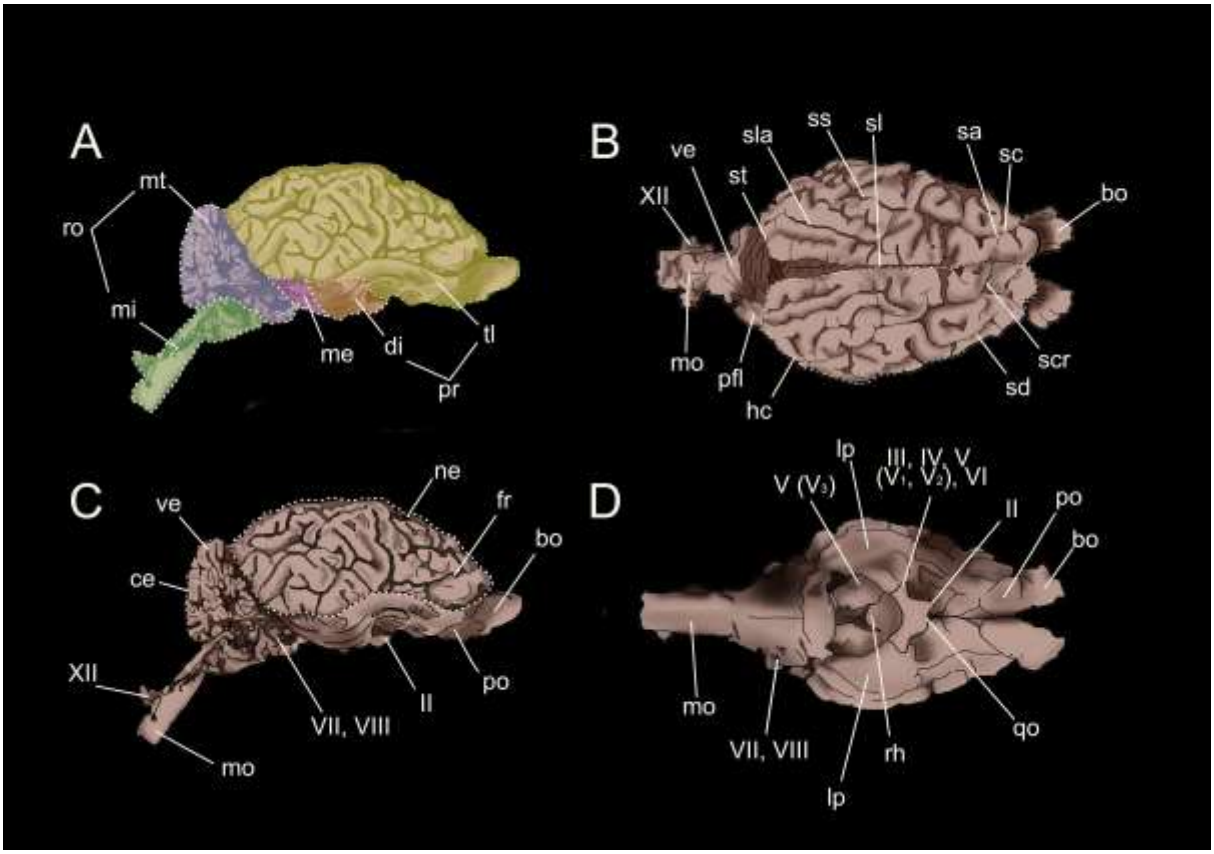

Figura 5. Ilustração do encéfalo de *Odocoileus virginianus*. **A**. vista lateral com subdivisões. *di* Diencéfalo, *me* Mesencéfalo, *mi* Mielencéfalo, *mt* Metencéfalo, *pr* Prosencéfalo, *ro* Rombencéfalo. *tl* Telencéfalo; **B**. vista dorsal; **C**. vista lateral; **D**. vista ventral com descrições anatômicas: *sa* sulco ansato, *bo* bulbos olfatórios, ce cerebelo, p*fl* paraflóculos, *fr* fissura rinal, *he* hemisfério cerebelar, *lp* lobo piriforme, *mo* medulla oblongata, *ne* neocórtex, *po* pedúculo olfatório, *qo* quiasma óptico, *rh* região hipofisiária, *sc* sulco coronal, *scr* sulco cruciato, *sd* sulco diagonal, *sl* sulco longitudinal, *sla* sulco lateral, *ss* sulco suprasilviano, *st* sulco transversal, *ve* vermis.

Nos últimos anos, devido ao desenvolvimento de tecnologias capazes de visualizar e analisar fósseis digitalmente através de escaneamento e *softwares* de renderização de modelos tridimensionais (CUNNINGHAM et al., 2014; DAS et al., 2017), tornou-se possível o estudo das cavidades endocranianas de maneira não-invasiva (ROWE, 2017). A tomografia computadorizada tem como princípio gerar inúmeros cortes virtuais bidimensionais do fóssil, onde é possível conectá-los e formar uma reconstrução tridimensional da área de interesse (e.g. encéfalo, cavidade nasal, ouvido interno, entre outros; CUNNINGHAM et al., 2014). O uso destas tecnologias amplia significativamente o conhecimento sobre as informações anatômicas dos fósseis e viabiliza o compartilhamento de dados, possibilitando análises das mais diversas formas, inclusive de fósseis considerados raros e com preservação frágil (CUNNINGHAM et al., 2014; DAVIES et al., 2017; DAS et al., 2017).

Embora o conhecimento sobre a evolução neurológica em mamíferos extintos tenha aumentado significativamente desde o advento da tomografia computorizada aplicada ao estudo dos fósseis (e.g. ROWE, 1996; MARINO et al., 2003; BLOCH e SILCOX, 2006; TSENG e WANG, 2010; ROWE et al., 2011; KOYABU et al., 2014), até então não havia estudos paleoneurológicos publicados de cervídeos sul-americanos.

1.2 OBJETIVOS

1.2.1 Objetivo Geral

O presente estudo tem o objetivo de reconstruir virtualmente um modelo do encéfalo do cervídeo extinto *Antifer* e estudar sua morfologia em comparação com cervídeos viventes.

1.2.2 Objetivos Específicos

i) Descrever e comparar a morfologia do molde endocraniano do encéfalo de *Antifer ensenadensis* em comparação com outros cervídeos;

ii) Testar o efeito do tamanho do encéfalo na forma do encéfalo (alometria) de *A. ensenadensis*;

iii) Analisar o tamanho relativo do encéfalo utilizando coeficientes de encefalização.

CAPÍTULO 2 – *ARTIGO CIENTÍFICO*

2.1 ARTIGO CIENTÍFICO

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RESEARCH ARTICLE

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Virtual brain endocast of *Antifer* (Mammalia: Cervidae), an extinct large cervid from South America

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Abstract

A diverse fossil record of Cervidae (Mammalia) has been documented in the South American Pleistocene, when these animals arrived during the Great American Biotic Interchange. Using computed tomography-scanning techniques, it is possible to access the endocranial morphology of extinct species. Here, we studied the brain endocast of the extinct late Pleistocene cervid *Antifer ensenadensis* from southern Brazil, one of the largest forms that lived on this continent, using comparative morphology, geometric morphometrics, and encephalization quotients. The analyzed endocasts demonstrate that *A. ensenadensis* had a gyrencephalic brain, showing a prominent longitudinal sinus (=sagittal superior sinus), which is also observed in the large South American cervid *Blastocerus dichotomus*. The encephalization quotient is within the variation of extant cervids, suggesting maintenance of the pattern of encephalization from at least the late Pleistocene. Geometric morphometric analysis suggested a clear and linear allometric trend between brain endocast size and shape, and highlights *A. ensenadensis* as an extreme form within the analyzed cervids regarding brain morphology.

KEYWORDS
allometry, endocast, endocranium, late Pleistocene, Odocoileini

1 | INTRODUCTION

Cervidae is a clade within Cetartiodactyla, which contains Cervinae and Capreolinae. The former includes two less-inclusive clades containing eight genera of European and Asian forms, while the latter includes four American clades (including Odocoileini, which is of major interest here) containing 10 genera (Gutiérrez et al., 2017; Heckeberg, Erpenbeck, Wörheide, & Rössner, 2016). Cervids are the only ruminants recorded in both tropical and subtropical environments of South America (Eisenberg & Redford, 1999; Wilson & Mittermeier, 2011). The first representatives of this clade arrived in South America in the early Pleistocene during the Great American Biotic Interchange (Goin, Gelfo, Chornogubsky, Woodburne, & Martin, 2012; Marshall et al., 1984; O'Dea et al., 2016; Tonni & Pasquali, 1999). Mainly after the middle Pleistocene, the South American Odocoileini underwent an adaptive radiation (Alcaraz & Carlini, 2003; Menegáz & Ortiz-Jaureguizar, 1995; Oliveira, Ribeiro, Ximenes, Viana, & Holanda, 2014).

The extant South American Odocoileini includes the genera *Mazama* Rafinesque, 1817, *Pudu* Gray, 1852, *Hippocamelus* Leuckart, 1816, *Blastocerus* Illiger, 1815, *Ozotoceros* Linnaeus, 1758, and *Odocoileus* Rafinesque, 1832 (Gutiérrez et al., 2017; Heckeberg et al., 2016). Meanwhile, the fossil record is composed of the genera *Antifer* Ameghino, 1889, *Charitoceros* Hoffstetter, 1963, *Morenelaphus*

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Carette, 1922, *Epieuryceros* Ameghino, 1889, *Agalmaceros* Hoffstetter, 1952, and *Paraceros* Ameghino, 1889 (Alcaraz, 2010; Menegáz & Ortiz-Jaureguizar, 1995). Menegáz and Ortiz-Jaureguizar (1995) included those extinct taxa in Odocoileini (Capreolinae). However, it is important to note that the phylogenetic relationships of these extinct cervids have not been studied to date using cladistic methodology.

Antifer is an extinct cervid characterized by wide and robust antlers that are more laterally positioned on the skull when compared to other Odocoileini and reach up to 60 cm in length (Alcaraz, 2010; Castellanos, 1945). The antlers have longitudinal sulci on the surface and dichotomic ramifications (Castellanos, 1945). According to Alcaraz (2010), two species are included in this genus: *Antifer ultra* Ameghino, 1889 and *Antifer ensenadensis* Ameghino, 1888, which are recorded in early/late Pleistocene of southern South America (Uruguay, Argentina, Chile, and Brazil; Aires & Lopes, 2012; Alcaraz, 2010; Alcaraz & Carlini, 2003; Alcaraz & Zurita, 2004; Casamiquela, 1984; Kerber & Oliveira, 2008; Labarca & Alcaraz, 2011; Pereira, Lopes, & Kerber, 2012; Ubilla, 2004). It is important to note that a taxonomic review of this genus is required since most diagnostic features are related to the antlers, which can be ontogenetically variable. The large size of the fossil specimens assigned to this genus suggests that *Antifer* is among the largest cervids that inhabited South America (Menegáz & Ortiz-Jaureguizar, 1995).

With the advance of technologies for visualizing and analyzing fossils using computed tomography (CT) and rendering software, it is now possible to noninvasively analyze the internal cavities of the skull of extinct species (Cunningham, Rahman, Lautenschlager, Rayfield, & Donoghue, 2014; Das, Murmann, Cohrn, & Raskar, 2017). The use of these approaches has increased the knowledge on the paleoneurology of extinct species significantly through anatomical reconstructions (Bertrand, Amador-Mughal, & Silcox, 2016; Orliac & Gilissen, 2012; Pierce, Williams, & Benson, 2017) and morphometric studies (Ahrens, 2014; Bertrand, San Martin-Flores, & Silcox, 2019; Iurino et al., 2015), as well as general interpretations of patterns and modes of neurological diversification through time (Rowe, 1996; Marino, Uhen, Pyenson, & Frohlich, 2003; Bloch & Silcox, 2006; Tseng & Wang, 2010; Rowe, Macrini, & Luo, 2011; Orliac & Gilissen, 2012; Koyabu et al., 2014, Dozo & Martinez, 2015; Fernández-Monescillo et al., 2017; Bertrand, Amador-Mughal, Lang, & Silcox, 2018; Rodrigues et al., 2018, among several others). However, data on the neuroanatomy and encephalization of extinct cervids are still quite scarce (Czyzewska, 1982; Palombo, Kohler, Moyà-Solà, & Giovinazzo, 2008), which is especially true for the South American forms. Hence, in this paper, we present the first approach to the study of the brain endocast of the extinct cervid *A. ensenadensis* from the late Pleistocene of southern Brazil. Specifically, our study aims to (a) describe and compare the morphology of the brain endocast of *A. ensenadensis* to other cervids; (b) describe the brain endocast shape and test the effect of brain size on the brain shape (= allometry) of *A. ensenadensis* in comparison to other cervids using 3D-geometric morphometrics; and (c) analyze the relative brain size using encephalization quotients.

2 | MATERIAL AND METHODS

2.1 | Location and geological remarks

The two fossil specimens of *A. ensenadensis* analyzed here were found in Touro Passo Creek, southern Brazil, in the 1990s by Édison Vicente Oliveira (U-4922; supporting information 1, Figure S1A; Table S1) (Oliveira, 1999) and in the 1970s by Miguel Bombin (MCN-PV 943; supporting information 1, Figure S1B) (Bombin, 1976). In this creek, Upper Pleistocene outcrops of the Touro Passo Formation are exposed (Bombin, 1976). The deposit has fluvial origin, consisting of sandstones, mudstones, and conglomerates (Oliveira & Kerber, 2009). The available numerical ages obtained by thermoluminescence, carbon-14, accelerator mass spectrometry, and electron spin resonance dating ranged from 43 to 10 ka (Kerber et al., 2011; Kerber, Pitana, Ribeiro, Hsiou, & Oliveira, 2014; Kotzian, Simões, Da-Rosa, & Milder, 2005; Milder, 2000; Miller, 1987).

2.2 | Specimens, scanning procedures, and 3D-modeling

Two specimens (U-4922 and MCN-PV 943) assigned to *A. ensenadensis* were studied using a medical CT scanner. Specimen U-4922 preserves the posterior portion of the cranium, but the region anterior to the orbit is missing. It preserves the base of the right antler (supporting information 1, Figure S1A). Specimen MCN-PV 943 preserves the dorsal aspect of the posterior portion of the cranium. The basicranium, as well as the region anterior to the orbit, are missing due to fragmentation (supporting information 1, Figure S1B). However, it comprises both antlers, which show diagnostic traits of this taxon (Ribeiro & Scherer, 2009).

For comparison, we also scanned skulls of selected South American, North American, and Eurasian cervids (supporting information 1, Table S1). All comparative specimens were adult males, except for specimen MCN 2965, a young individual of undefined sex. The taxonomic identification of the comparative specimens follows the collection labeling. Anatomical nomenclature of the endocast follows Dozo and Martínez (2015) (Figure 1), which is modified from other sources.

The specimens were scanned using a Philips Brilliance 16-Slice CT scanner (scanner settings in supporting information 1, Table S1). The raw scan data were exported from the scanner computer in DICOM format. Segmentation of the endocranial cavity of each specimen was performed using the software Avizo 8.1 in order to generate the 3D models. The 3D models of the brain endocast of *A. ensenadensis* are available in Fontoura, Ferreira, Bubadué, Ribeiro, and Kerber (2020).

2.3 | Geometric morphometrics

Based on Bertrand et al. (2019), we used Landmark Editor (Wiley et al., 2005) to position 13 homologous landmarks on the left side of

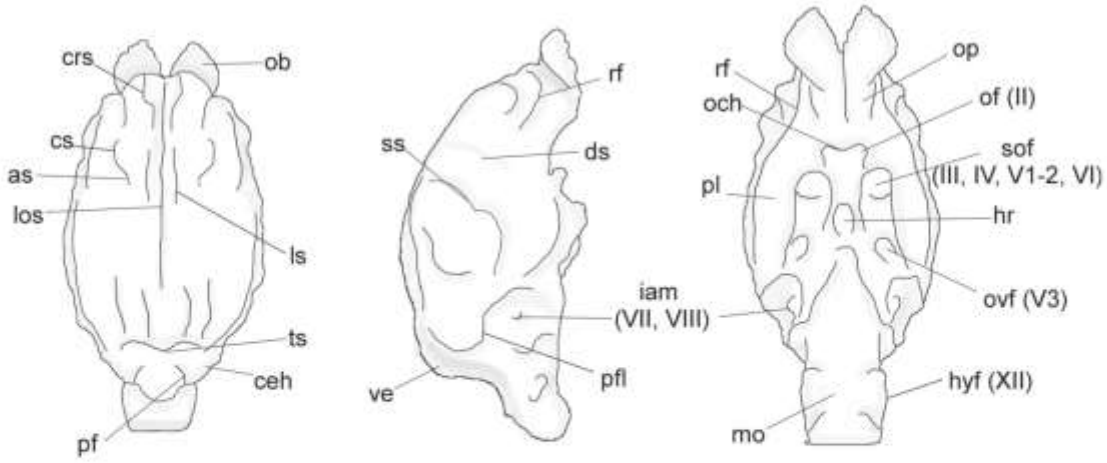

FIGURE 1 Anatomical nomenclature of brain endocasts. as, ansate sulcus; ceh, cerebellar hemisphere; crs, cruciate sulcus; cs, coronal sulcus; ds, diagonal sulcus; hr, hypophyseal region; hyf, cast of hypoglossal foramen; iam, cast of internal auditory meatus (exit of cranial nerves VII and VIII); los, longitudinal sinus; ls, lateral sulcus, mo, medulla oblongata; ob, olfactory bulb; och, optic chiasm; of, cast of optic foramen (exit of cranial nerve II); op, olfactory peduncles; pf, paramedian fissure; pfl, paraflocculus; pl, pyriform lobe; rf, rhinal fissure; sof, cast of sphenorbital fissure (exit of cranial nerves III, IV, V1 and V2, VI); ss, sylvian sulcus; ovf, cast of oval foramen (exit of cranial nerve V3); ts, transverse sinus; ve, vermis

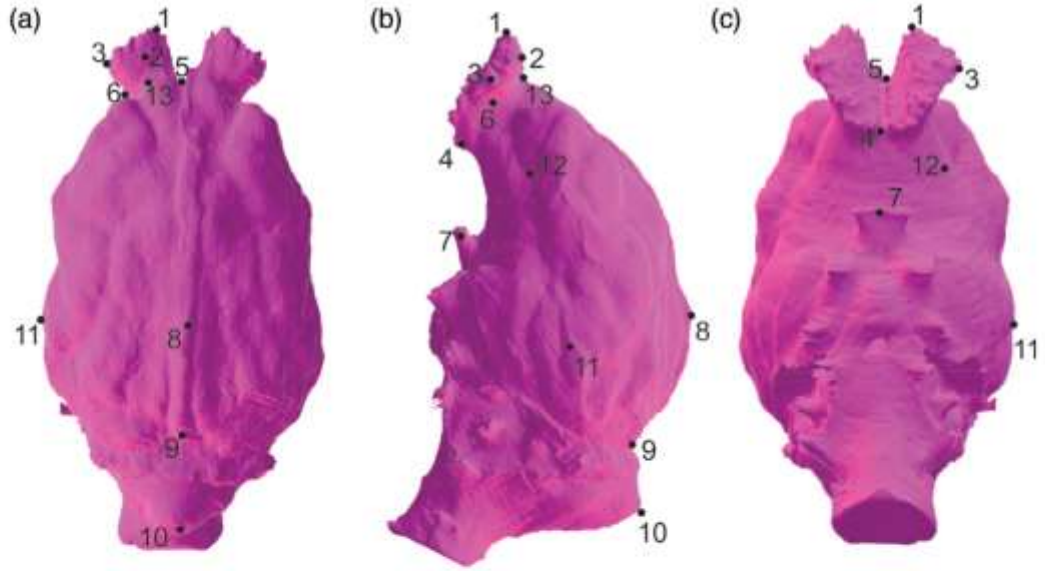

FIGURE 2 Brain endocast of *Blastocerus dichotomus* (a. dorsal, b. lateral, and c. ventral views) showing the location of the 13 landmarks used in the geometric morphometrics analyses (Modified from Bertrand et al., 2019). 1. Anteriormost point of olfactory bulb; 2. Dorsalmost point of the olfactory bulb; 3. Lateralmost point of the olfactory bulb; 4. Inferior fossa of the olfactory bulb; 5. Confluence of the circular and sagittal fissure; 6. Lateral constriction of the olfactory bulb; 7. Bifurcation of the optic nerves; 8. Dorsalmost point on endocast; 9. Confluence of the sinuses; 10. Posteriormost point of the vermis; 11. Lateralmost point on endocast; 12. Sylvian fossa; 13. Anteriormost point on the neocortex

the cranial cavity endocast 3D models (Figure 2). We chose not to use landmarks on the ventral posterior region of the endocast because MCN-PV 943 does not preserve that area. Due to deformations on the right side of specimen U-4922, we limited our landmark configuration to the left side of the endocast. We performed a generalized Procrustes analysis in order to rotate, translate, and scale our raw landmark configuration to obtain the Procrustes shape coordinates (Zelditch, Swiderski, & Sheets, 2012). From this procedure, we

extracted the brain endocast size, recorded as centroid size (= square root of the sum of the squares of the distances from the landmarks to their centroid), and shape, as Procrustes coordinates (Zelditch et al., 2012) (supporting information 2).

We evaluated the overall shape variation and the position of U-4922 and MCN-PV 943 in relation to other Cervidae species using principal component analysis (PCA). We also evaluated the brain endocast shape vs. size of *A. ensenadensis* in relation to other cervids. This was done in order to understand how size impacts shape variation within the Cervidae brain and to estimate if the shape of *A. ensenadensis* is in accordance with what is expected within an interspecific allometric slope of shape change in relation to size. All geometric morphometric analyses were performed in the R statistical computing environment using the software package "geomorph" (Adams & Otarola-Castillo, 2012).

2.4 | Encephalization and body mass

The analysis of the relative size of the brain endocast was carried out using the encephalization quotients (EQ) developed by Jerison (1973): [$EQ = EV/(0.12 \times BM^{0.67})$] and Eisenberg (1981) [$EQ = EV/(0.0553 \times BM^{0.74})$] (BM, body mass; EV, encephalic volume). The volume of the endocast (EV; mm^3) was converted to brain mass (g) by the division of the volume by 1.05 (Bertrand & Silcox, 2016; Falk, 2007; Hofman, 1983).

The body mass of the extant and extinct cervids used for the EQ calculation was estimated following Janis (1990) using the variable occipital height (OCH). We applied the linear regression of the OCH (slope = 0.315, intercept = 0.234, $r^2 = 0.854$) because this portion of the cranium is preserved in U-4922, and it reflects the body size of the extant cervids. To standardize the data used in the EQ equations, we applied the same equation for the extant comparative specimens, producing body mass estimates similar to the mass variation expected for those species (supporting information 1, Table S2).

2.5 | Quantification of surface areas and volume of the endocast

The neocortical surface area was estimated based on Jerison (2012), in which the rhinal fissure delimits the separation between the paleo- and neocortex, excluding the superior sagittal sinus (Orliac et al., 2014). The percentage of neocortical area in relation to the total area of the endocast was calculated with and without the olfactory bulbs, following Jerison (2012) and Long, Bloch, and Silcox (2015) (supporting information 1, Table S3). We also calculated the area and volume of the olfactory bulbs in relation to the total area and volume of the endocast, respectively. Geomagic Editor was used to delimit the areas and volumes of the endocast in order to make the percentage calculations. Additionally, we provided linear measurements and ratios (taken according Dozo & Martinez, 2015 and Bertrand & Silcox, 2016; supporting information 1, Table S4).

2.6 | Institutional abbreviations

MAMM, Museu Anchieta de Ciências Naturais, Porto Alegre, Brazil; MCN, mammal collection of the Mastozoology Sector of the Museu de Ciências Naturais do Rio Grande do Sul (MCN), Secretaria do Meio Ambiente e Infraestrutura (SEMA), Porto Alegre, Brazil; MCN-PV, paleontological collection of the Paleontology Section of the MCN/SEMA, Porto Alegre, Brazil; U, paleontological collection of the Universidade do Vale do Rio dos Sinos (UNISINOS), São Leopoldo, Brazil.

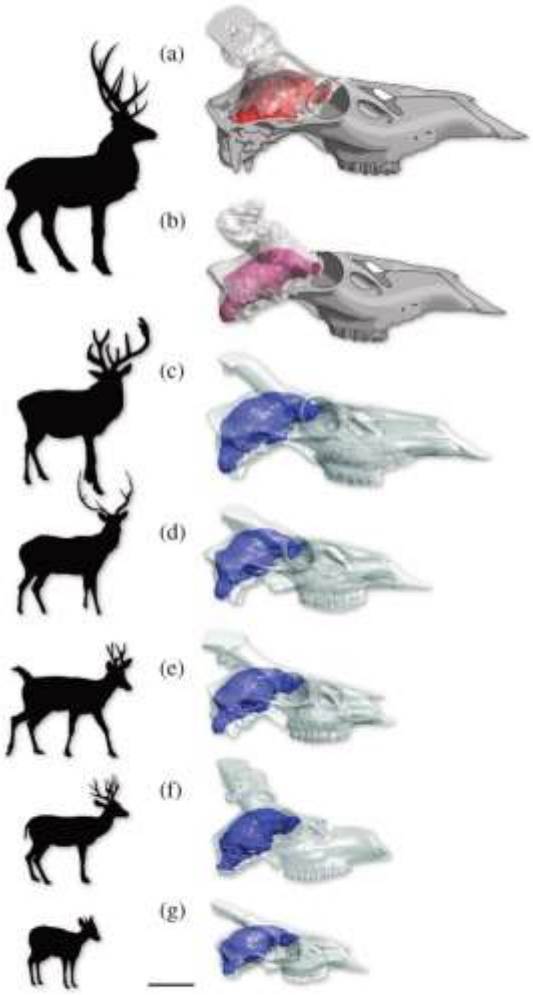

FIGURE 3 Virtual brain endocast inside of the transparent skull of extinct and extant cervids. (a) *Antifer ensenadensis* (U-4922); (b) *Antifer ensenadensis* (MCN-PV 943); (c) *Cervus elaphus* (MCN 3312); (d) *Axis axis* (MCN 3310); (e) *Blastocerus dichotomus* (MCN 3009); (f) *Ozotoceros bezoarticus* (MAMM 0099); (g) *Mazama nana* (MCN 3493). Scale-bar = 50 mm

3 | RESULTS

3.1 | Comparative morphology of the brain endocast of *A. ensenadensis*

3.1.1 | General remarks

After applying the methodology to reconstruct the brain endocast of *A. ensenadensis*, two endocasts were generated (Figures 3–5). From specimen U-4922, it was possible to reconstruct the entire endocast (Figure 4), while for specimen MCN-PV 943, which does not preserve the basicranial region, only the dorsal portion of the endocast was reconstructed (Figure 5). Casts of the olfactory bulbs and cerebral hemispheres were reconstructed, but not the cerebellar region and nerves on the ventral portion of the endocast. Although MCN-PV 943 lacks some regions, the neopallium morphology was better preserved in this specimen.

The endocasts studied here show a gyrencephalic pattern. In relation to the comparative specimens (Figures 3, 6–8), the brain endocast of U-4922 (slightly more elongated than MCN-PV 943) is anteroposteriorly elongated, as in *Axis axis* (Figure 7g,h), and different from the pattern observed in *Ozotoceros bezoarticus*, which shows an anteroposteriorly more compressed endocast (Figure 8a–f). In dorsal view, the brain endocast of *A. ensenadensis* (U-4922) has a rhomboid outline. In contrast, *O. bezoarticus* (Figure 8a–f) and *Mazama nana* (Figure 6g,h) have a rounded outline, and *Cervus elaphus* (Figure 8g,h), *Blastocerus dichotomus* (Figure 7a–f), and *A. axis* (Figure 7g,h) are more quadrangular.

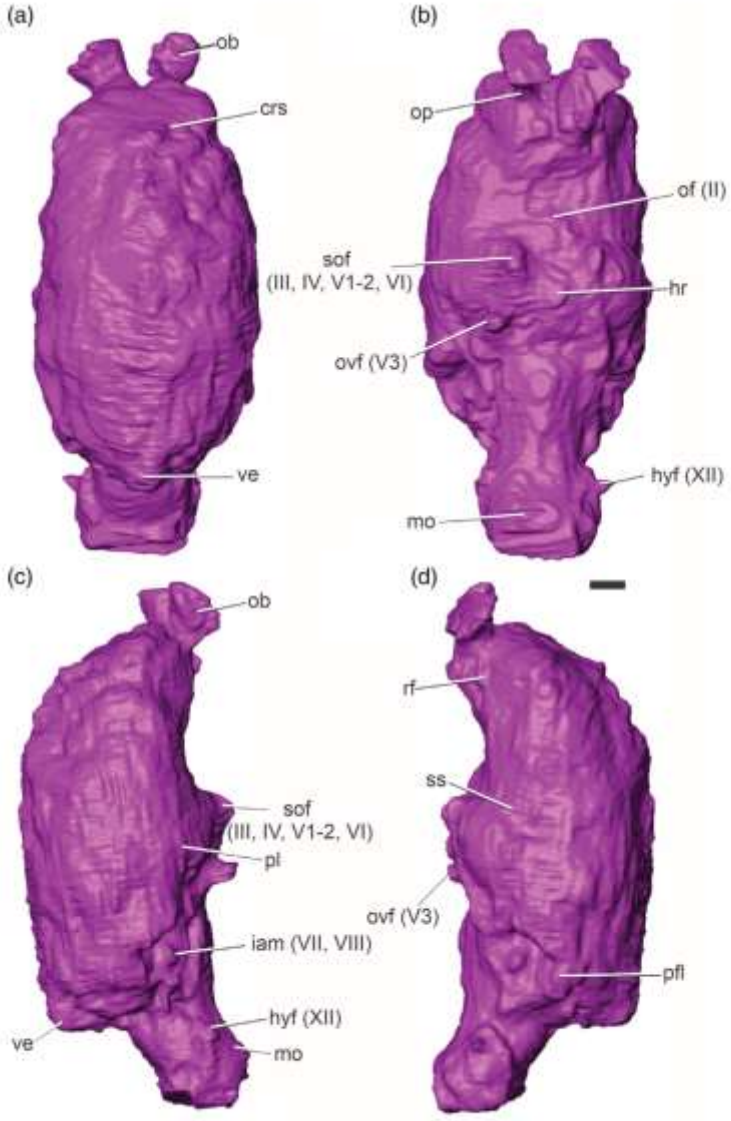

FIGURE 4 *Antifer ensenadensis*, brain endocast (U-4922), in dorsal (a), ventral (b), right lateral (c), and left lateral (d) views. Scale-bar: 10 mm. crs, cruciate sulcus; hr, hypophyseal region; hyf, cast of hypoglossal foramen; iam, cast of internal auditory meatus; mo, medulla oblongata; ob, olfactory bulb; of, cast of optic foramen (exit of cranial nerve II); op, olfactory peduncles; pfl, paraflocculus; pl, pyriform lobe; rf, rhinal fissure; sof, cast of sphenorbital fissure (exit of cranial nerves III, IV, V1 and V2, VI); ss, sylvian sulcus; ovf, cast of oval foramen (exit of cranial nerve V3); ve, vermis

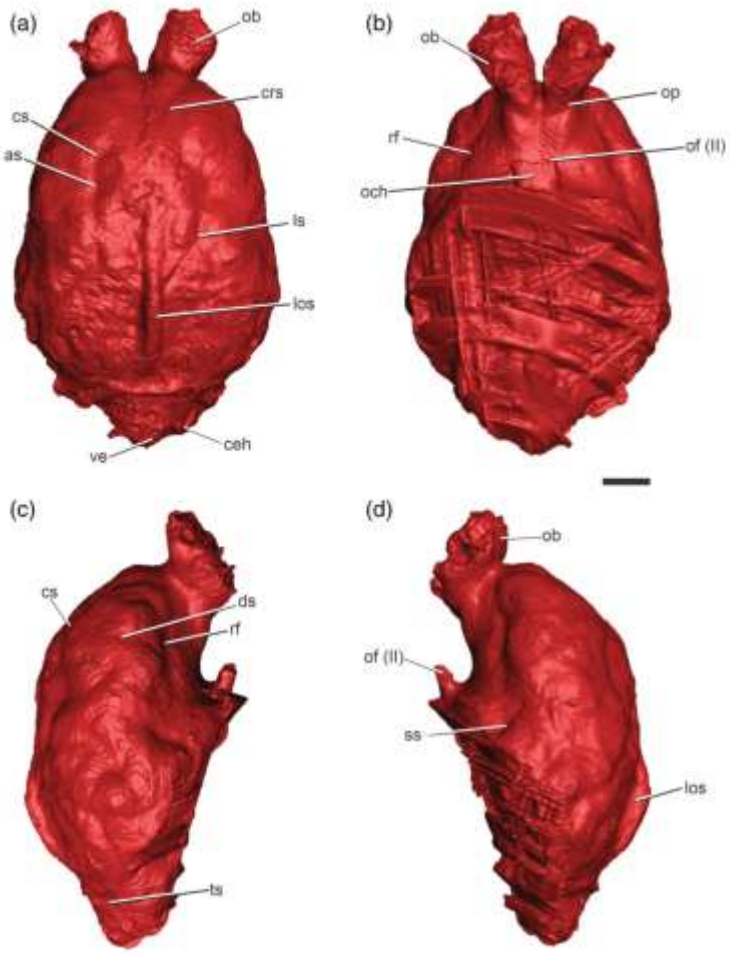

FIGURE 5 *Antifer ensenadensis*, brain endocast (MCN-PV 943), in dorsal (a), ventral (b), right lateral (c), and left lateral (d) views. Scale-bar: 10 mm. as, ansate sulcus; ceh, cerebellar hemisphere; crs, cruciate sulcus; cs, coronal sulcus; ds, diagonal sulcus; los, longitudinal sinus; ls, lateral sulcus; ob, olfactory bulb; och, optic chiasm; of, cast of optic foramen (exit of cranial nerve II); op, olfactory peduncles; rf, rhinal fissure; ss, sylvian sulcus; ts, transverse sinus; ve, vermis

In some cervids, the temporal region of the cerebral hemispheres is more developed than the occipital portion (e.g., *A. ensenadensis* MCN-PV 943, *M. nana*, *Mazama americana*, *Mazama gouazoubira*, and *C. elaphus*; Figures 5, 6 and 8g,h).

3.1.2 | Rhinencephalon

The brain endocast of *A. ensenadensis* has a well-marked rhinencephalon, as in other cervids. The pyriform lobe in extant cervids and *A. ensenadensis* is ventrally delimited by the posterior region of the rhinal fissure.

The pyriform lobe of *A. ensenadensis* (U-4922) is not as developed as the temporal-occipital region of the cerebral hemisphere. However, it forms a small salient feature on the endocast, which is anteroventrally oriented, differing from other species of cervids, in which it is ventrally oriented (e.g., *A. axis*, Figure 7g,h; *C. elaphus*, Figure 8g,h; and *M. gouazoubira*, Figure 6a–c) or posteroventrally oriented (e.g., *M. americana*, *M. nana*, Figure 6d–h; *O. bezoarticus*, Figure 8a–f; and *B. dichotomus*, Figure 7a–f). In MCN-PV 943, the pyriform lobe is not completely preserved.

The olfactory peduncle is short and robust, and does not present a marked circular fissure. Both specimens are similar; however, in MCN-PV 943 the olfactory bulbs are more robust and anteriorly elongated than in U-4922. In addition, in U-4922 they are located more ventrally than in MCN-PV 943, and the olfactory penduncle is more inclined. The olfactory penducle of *A. ensenadensis* is short and is distinct from *M. americana* (Figure 6d–f) and *C. elaphus* (Figure 8g,h), in which this structure is more elongated.

The olfactory bulbs are individualized and located ventrally on the anteriormost region of the endocast (Figures 4–5). In all cervid species analyzed in this study, the olfactory bulbs are slightly laterally oriented. They are ventrally oblique in relation to the horizontal axis passing through the brain endocast, such as in *A. axis* (Figure 7g, h), *M. gouazoubira* (Figure 6a–c), and *O. bezoarticus* (Figure 8a–f). In contrast, *B. dichotomus* (Figure 7a–f), *M. americana*, *M. nana* (Figure 6d–h), and *C. elaphus* (Figure 8g–f) have more horizontally oriented bulbs.

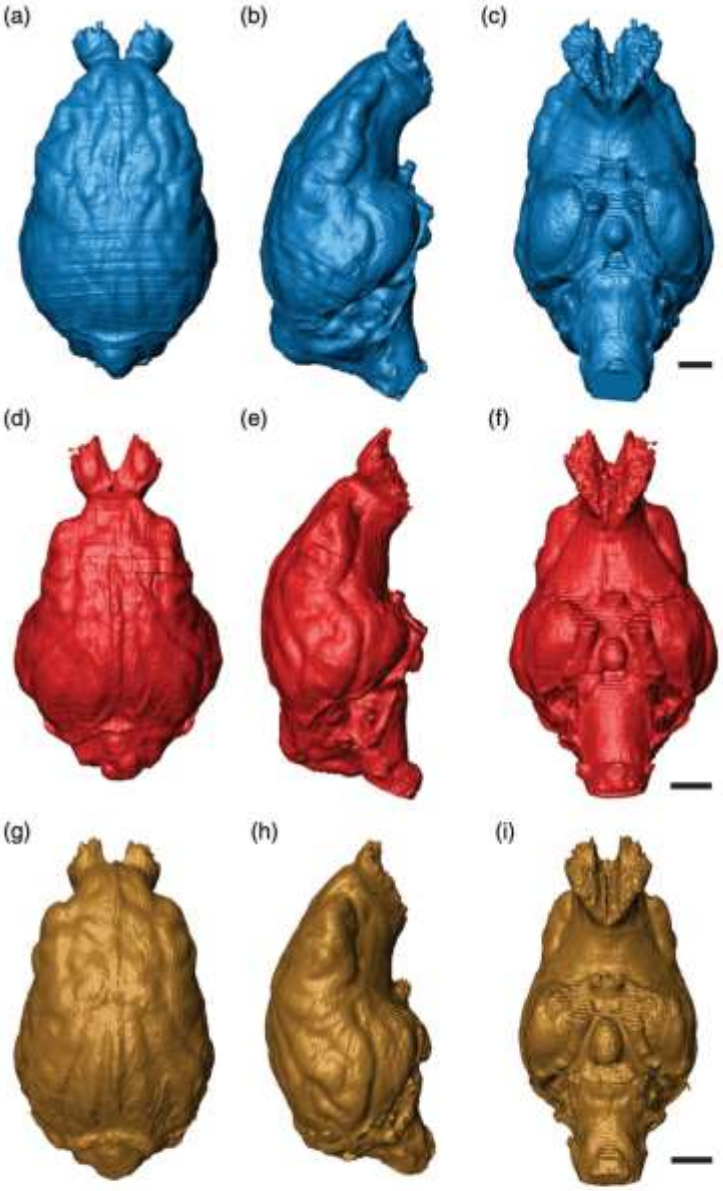

FIGURE 6 Diversity of brain endocast morphology of comparative extant cervids, in dorsal (a, d, g), lateral (b, e, h), and ventral (c, f, i) views. a–c, *Mazama gouazoubira* (MCN 3000); d–f, *Mazama americana* (MCN 2975); g–h, *Mazama nana* (MCN 3493). Scale-bars = 10 mm

3.1.3 | Neopallium

It was not possible to reconstruct the surface of the brain endocast of U-4922 with precision. The neocortical sulci cannot be distinguished properly. However, in MCN-PV 943 the surface was reconstructed with more detail (Figure 5).

The longitudinal sinus (=superior sagittal sinus) is visible on the sagittal line of the brain, dividing the cerebral hemispheres. In MCN-PV 943, dorsally, this sinus is the most prominent structure of the dorsal region of the endocast, as in *B. dichotomus* (Figure 7a–f). In its posteriormost region, the sinus divides into two structures corresponding to the transverse sulci.

Like in other cervids, the rhinal fissure is visible anteriorly in specimen MCN-PV 943 (Figure 5), showing a deep and anteroposteriorly oriented sulcus. However, *C. elaphus* (MCN 3312) has a shallow rhinal fissure (Figure 8g,h).

There is a slope on the anterior region of the neopallium that is more accentuated in U-4922 than in MCN-PV 943. In MCN-PV 943 (Figure 5), it is possible to observe the cruciate sulcus, which runs anterolaterally, as in other mammals (Dozo & Martínez, 2015; Kuhlenbeck, 1978).

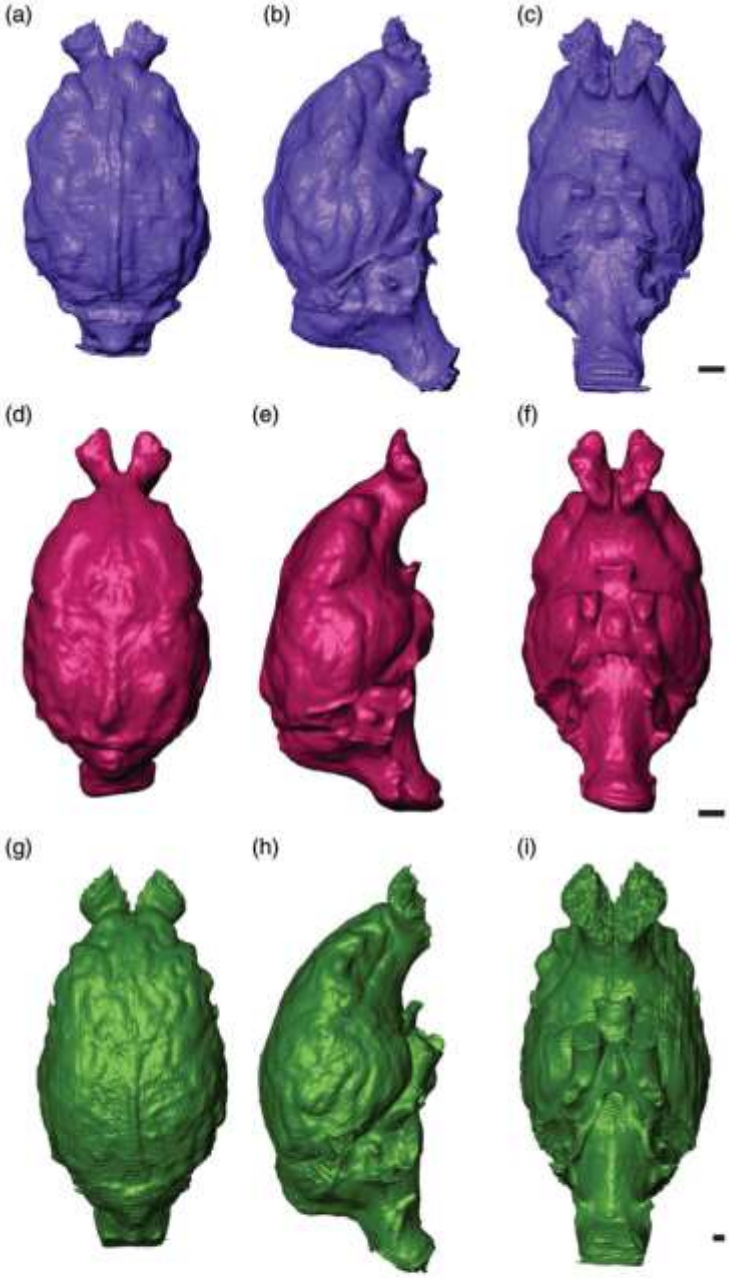

FIGURE 7 Diversity of brain endocast morphology of comparative extant cervids, in dorsal (a, d, g), lateral (b, e, h), and ventral (c, f, i) views. a–c, *Blastocerus dichotomus* (MCN 3009); d–f, *Blastocerus dichotomus* (MAMM 0160); g–h, *Axis axis* (MCN 3310). Scale-bars = 10 mm

The ansate sulcus is dorsally positioned on the anterior region of the endocast. It is deep and anteriorly confluent with the coronal sulcus, which is laterally oriented. The ansate sulcus in U-4922 is deeper than in MCN-PV 943. The coronal sulcus is continuous and is confluent with the ansate sulcus, as in other mammals (Kuhlenbeck, 1978). In lateral view, we observed that the diagonal sulcus is parallel to the suprasylvian sulcus. The suprasylvian sulcus delimits the temporal lobe. In the dorsal view of the neopallium, the lateral sulcus is parallel to the median line of the brain. It is shallow and extends across the entire dorsal surface of the neocortex.

In the posterior region of the cerebral hemisphere, the cerebra of *Mazama* spp. and *O. bezoarticus* present radial convolutions (Figures 6 and 8a–f), while *Antifer* and the other comparative species show no such pattern.

In all specimens, the mesencephalon is covered by the neocortex.

3.1.4 | Cerebellum

The cerebellar region is better preserved in U-4922 than in MCN-PV 943. However, it is possible to observe the posteriormost region of the vermis in MCN-PV 943 (Figure 5).

The cerebellum is partially covered by the neocortex. It is composed of a central vermis, more prominent dorsally, and two lateral cerebellar hemispheres, which are poorly marked. In dorsal view, the vermis is the most prominent structure of the cerebellum, while the paramedian fissures are shallow.

The transversal fissure is not visible in U-4922, but it is well marked in MCN-PV 943 and comparative specimens. The parafloccular cast is evident on the lateral surface of the cerebellar region but is not well delimited.

3.1.5 | Cranial nerves and brainstem

The cast of the foramina represents the impression of nerves and vessels associated with the brain. The impression of the optic foramen (exit of cranial nerve II) is present on the anterior region of the ventral face of the endocasts, and it is more clearly visible in MCN-PV 943, which preserves the chiasma. In our sample, *A. ensenadensis* has the smallest distance between the chiasma and olfactory bulbs, while

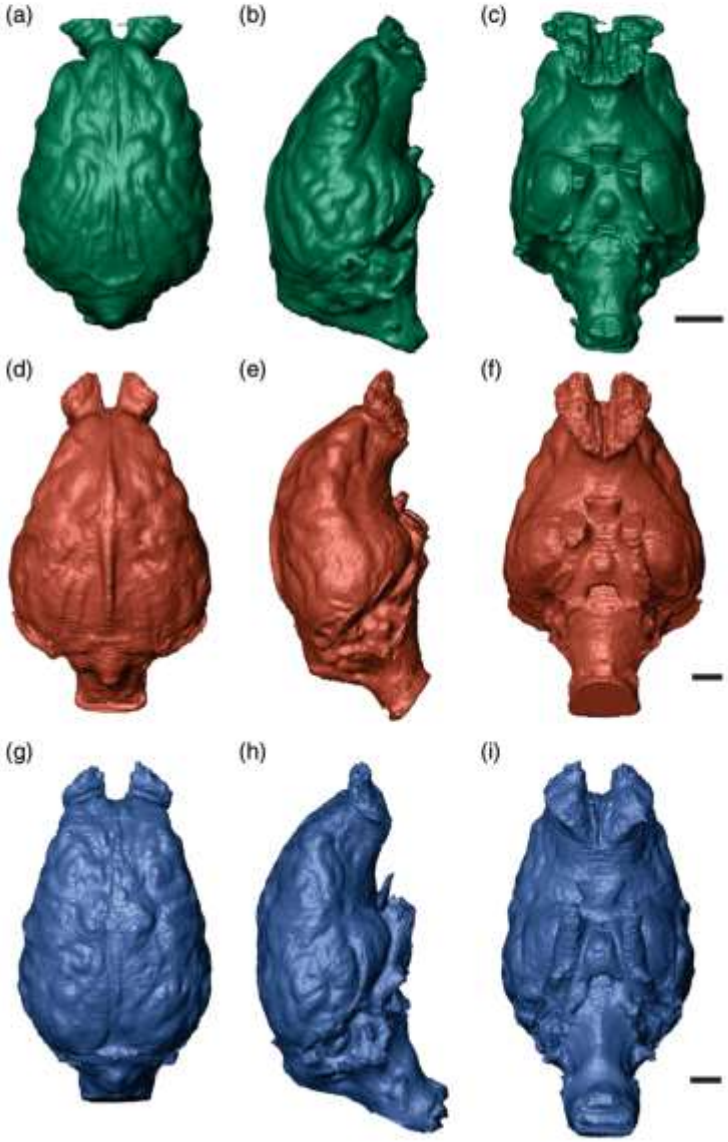

FIGURE 8 Diversity of brain endocast morphology of comparative extant cervids, in dorsal (a, d, g), lateral (b, e, h), and ventral (c, f, i) views. a–c, *Ozotocerus bezoarticus* (MCN 2965); d–f, *Ozotocerus bezoarticus* (MAMM 0099); g–h, *Cervus elaphus* (MCN 3312). Scale-bar: 10 mm

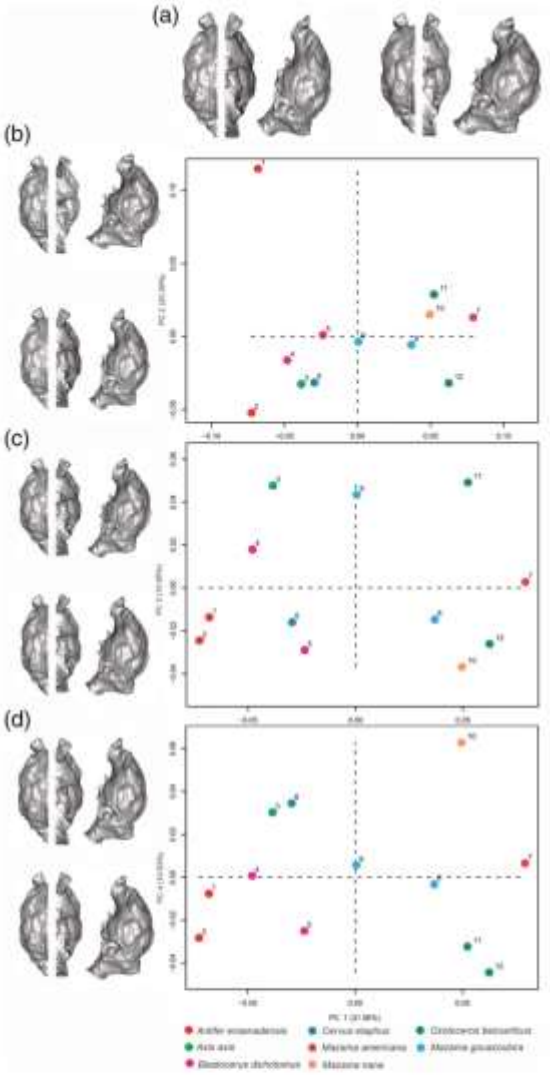

FIGURE 9 Scatter plots of PC1 versus PC2, PC3, and PC4. Brain endocast deformations (left side in dorsal, ventral and lateral views, respectively) are plotted in relation to the 3D model of specimen 9 and they represents the mean at the extreme positive and negative of each principal component. 1. *Antifer ensenadensis* (U-4922); 2. *Antifer ensenadensis* (MCN-PV 943); 3. *Axis axis* (MCN 3310); 4. *Blastocerus dichotomus* (MAMM-0160); 5. *B. dichotomus* (MCN 3009); 6. *Cervus elaphus* (MCN 3312); 7. *Mazama americana* (MCN 2975); 8. *Mazama gouazoubira* (MAMM-0123); 9. *M. gouazoubira* (MCN 3000); 10. *Mazama nana* (MCN 3493); 11. *Ozotocerus bezoarticus* (MAMM-0099); 12. *Ozotocerus bezoarticus* (MCN 2965)

M. nana and *M. americana* (Figure 6d–h) have the greatest distances (supporting information 1, Table S4).

In U-4922, posterolaterally to the impression of the CN II, there is the impression of the sphenorbital fissure, which in terrestrial cetartiodactyls transmits the oculomotor (CN III), trochlear (CN IV), ophthalmic (CN V1) and maxillary (CN V2) branches of the trigeminal (CN V), and abducens (CN VI) nerves (Orliac & Gilissen, 2012). Posterior to the sphenorbital fissure, there is the cast of the oval foramen that transmits the third branch of the trigeminal nerve (CN V3; Orliac & Gilissen, 2012).

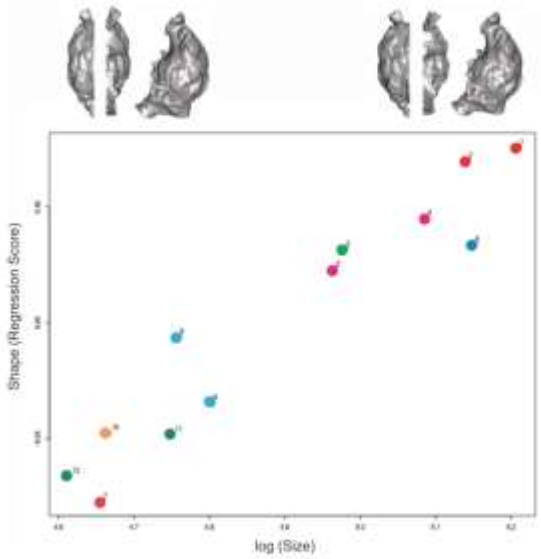

FIGURE 10 Regression plot between brain shape and size. Brain endocast deformations (left side in dorsal, ventral and lateral views, respectively) are plotted in relation to specimen 9. 3D model and represents shape changes from the smallest (left, 12) to the largest (right, 1. *Antifer ensenadensis*) individual. 1. *Antifer ensenadensis* (U-4922); 2. *Antifer ensenadensis* (MCN-PV 943); 3. *Axis axis* (MCN 3310); 4. *Blastocerus dichotomus* (MAMM-0160); 5. *B. dichotomus* (MCN 3009); 6. *Cervus elaphus* (MCN 3312); 7. *Mazama americana* (MCN 2975); 8. *Mazama gouazoubira* (MAMM-0123); 9. *M. gouazoubira* (MCN 3000); 10. *Mazama nana* (MCN 3493); 11. *Ozotoceros bezoarticus* (MAMM-0099); 12. *O. bezoarticus* (MCN 2965)

The cast of the hypophysis (=pituitary gland) is located at the midline of the ventral surface of the endocast between the casts of the sphenorbital fissure and the oval foramen (Figure 4). *Antifer ensenadensis* (U-4922) has a smaller hypophysis length-to-width ratio in our sample, compared to *C. elaphus*, which shows the highest ratio (supporting information 1, Table S4).

Posterolateral to this region, there is the impression of the internal auditory meatus, a passage for the facial (VII) and vestibulocochlear (VIII) nerves. The cast of the hypoglossal nerve (XII) is located laterally to the medulla oblongata (Figure 4).

The brainstem (medulla oblongata) is long, forming a rod at the base of the brain endocast (Figure 4).

3.2 | Geometric morphometrics results

The first four principal components of shape cumulatively explain 73.43% of total shape variance. PC1 explains 31.56% of shape variance

(Figure 9a) and positions U-4922 (Figure 9, number 1) and MCN-PV 943 (Figure 9, number 2) in the same region of the PC1 axis (negative scores), while other cervids such as *Mazama* spp. and *O. bezoarticus* (Figure 9, numbers 10, 11) show extreme positive scores on the same axis. Cervids with negative PC1 scores have a brain endocast that is anteroposteriorly elongated, dorsoventrally compressed, and laterally wide. The olfactory tract is elongated and the dorsal profile of the endocast is less convex than in specimens with positive PC1 scores. Cervids with positive PC1 scores have the opposite features (Figure 9a). PC2 (20.39%) suggests clear shape differences between U-4922 (Figure 9, number 1; positive score) and other cervids (negative scores). The brain endocasts with lower PC2 scores are anteroposteriorly more elongated than those with positive PC2 scores, which are anteroposteriorly compressed and dorsoventrally expanded. U-4922, in relation to other cervids, has a more robust brain endocast, especially in the ventro-dorsal plane (Figure 9b). For PC3 (10.95%), the *A. ensenadensis* specimens are closely clustered (negative scores). Positive PC3 scores apply to *A. axis* (Figure 9, number 3), *M. americana* (Figure 9, number 3), and *O. bezoarticus* (Figure 9, numbers 10, 11). Cervids with lower PC3 scores have anteroposteriorly elongated brain endocasts, more robust olfactory bulbs, and a cerebellar region that projects slightly posteriorly. Cervids with positive PC3 scores have the opposite features (Figure 9c). For PC4 (10.53%), U-4922 shows values near zero (but negative), being comparable especially to *B. dichotomus* (Figure 9, number 4). MCN-PV 943 has a similar score to *B. dichotomus* (Figure 9, number 5), but more toward the extreme negative of the plot. At the positive end of the axis, the specimen of *M. nana* (Figure 9, number 10) is isolated from the other taxa (Figure 9c). PC4 positions U-4922 and MCN-PV 943 in the same region of the axis (negative scores), while other cervids such as *C. elaphus*, *A. axis* (Figure 9, number 6), and *M. nana* (Figure 9, number 10) show extreme positive scores. Cervids with lower PC4 scores have a dorsoventrally expanded endocast when compared to those with positive PC4 scores (Figure 9d).

The allometric slope for the endocast is strong and significant, with size explaining 28.5% of brain shape variation (R^2 = 0.285, F = 3.996, p < .001). *Antifer ensenadensis* (Figure 10, numbers 1 and 2) is shown at the positive extremes of this plot. Overall, the allometric pattern of the sampled cervids shows that the increase in brain endocast size (centroid size) is associated with a proportional expansion of the cerebral hemispheres, along with a more lateral positioning of the olfactory bulbs (Figure 10).

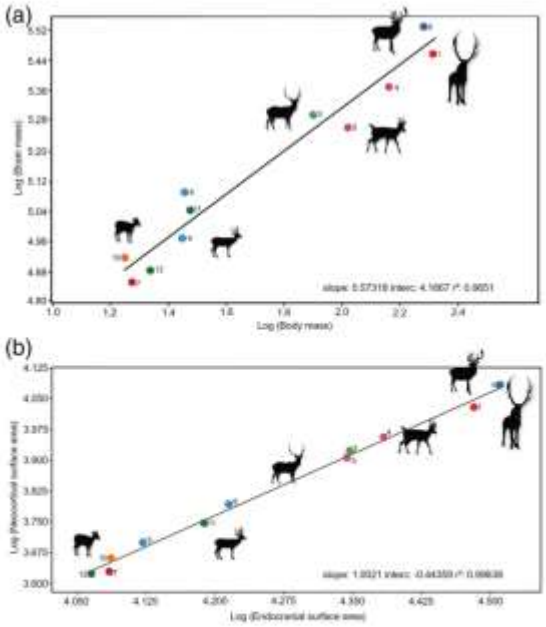

FIGURE 11 Bivariate plots (log) of brain mass versus body mass (a); neocortical surface versus total endocranial surface (b). The identification of the dots is the same as the Figure 9

3.3 | Encephalization quotients and brain size

The estimated volume of the brain endocast of the *Antifer* specimen U-4922 is 313,327.96 mm^3. We estimated the body mass of *Antifer* as 206 kg. Based on this mass, its EQ is 0.68 using the Jerison (1973) equation, and 0.63 using the Eisenberg (1981) equation. These values are within the range of the comparative extant cervid EQs (Figures 11a and 12; Table 1, supporting information 1, Table S2). The highest EQs are present in *M. nana* and *M. gouazoubira*, and the lowest in *B. dichotomus*, followed by *A. ensenadensis*.

The olfactory bulbs represent about 1.9% of the total volume of the brain endocast in U-4922, and represent 7.39% of the total surface area (Figure 13; Table 1, supporting information 1, Table S3). *Ozotocerus bezoarticus* (MAMM 0160) presents the highest olfactory bulb volume percentage in relation to other cervids (2.94%; Table 1, supporting information 1, Table S3), which represents 8.20% of the total endocast surface area, followed by *A. axis* (2.84% in volume, and 9.11% in surface area; Figures 11 and 13).

In general, there is no evident variation in the neocortical surface area of the specimens here analyzed (Figure 13). Nevertheless, the neocortical surface area of *A. ensenadensis* is the smallest in relation to the other analyzed taxa (35.35%; Figure 13; Table 1, supporting information 1, Table S3). On the other hand, *M. gouazoubira* presents the widest surface area of the sample (37.72%; Figure 13). The brain mass and the neocortical surface area increase proportionally in relation to the body mass and total endocranial surface in our sample, respectively (Figure 11a–b).

4 | DISCUSSION

The neurosensorial evolution of extinct South American Cenozoic mammals (e.g., notoungulates, caviomorph rodents, xenarthrans, and primates) has been studied using natural or artificial brain endocasts (usually produced with latex; Dechaseaux, 1958, 1962; Dozo, 1987, 1994, 1997; Dozo, Vucetich, & Candela, 2004; Patterson, 1937;

Radinsky, 1981) and more recently using virtual endocasts (Aristide et al., 2019; Boscaini et al., 2018; Fernández-Monescillo et al., 2017; Ferreira, Negri, Sánchez-Villagra, & Kerber, 2020; Tambusso & Fariña, 2015a, 2015b). Although terrestrial cetartiodactyls are a conspicuous component of the mammalian fauna of this continent (Menegáz & Ortiz-Jaureguizar, 1995), no paleoneurological data have been provided to date. In this regard, this paper presents the first comparative paleoneurological study of South American cervids.

Antifer ensenadensis has a gyrencephalic brain endocast, like in all other species we analyzed here (see also Czyzewska, 1982 and Palombo et al., 2008 for endocast morphology of European extinct cervids), showing a prominent longitudinal sinus, which is also observed in the large South American cervid *B. dichotomus*. Also, intraspecific variation in the brain endocast is recorded, both in extinct and extant forms, for which we have more than one specimen in our sample. For example, in *A. ensenadensis* the endocast of MCN-PV 943 shows more developed olfactory bulbs than in U-4922. On the other hand, U-4922 is anteroposteriorly more elongated than MCN-PV 943 (Figures 4–5). In the extant comparative specimens, both adult males of *B. dichotomus* have similar endocasts, and the most significant difference between them is the superior sagittal sinus of MCN 3009, which is more developed than in MAMM 0160

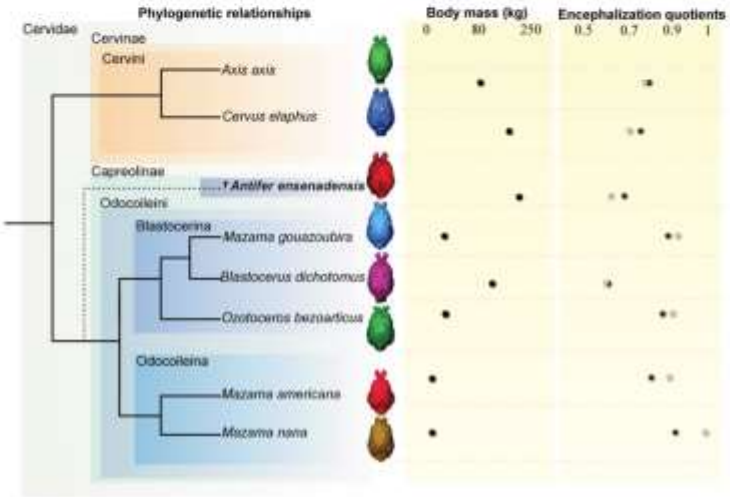

FIGURE 12 Phylogenetic relationships (based on Heckeberg et al., 2016 and Gutiérrez et al., 2017) of the taxa analyzed here, body mass, and encephalization quotients. The phylogenetic position of *Antifer ensenadensis* was not studied using cladistic methodology, and for this reason, it is represented by the dashed line. Black circles are the EQs of Jerison (1973) and gray ones are Eisenberg (1981). Other data are compiled in the Table 1 and supporting information 1, Table S2

TABLE 1 Analyzed specimens and summary of main data

Specimens	Taxa	Body mass (kg)	Brain mass (g)	EQ Jerison	EQ Eisenberg	Olfactory bulbs volume (%)	Neocortex surface area (%)
U-4922	*Antifer ensenadensis*	206.93	298.4	0.68	0.63	1.90	35.35
MCN 3493	*Mazama nana*	18.12	77.86	0.91	0.99	2.40	37.22
MCN 2975	*Mazama americana*	18.50	69.56	0.8	0.87	2.75	35.66
MCN 3000	*Mazama gouazoubira*	27.88	87.43	0.77	0.81	2.50	37.60
MCN 3312	*Cervus elaphus*	197.28	322.8	0.76	0.7	2.10	37.28
MCN 3310	*Axis axis*	82.89	187.9	0.79	0.78	2.84	37.53
MCN 3009	*Blastocerus dichotomus*	105.54	175.1	0.63	0.61	2.37	36.60
MCN 2965	*Ozotoceros bezoarticus*	21.22	72.41	0.76	0.82	2.48	36.13
MAMM 0160	*Blastocerus dichotomus*	146.05	221.8	0.64	0.6	2.13	37.15
MAMM 0099	*Ozotoceros bezoarticus*	30.80	104.2	0.85	0.9	2.94	35.94
MAMM 0123	*Mazama gouazoubira*	29.07	117.8	1.00	1.06	2.53	37.72

(Figure 7a–f). In *Ozotocerus bezoarticus*, the young specimen of indeterminate sex (MCN 2965) has a more anteriorly projected anterior lobe and more poorly developed superior sagittal sulcus in comparison to the adult (MAMM 0099; Figure 8a–f). The young specimen has a greater neocortex and olfactory bulb area in relation to the total area of the endocast compared to the adult (supporting information 1, Table S3). In general, the analyzed endocasts show similar morphologies, but subtle differences among them are present.

Considering the size variation of cervids, by applying geometric morphometrics we were able to identify morphological tendencies unbiased by scale factors, which allowed us to compare the *A. ensenadensis*' brain endocast to other cervids in a more controlled way. The comparative approach of geometric morphometrics evidenced a clear and linear allometric trend between brain size and shape in our data. This was expected, as strong allometry was also found in the overall skull shape of cervids (Merino, Milne, & Vizcaíno, 2005). In our case, the largest South American cervids, such as *A. ensenadensis* and *B. dichotomus*, are closer to the Cervini *A. axis* and *C. elaphus* than to their closer relatives Odocoileini, sharing expansion of the cerebral hemispheres and more laterally positioned olfactory bulbs. Interestingly, *A. ensenadensis* shows the extreme variations of the analysis, as expected within a strong allometric trend, as it is the largest South American species sampled.

The body mass estimate performed to calculate the encephalization of *A. ensenadensis* indicates that this species was one of the largest cervids that inhabited South America, surpassing the largest extant South American forms, *B. dichotomus* and *Odocoileus virginianus*, with a similar body mass to the cervids from the northern

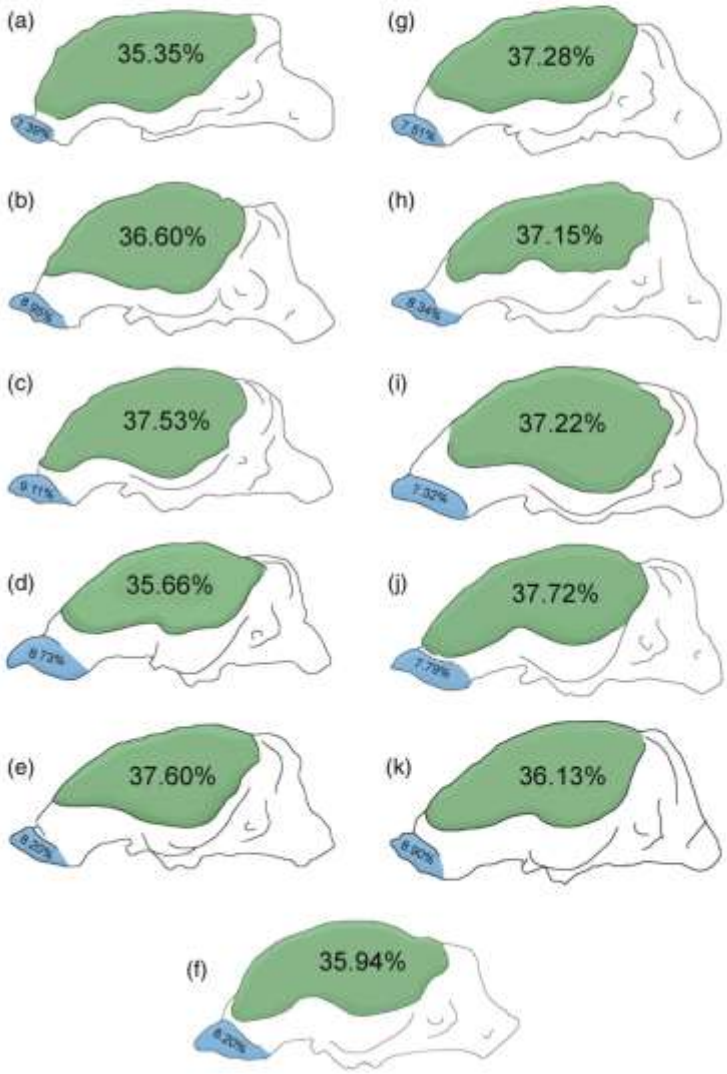

FIGURE 13 Comparison of neocortical (green) and bulbs (blue) surface of the endocast of *Antifer ensenadensis* and other cervids, in lateral view. (a). *Antifer ensenadensis* (U-4922); (b). *Blastocerus dichotomus* (MCN 3009); (c). *Axis axis* (MCN 3310); (d). *Mazama americana* (MCN 2975); (e). *Mazama gouazoubira* (MCN 3000); (f). *Ozotoceros bezoarticus* (MAMM 0099); (g). *Cervus elaphus* (MCN 3312); (h). *B. dichotomus* (MAMM 0160); (i). *Mazama nana* (MCN 3493); (j). *M. gouazoubira* (MAMM 0123); (k). *O. bezoarticus* (MCN 2965)

hemisphere, such as *Cervus elaphus* (Figure 12). A body mass of more than 200 kg is much higher than previous estimates for *Antifer* (50 kg, Fariña, Czerwonogora, & Giacomo, 2014; 120 kg, Vizcaino, Cassini, Toledo, & Bargo, 2012), which is in accordance with it having a larger skull than that of extant forms.

Our results suggest that the relative brain size of *A. ensenadensis* is expected for extant cervids with similar skull dimensions (Figures 11 and 12). In comparison with the available data on encephalization in other extant cervids and terrestrial cetartiodactyls (Orliac & Gilissen, 2012; their Table S7 and references therein), the EQ of *A. ensenadensis* is within the variation (or close to that) of representatives of most clades (Figure 14). Considering this sample, exceptions are found in comparison to hippopotamids, which seem to have a low EQ, and tayassuids, for which available data are limited (see also Finarelli, 2011 for estimates of the relative brain size of cetartiodactyls based on skull measurements). Other extinct cervids with EQs available show values similar to the extinct species, such as *Dicrocerus* Lartet, 1837 from the Neogene of Europe (EQ: 0.96; Jerison, 1973). The insular Pleistocene cervid *Candiacervus* Kuss, 1975 from Crete shows only minor changes in relative brain size in comparison to other insular mammals, such as the bovid *Myotragus* Bate, 1909, which shows a reduced relative brain size (Palombo et al., 2008). However, it does show a reduction in the size of the orbit and foramen magnum.

The EQ of *A. ensenadensis* is similar to extant forms, which suggests a maintenance of the pattern within the clade, at least over the last ~40 ka (late Pleistocene). This is in accordance with the presence of complex continental environments and communities with trophic relationships in the Pleistocene of South America (Prevosti & Vizcaino, 2006) that require complex brain structures involved in vigilance and the mobility of ungulates (Palombo et al., 2008). Data on the encephalization of the early South American cervids are necessary to analyze changes that could have occurred in Pleistocene times. In the extant comparative forms, the results for encephalization follow previous interpretations of the relative brain size of cervids (Merino et al., 2005; Wemmer & Wilson, 1987), demonstrating that smaller species have higher EQs than larger species.

Changes in encephalization through time, such as an increase in the endocranial volume under the selective pressure of predators and competition, or stabilization/reduction (negative or neutral selection)

FIGURE 15 Artistic reconstruction of the lifestyle and brain morphology of *Antifer ensenadensis* from southern Brazil. Reconstruction of the antlers is based on the specimen MCN-PV 943. Art by Márcio L. Castro

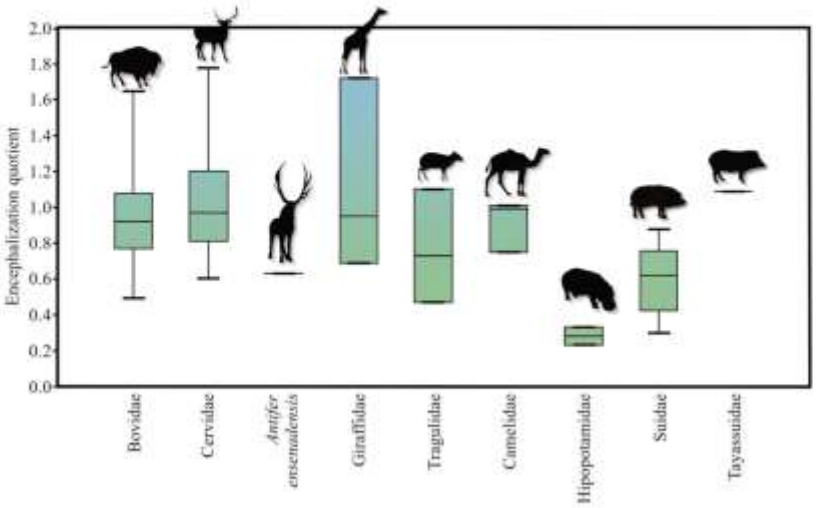

FIGURE 14 Box plot of the encephalization quotient (Eisenberg, 1981) of extant terrestrial Cetartiodactyla and the extinct *Antifer ensenadensis*. The data on the EQ is based on Orliac and Gilissen (2012; their Table S7 and references cited therein) and this study

in the cases of the absence of predators, domestication, and/or fossorial lifestyles (among others), have been documented in several mammalian groups (Bertrand et al., 2018; Dunbar, 2009; Jerison, 1973; Köhler & Moyà-Solà, 2004; Kruska, 2005; Palombo et al., 2008; Weston & Lister, 2009). However, few studies have analyzed changes in mammalian encephalization during the Cenozoic of South America (Dozo & Martínez, 2015; Fernández-Monescillo et al., 2017; Ferreira et al., 2020). It is hypothesized that, before the Great American Biotic Interchange, the predatory pressures were distinctly different (low) when compared with the moment after the arrival of the placental carnivores, which are more active predators (Fernández-Monescillo et al., 2017; Ferreira et al., 2020). Cervids, other ungulates, and large carnivorous mammals arrived in South America at a similar time and evolved in parallel over the last 2 million years. Further studies investigating cerebral changes associated with the factors mentioned above are necessary to better understand the evolution of the sensory systems of the mammals that inhabited this continent with a complex geological and biological history.

5 | CONCLUSION

In this paper, the brain endocast of the late Pleistocene extinct cervid *A. ensenadensis* (Figure 15) from southern Brazil was studied through comparative morphology, geometric morphometrics, and encephalization quotients. Our results show that this large cervid, which could have reached about 200 kg in body mass, had a brain morphologically similar to the extant forms, which show a linear allometric trend between size and shape. The pattern of encephalization of extant South American cervids was already established during the late Pleistocene.

In the future, a multidisciplinary study on the interaction between the endocranial morphology and the cranial shape, including more species and a phylogenetic approach, can potentially reveal interesting morphological integration patterns in this group. Further studies on the ontogeny and sexual dimorphism of extant forms, as well as the description of endocasts of other extinct taxa, are necessary for a better understanding of morphological variation, encephalization, and the functional implications for morphological change in the brain of these mammals that have been inhabiting the South American continent since the early Pleistocene.

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Emmanuelle Fontoura: Conceptualization; formal analysis; investigation; methodology; validation; visualization; writing-original draft; writing-review and editing. **José Ferreira:** Conceptualization; data curation; formal analysis; investigation; methodology; validation; visualization; writing-original draft; writing-review and editing. **Jamile Bubadué:** Formal analysis; investigation; methodology; validation; visualization; writing-original draft; writing-review and editing. **Ana Ribeiro:** Conceptualization; data curation; writing-review and editing. **Leonardo Kerber:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; visualization; writing-original draft; writing-review and editing.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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Supporting Information

Virtual brain endocast of *Antifer ensenadensis* (Mammalia: Cervidae), an extinct large cervid from South America

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Figure S1. Analyzed crania of *Antifer ensenadensis*. **A**. U-4922; **B**. MCN-PV 943. Scale-bar = 10 cm.

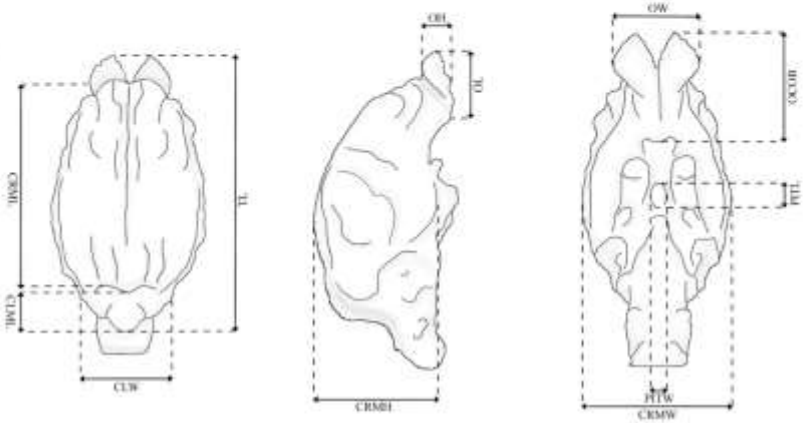

Figure S2. Linear measurements (modified from Dozo & Martinez, 2015). Abbreviations: **CRMW**, cerebrum maximum width; **PITW**, pituitary (hypophysis) total width; **PITL**, pituitary (hypophysis) total length; **OCOB**, optic chiasma length to olfactory bulbs; **OW**, olfactory bulbs width; **TL**, total length; **CLW**, cerebellum width; **CLML**, cerebellum maximum length; **CRML**, cerebrum maximum length; **CRMH**, cerebrum maximum height; **OL**, olfactory bulbs length; **OH**, olfactory bulbs height.

Taxa	Collection number	Nº slices	Voltage (KV)	Amperage (mAs)	Pixel size	Slice thickness
Antifer ensenadensis	MCN-PV 943	216	120	171.17	0.46	0.63
Antifer ensenadensis	U-4922	498	120	356.67	0.62	0.63
Mazama nana	MCN 3493	248	120	171.17	0.23	0.63
Mazama americana	MCN 2975	270	120	171.17	0.23	0.63
Mazama gouazoubira	MCN 3000	320	120	171.17	0.24	0.63
Mazama gouazoubira	MAMM 0123	330	120	191.63	0.27	0.63
Ozotocerus bezoarticus	MCN 2965	240	120	171.17	0.19	0.63
Ozotocerus bezoarticus	MAMM 0099	330	120	171.17	0.33	0.63
Blastoceus dichotomus	MCN 3009	496	120	171.17	0.27	0.63
Blastoceus dichotomus	MAMM 0160	553	120	191.63	0.64	0.63
Cervus elaphus	MCN 3312	632	120	171.17	0.40	0.63
Axis axis	MCN 3310	406	120	171.17	0.30	0.63

Table S1. Analyzed specimens and computed tomography (CT) scan parameters

Specimens	Taxa	Body mass acoording to the literature	Occipital Height (OCH) (mm)	Estimated Body mass (kg)	Estimated Brain mass (g)	EQ Jerison	EQ Eisenberg
U-4299	*Antifer ensenadensis*	120 kg (Vizcaíno, Cassini, Toledo, & Bargo, 2012)	81	206.93	298.4	0.68	0.63
MCN 3493	*Mazama nana*	15 kg (Merino, Milne, & Vizcaíno, 2005)	37.61	18.12	77.86	0.91	0.99
MCN 2975	*Mazama americana*	30-40 (kg) (Duarte & Vogliotti, 2016)	37.86	18.50	69.56	0.8	0.87
MCN 3000	*Mazama gouazoubira*	11-25kg (Black-Decima & Vogliotti, 2016)	43.08	27.88	87.43	0.77	0.81
MCN 3312	*Cervus elaphus*	126.2-186.1kg (Klinkhamer et al 2019)	79.79	197.28	322.8	0.76	0.7
MCN 3310	*Axis axis*	72-98 kg (Waring, 1996)	60.72	82.89	187.9	0.79	0.78
MCN 3009	*Blastocerus dichotomus*	100-150 kg (Duarte, Varela, D., Piovezan, Beccaceci & Garcia, 2016)	65.52	105.54	175.1	0.63	0.61
MCN 2965	*Ozotoceros bezoarticus*	30 kg (Merino, Milne, & Vizcaíno, 2005)	39.53	21.22	72.41	0.76	0.82
MAMM 0160	*Blastocerus dichotomus*	100-150 kg (Duarte, Varela, D., Piovezan, Beccaceci & Garcia, 2016)	72.58	146.05	221.8	0.64	0.6
MAMM 0099	*Ozotoceros bezoarticus*	30 kg (Merino, Milne, & Vizcaíno, 2005)	44.45	30.80	104.2	0.85	0.9
MAMM 0123	*Mazama gouzoubira*	11-25kg (Black-Decima & Vogliotti, 2016)	43.65	29.07	117.8	1	1.06

Table S2. Specimens, body and brain mass data, and encephalization coefficients.

	Antifer ensenadensis (UFMG 721)	*Mazama nana* (MCN 3493)	*Mazama americana* (MCN 2675)	*Mazama gouazoubira* (MCN 3000)	*Cervus elaphus* (MCN 3312)	*Axis axis* (MCN 3310)	*Blastocerus dichotomus* (MCN 2809)	*Ozotoceros bezoarticus* (MCN 2805)	*Blastocerus dichotomus* (MAMM 01060)	*Ozotoceros bezoarticus* (MAMM 00099)	*Mazama gouazoubira* (MAMM 01123)
Surface areas (mm²) and volume (mm³)											
Total endocast surface area	31089.10	12224.97	11881.05	13235.41	32433.70	22217.84	22069.63	11614.00	24180.03	15463.10	16382.50
Surface of the olfactory bulbs	2299.09	895.21	1037.96	1086.47	2436.35	2024.07	1976.10	2017.91	2017.91	1268.64	1277.37
Total surface area without the olfactory bulbs	28790.9	11329.76	10843.09	12148.94	29997.35	20193.76	20093.53	10580.11	22162.13	14194.46	15105.14
Neocortical surface area (both sides)	10992.08	4551.35	8339.15	4976.65	12093.86	8339.15	8079.53	4196.63	8984.89	5558.76	6180.02
Total endocast volume	313327.96	81756.65	73037.77	91797.65	338989.42	197285.74	183872.87	76025.72	232925.62	109450.25	123729.50
Olfactory bulbs volume	5964.56	1958.24	4237.76	4976.65	12093.86	8339.15	8079.53	4196.63	8984.89	5558.76	6180.02
Ratios surface areas and volumes (%)											
Neocortical surface / Total endocast surface area	35.35	37.22	35.66	37.60	37.28	37.53	36.60	36.13	37.15	35.94	37.72
Olfactory bulbs surface / Total endocast surface area	7.39	7.32	8.73	8.20	7.51	9.11	8.95	8.90	8.34	8.20	7.79
Olfactory bulbs / Total endocast volume	1.90	2.40	2.75	2.50	2.10	2.84	2.37	2.48	2.13	2.94	2.53

Table S3. Quantification of the area and volume of the analyzed endocasts.

	Antifer ensenadensis (U-4922)	*Antifer ensenadensis* (MCN PV 943)	*Mazama nana* (MCN 3493)	*Mazama americana* (MCN 2975)	*Mazama gouazoubira* (MCN 3000)	*Cervus elaphus* (MCN 3312)	*Axis axis* (MCN 3310)	*Blastocerus dichotomus* (MCN 3009)	*Ozotoceros bezoarticus* (MCN 2965)	*Blastocerus dichotomus* (MAMM 0160)	*Ozotoceros bezoarticus* (MAMM 0099)	*Mazama gouazoubira* (MAMM 0123)
PITL	9.35	----	8.51	7.03	7.29	14.39	8.053	11.32	6.49	10.93	7.98	9.12
PITW	9.88	----	12.06	8.95	9.25	18.59	12.69	14.45	7.75	16.98	10.48	11.32
OCOB	54.41	51.51	38.66	44.24	38.68	53.95	47.93	47.58	34.91	51.97	39.04	43.74
CRMW	73.41	82.74	51.67	54.14	53.16	82.06	64.55	64.77	50.66	72.05	61.94	59.84
OW	41.82	45.35	23.13	23.62	26.85	46.66	35.9	36.76	32.02	36.11	29.82	30.15
TL	143.99	137.45	87.22	90.46	95.62	140.71	122.16	115.11	80.32	130.68	95.53	102.51
CRML	111.35	101.22	65.89	58.08	73.13	110.27	93.53	84.61	67.93	105.1	67.82	92.38
CLML	23.49	21.54	17.57	18.96	15.05	21.09	20.02	20.61	12.47	13.78	19.64	22.53
CLW	35.51	44.87	23.15	24.81	30.38	46.8	34.71	42.19	24.72	43.52	26.87	31.13
OL	10.98	11.98	8.75	14.38	8.91	17.402	10.48	11.58	6.051	14.73	13.82	11.08
OH	18.6	30.82	13.82	14.82	16.67	21.63	21.9	22.11	16.28	26.12	18.71	16.49
CRMH	69.73	----	39.77	39.43	39.67	60.03	51.16	52.97	40.22	71.97	44.74	46.08
Ratios linear measurements (%)												
OCOB/ TL	37.79	37.48	44.32	48.91	40.45	38.34	39.24	41.33	43.46	39.77	40.87	42.67
OL/ TL	7.63	8.72	10.03	15.90	9.32	12.37	8.58	10.06	7.53	11.27	14.47	10.81
CRML/TL	77.33	73.64	75.54	64.21	76.48	78.37	76.56	73.50	84.57	80.43	70.99	90.12
CLML/ TL	16.31	15.67	20.14	20.96	15.74	14.99	16.39	17.90	15.53	10.54	20.56	21.98
CLW/CRMW	48.37	54.23	44.80	45.83	57.15	57.03	53.77	65.14	48.90	60.40	43.38	52.02
OW/ CRMW	56.97	54.81	44.76	43.63	50.51	56.86	55.62	56.75	63.21	50.12	48.14	50.38
OW/ CLW	117.77	----	99.91	95.20	88.38	99.70	103.43	87.13	129.53	82.97	110.98	96.85
OL/ CRMH	15.75		22.00	36.47	22.46	28.99	20.48	21.86	15.04	20.47	30.89	24.05

Table S4. Linear measurements and ratios of the analyzed endocasts.

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-1.7089319e+001 7.5167876e-001 6.8575798e+001
-1.6819349e+001 1.8461773e+001 8.0812500e+001
-1.7142305e+001 3.6980324e+001 9.2062500e+001
1.5931564e+001 1.7855946e+001 4.5748966e+001
-3.9332733e+000 2.2368126e+000 8.4270668e+000
-1.1070204e+001 -7.7333517e+000 -5.6190834e+000
ID = *Axis axis* (MCN 3310)

LM3=13
-5.8567009e+000 -2.9660364e+001 -3.6517277e+001
-5.7355938e+000 -1.9345615e+001 -4.2860489e+001
-1.5150661e+001 -2.2401585e+001 -4.3045654e+001
-5.5083008e+000 1.5517963e+000 -3.1110550e+001
6.6284943e-001 -1.2529979e+001 -3.8229321e+001
-9.0766068e+000 -9.0461912e+000 -4.2114075e+001
-1.0613098e+001 2.1612804e+001 -2.9532196e+001
6.9808083e+000 5.4888260e+001 -8.1852707e+001
-2.7214813e-001 7.7436096e+001 -8.0238373e+001
-6.2636108e+000 9.5751617e+001 -7.4111237e+001
-3.7006683e+001 5.3713867e+001 -7.1983566e+001
-1.6751556e+001 5.7073030e+000 -5.2111893e+001
-5.2158127e+000 -1.3407061e+001 -4.3165253e+001
ID = *Blastocerus dichotomus* (MAMM-0160)

LM3=13
3.1676865e+000 -3.0347607e+001 1.8591179e+001
1.0523079e+001 -3.0682024e+001 2.4168587e+001
1.3796722e+001 -2.2106810e+001 2.3942564e+001
-4.1864142e+000 -1.0647077e+001 3.7425232e+001
-3.7776489e+000 -2.7717148e+001 3.0921097e+001
6.3353119e+000 -2.3955996e+001 3.3034359e+001
-4.4347610e+000 3.0488217e+000 5.2163227e+001
-4.3529701e+000 -3.6456020e+001 9.6519363e+001
-4.1321397e+000 -1.7501842e+001 1.1321109e+002
-3.0447922e+000 -4.6749406e+000 1.3025055e+002
2.7520416e+001 -8.7374096e+000 9.5542244e+001
1.3186501e+001 -2.1630302e+001 4.8483032e+001
3.5428505e+000 -2.7653475e+001 2.9059807e+001
ID = *Blastocerus dichotomus* (MCN 3009)

LM3=13
1.3389333e+001 -3.4113358e+001 3.7530540e+001
1.6326458e+001 -3.7441616e+001 4.2735016e+001
2.6583954e+001 -3.0549152e+001 4.9282375e+001
3.0156412e+000 -1.1432748e+001 6.6180786e+001
3.7996550e+000 -3.1720572e+001 5.2456425e+001

Supplementary data and results of geometric morphometrics analyses

Supplementary Data 1. 3D geometric morphometrics coordinates positioned in the left side of the braincast for each specimen in TPS format

LM3=13
-4.5632530e+001 1.2000856e+001 9.0704414e+001
-4.3704334e+001 1.0769723e+001 8.9588905e+001
-5.2369583e+001 1.3458234e+001 8.0405807e+001
-2.9228584e+001 2.2396786e+001 6.2234207e+001
-2.6802248e+001 1.3323026e+001 7.9545120e+001
-4.5462296e+001 1.6017319e+001 7.5935486e+001
-2.8306393e+001 1.9646994e+001 2.5374802e+001
-7.4143486e+000 -3.4382790e+001 2.3847061e+001
-6.5477371e+000 -3.3475567e+001 -2.6610846e+001
-4.9896088e+000 -3.0001328e+001 -3.8729794e+001
-4.4051727e+001 -2.6563282e+001 -5.1444721e-001
-4.4722443e+001 2.6256652e+000 5.6431885e+001
-3.8033485e+001 1.3793327e+001 8.1313026e+001
ID = *Antifer ensenadensis* (U-4922)

LM3=13
-3.8854336e+001 -5.0286591e+001 3.0249451e+001
-4.1615414e+001 -4.3750175e+001 2.2260506e+001
-5.2726940e+001 -3.9613041e+001 2.6972137e+001
-3.1126671e+001 -2.0022617e+001 2.8783203e+001
-2.7701494e+001 -3.2482197e+001 2.1491779e+001
-4.1868263e+001 -3.1907768e+001 1.9528172e+001
-3.2972588e+001 3.0936072e+000 2.5367798e+001
-1.2321125e+001 1.0513676e+001 -4.8116638e+001
-1.6566906e+001 3.5982616e+001 -4.5603729e+001
-1.9344170e+001 6.2033791e+001 -4.4862885e+001
-5.9294998e+001 1.6022461e+001 -3.7892731e+001
-4.7089218e+001 -2.3254820e+001 5.5013275e+000
-3.5582390e+001 -3.7430092e+001 1.9377968e+001
ID =*Antifer ensenadensis* (MCN-PV 943)

LM3=13
-1.0599878e+001 -1.1880072e+001 -1.9114731e+001
-6.4189110e+000 -1.0849594e+001 -8.1710014e+000
2.1133423e-002 -3.2077060e+000 -7.1309948e+000
-1.7102390e+001 9.8380699e+000 7.2440338e-001
-1.7710754e+001 -5.6951885e+000 -5.3051300e+000
-5.0638275e+000 -2.5035422e+000 -1.2348728e+000
-1.6619465e+001 2.2943350e+001 1.4665985e+001

2.3276962e+001 -2.8296663e+001 5.3890461e+001
4.9216957e+000 -1.6760918e+000 7.9528633e+001
7.0209885e+000 -3.6234982e+001 1.3742120e+002
8.5396175e+000 -2.2504684e+001 1.5052780e+002
1.0836123e+001 -2.0237909e-001 1.7315372e+002
4.9360886e+001 -1.7303328e+001 1.2865833e+002
2.3969437e+001 -2.1732155e+001 7.3116470e+001
1.4166608e+001 -3.3731949e+001 4.9778454e+001
ID = *Cervus elaphus* (MCN 3312)

LM3=13
5.3964157e+000 -7.9599552e+000 -2.4203724e+001
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1.1652756e+001 -6.3115716e+000 -1.6508926e+001
1.8696404e-001 6.0340838e+000 -4.8894958e+000
2.3869038e-002 -8.8955011e+000 -1.5369560e+001
6.6699600e+000 -7.2716727e+000 -7.7774515e+000
-6.3252795e-001 1.4896349e+001 1.2041512e+001
-2.2605104e+000 -1.5307379e+001 3.4027214e+001
-2.4390059e+000 -4.5256815e+000 4.6231750e+001
-2.6685486e+000 7.4615016e+000 6.3588764e+001
2.5388184e+001 6.5158496e+000 3.3247246e+001
9.6151695e+000 -1.6814378e+000 2.1700592e+000
4.9163895e+000 -9.4061432e+000 -1.0224719e+001
ID = *Mazama americana* (MCN 2975)

LM3=13
7.0298676e+000 -3.2856041e+001 -1.0800197e+002
7.7877531e+000 -3.5534405e+001 -1.0000927e+002
1.6165157e+001 -2.8793743e+001 -9.9395515e+001
8.5888100e-001 -1.7617239e+001 -8.6825684e+001
1.6121030e+000 -3.3809120e+001 -9.6213448e+001
1.0189781e+001 -2.7927771e+001 -9.0410751e+001
-2.5728646e-001 -9.5064011e+000 -7.1443054e+001
-2.7082634e+000 -4.6292004e+001 -4.3222431e+001
-3.2119780e+000 -3.4582943e+001 -2.6401804e+001
-2.9422512e+000 -2.0708887e+001 -5.9375000e+000
2.8298477e+001 -2.2735403e+001 -4.1627235e+001
1.3979881e+001 -2.6987190e+001 -7.8201637e+001
6.8724613e+000 -3.5099129e+001 -9.5257706e+001
ID = *Mazama gouazoubira (*MAMM-0123)

LM3=13
6.5446229e+000 -1.5589555e+001 -7.9688766e+001
8.8072348e+000 -1.6311483e+001 -7.3453484e+001
1.4977116e+001 -1.2092788e+001 -7.4874626e+001

3.7615039e+000 5.2429914e-001 -6.0105099e+001
1.2909188e+000 -1.3390829e+001 -6.9544037e+001
1.0264420e+001 -1.3733306e+001 -6.7610886e+001
4.9706006e+000 8.3591852e+000 -4.8807320e+001
5.2098885e+000 -1.7031967e+001 -1.3431164e+001
6.9786158e+000 -6.9752226e+000 2.9601669e-001
8.2204275e+000 3.0979738e+000 1.2885986e+001
3.3421112e+001 3.1295099e+000 -2.2638729e+001
1.3329674e+001 -9.5228682e+000 -5.7298920e+001
6.0292130e+000 -1.4940866e+001 -7.0836685e+001
ID = *Mazama gouazoubira* (MCN 3000)

LM3=13
6.4343967e+000 -7.1414375e+000 -1.4118748e+001
8.1521969e+000 -9.5698509e+000 -1.0111309e+001
1.2848225e+001 -5.7163258e+000 -6.1979094e+000
2.0527220e+000 7.6106935e+000 5.1269617e+000
1.3848639e+000 -9.6417589e+000 -7.6571159e+000
1.1303837e+001 -6.2977934e+000 -3.4159555e+000
2.0581975e+000 1.5359430e+001 1.7939728e+001
4.3716211e+000 -1.6755791e+001 4.3629211e+001
3.8876326e+000 -4.9392467e+000 5.6166782e+001
4.8519669e+000 5.9733405e+000 7.1227913e+001
2.9139160e+001 3.2842839e+000 3.8486526e+001
1.6020035e+001 -1.3995048e+000 1.3335207e+001
6.7917957e+000 -9.5890932e+000 -7.2737637e+000
ID = *Mazama nana* (MCN 3493)

LM3=13
2.7836690e+000 -1.7278084e+001 -1.0061198e+002
4.3313808e+000 -1.9181540e+001 -9.3307320e+001
1.1007038e+001 -1.7033285e+001 -9.2308159e+001
-3.2014170e+000 1.6013132e-001 -8.1809319e+001
-3.7701879e+000 -1.6829454e+001 -8.8877754e+001
6.8417587e+000 -1.5244539e+001 -8.6580307e+001
-3.2372265e+000 8.7500010e+000 -7.2312500e+001
-5.0801086e+000 -2.0276472e+001 -4.1200630e+001
-5.3490200e+000 -2.9261690e-001 -2.2937500e+001
-5.4914675e+000 1.4759501e+001 -1.1069092e+001
2.6461037e+001 8.3453522e+000 -4.2911118e+001
6.1803665e+000 -9.8931618e+000 -7.9827736e+001
3.4433136e+000 -1.7534264e+001 -8.9210602e+001
ID = *Ozotocerus bezoarticus* (MAMM-0099)
LM3=13
5.6926403e+000 -1.4229033e+001 -2.6372940e+001
7.2353668e+000 -1.4995184e+001 -2.1686329e+001

1.4417175e+001	-1.0664001e+001	-2.5155296e+001
2.9089260e-001	1.2820542e+000	-1.3746098e+001
-1.0690427e+000	-1.4572864e+001	-2.0778553e+001
7.1101456e+000	-1.2919920e+001	-1.7128517e+001
2.9660749e-001	9.4925413e+000	-2.8177834e-001
1.9394689e+000	-2.2212023e+001	2.5051634e+001
2.7951372e+000	-1.6950975e+001	3.5720531e+001
3.0198405e+000	-5.1363152e-001	5.3684399e+001
2.7374191e+001	-3.3975008e+000	2.2561464e+001
1.0308754e+001	-8.0152922e+000	-9.4630508e+000
3.9101162e+000	-1.4809896e+001	-2.0493618e+001

ID = *Ozotocerus bezoarticus* (MCN 2965)

Table S1. Centroid size and log centroid size from the 13 landmarks positioned in the left side of the braincast for each specimen

Specimen	Centroid Size	Log Centroid Size
Antifer ensenadensis (U-4922)	182.798	5.208
Antifer ensenadensis (MCN-PV 943)	170.825	5.141
Axis axis (MCN 3310)	145.177	4.978
Blastocerus dichotomus (MAMM-0160)	161.772	5.086
Blastocerus dichotomus (MCN 3009)	143.227	4.964
Cervus elaphus (MCN 3312)	172.319	5.149
Mazama americana (MCN 2975)	105.244	4.656
*Mazama gouazoubira (*MAMM-0123)	121.760	4.802
Mazama gouazoubira (MCN 3000)	116.480	4.758
Mazama nana (MCN 3493)	106.045	4.664
'Ozotocerus bezoarticus (MAMM-0099)	115.312	4.748
Ozotocerus bezoarticus (MCN 2965)	100.636	4.612

Table S2. Variance loadings for all principal components.

	Standard deviation	Proportion of Variance	Cumulative Proportion
PC1	0.054	0.316	0.316
PC2	0.043	0.204	0.520
PC3	0.032	0.110	0.629
PC4	0.031	0.105	0.734
PC5	0.026	0.074	0.808
PC6	0.024	0.061	0.870
PC7	0.022	0.054	0.924
PC8	0.017	0.033	0.957
PC9	0.013	0.019	0.975
PC10	0.013	0.017	0.993
PC11	0.008	0.007	1.000

Table S3. PC scores for each specimen included in the analysis.

Specimen	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
A. ensenadensis (U-4922)	-0.068	0.115	-0.014	-0.008	0.008	0.018	0.005	-0.010	0.001	-0.002	-0.001
A. ensenadensis (MCN-PV 943)	-0.073	-0.052	-0.025	-0.028	0.011	0.000	-0.028	0.004	-0.012	-0.015	-0.009
A. axis (MCN 3310)	-0.038	-0.033	0.048	0.030	0.018	0.044	-0.015	0.005	0.002	0.007	0.008
B. dichotomus (MAMM-0160)	-0.048	-0.016	0.018	0.001	-0.050	-0.021	0.004	-0.011	0.016	-0.014	0.008
B. dichotomus (MCN 3009)	-0.024	0.001	-0.029	-0.025	-0.017	-0.015	0.001	0.028	-0.007	0.023	0.010
C. elaphus (MCN 3312)	-0.030	-0.031	-0.016	0.035	0.035	-0.031	0.028	-0.025	-0.006	0.008	0.002
M. americana (MCN 2975)	0.079	0.013	0.003	0.007	-0.029	0.005	-0.021	-0.023	-0.025	0.001	0.003
M. gouazoubira (MAMM-0123)	0.037	-0.006	-0.015	-0.003	0.000	-0.003	-0.030	-0.012	0.025	0.018	-0.010
M. gouazoubira (MCN 3000)	0.001	-0.004	0.043	0.006	-0.023	0.002	0.032	0.013	-0.007	0.005	-0.017
M. nana (MCN 3493)	0.049	0.015	-0.037	0.063	0.001	-0.001	-0.002	0.026	0.004	-0.015	0.000
O. bezoarticus (MAMM-0099)	0.052	0.029	0.049	-0.032	0.038	-0.033	-0.009	0.010	0.002	-0.008	0.004
O. bezoarticus (MCN 2965)	0.062	-0.032	-0.026	-0.044	0.008	0.035	0.034	-0.005	0.007	-0.007	0.004

Table S4. Regression scores for each specimen from allometric model

Specimen	Regression Score	Log Centroid Size
Antifer ensenadensis (U-4922)	0.076	5.208
Antifer ensenadensis (MCN-PV 943)	0.070	5.141
Axis axis (MCN 3310)	0.032	4.978
Blastocerus dichotomus (MAMM-0160)	0.045	5.086
Blastocerus dichotomus (MCN 3009)	0.023	4.964
Cervus elaphus (MCN 3312)	0.034	5.149
Mazama americana (MCN 2975)	-0.077	4.656
Mazama gouazoubira (MAMM-0123)	-0.034	4.802
Mazama gouazoubira (MCN 3000)	-0.006	4.758
Mazama nana (MCN 3493)	-0.047	4.664
Ozotocerus bezoarticus (MAMM-0099)	-0.048	4.748
Ozotocerus bezoarticus (MCN 2965)	-0.066	4.612

2.2 DATASET

morphomuseum

Dataset

3D models related to the publication: Virtual brain endocast of *Antifer* (Mammalia: Cervidae), an extinct large cervid from South America

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Abstract
The present 3D Dataset contains the 3D models of the brain endocast analyzed in "Virtual brain endocast of Antifer (Mammalia: Cervidae), an extinct large cervid from South America".

Keywords: *Antifer* ensenadensis, brain endocast, Cervidae, late Pleistocene

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Inv nr.	Collection
U-4922	UNISINOS
MCN-PV943	MCN-PV

Table 1. List of brain endocasts of *Antifer ensenadensis*. **MCN-PV**: paleontological collection of the Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **UNISINOS**: paleontological collection of the Universidade do Vale do Rio dos Sinos, São Leopoldo, Brazil.

INTRODUCTION

A diverse fossil record of Cervidae (Mammalia) has been recorded in South America since the early Pleistocene after these animals arrived during the Great American Biotic Interchange. With the advent of the CT-Scanning techniques, it is now possible to access the endocranial morphology of extinct species. *Antifer ensenadensis* is an extinct South American cervid characterized by the wide and robust antlers lateralized on the skull when compared to other Odocoileini. Foutoura et al. (2020) analyzed the brain endocast of this extinct cervid generated using computed tomography scan data. This contribution contains the 3D models studied by them (Fig. 1 and table 1; Fontoura et al. 2020).

METHODS

Two specimens of *Antifer ensenadensis* from the late Pleistocene of southern Brazil were studied. The specimens (U-4922 and MCN-PV 943) were analyzed using a Philips Brilliance 16-Slice CT Scanner. The analysis (parameters: voltage 120 kV; amperage 356.67 mAs; pixel size 0.62 µm) generated a total of 498 slices for U-4922, and 216 slices (parameters: voltage 120 kV; amperage 171.17 mAs; pixel size 0.46 µm) for MCN-PV 943. The tomograms were imported into software Avizo for virtual reconstruction and virtual segmentation of structures. After applying the methodology to reconstruct the brain endocast of *Antifer ensenadensis*, two endocasts were generated. From specimen U-4922, it was possible to reconstruct the entire endocast (although it was not possible to reconstruct the dorsal surface precisely due to the preservation of the specimen), while for specimen MCN-PV 943, which does not preserve the basicranial region, only the dorsal portion of the endocast was reconstructed. Casts of the olfactory bulbs and cerebral hemispheres were reconstructed, but not the cerebellar region and nerves on the ventral portion of the endocast. Although MCN-PV 943 lacks some regions, the neopallium morphology was better preserved in this specimen (see Fontoura et al. 2020 for details). The 3D surface models are provided in .ply format, and can therefore be opened with a wide range of freeware.

ACKNOWLEDGEMENTS

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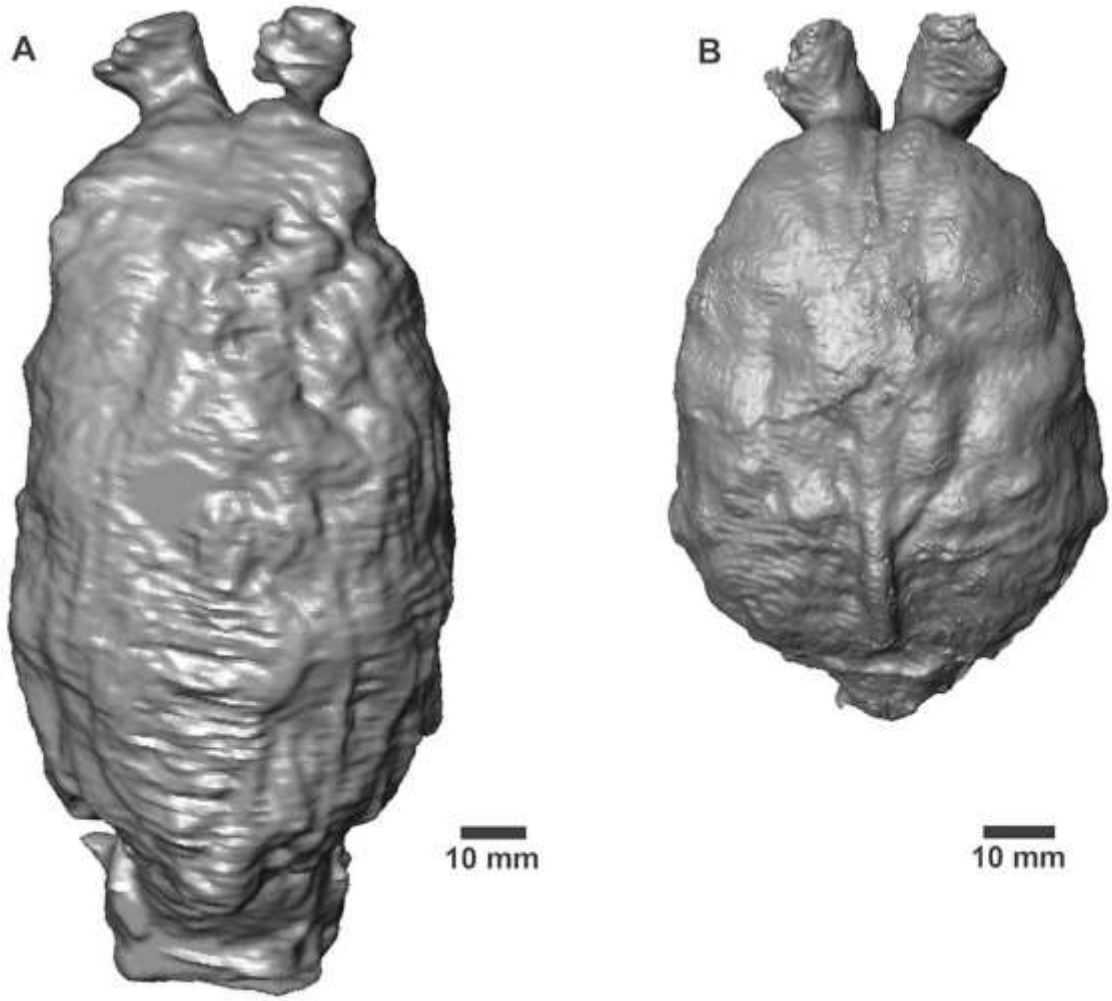

Figure 1. 3D models of the brain endocast of *Antifer ensenadensis* from the late Pleistocene of southern Brazil. Brain endocast of U-4922 (A) and MCN PV 943 (B), in dorsal views.

CAPÍTULO 3 – *CONSIDERAÇÕES FINAIS*

3. CONSIDERAÇÕES FINAIS

Este trabalho é o primeiro estudo comparativo de paleoneurologia de cervídeos sul-americanos. Em suma, os resultados desta dissertação demonstram que *A. ensenadensis* foi um dos maiores cervídeos sul-americanos e seu molde endocraniano assemelha-se as formas de cervídeos atuais, sendo que a forma e o tamanho dos moldes endocranianos estão fortemente relacionados. O coeficiente de encefalização dos cervídeos sul-americanos demonstra estabilidade desde o final do Pleistoceno.

3.1 MORFOLOGIA COMPARADA

O molde endocraniano de *Antifer ensenadensis* foi analisado na presente dissertação, em comparação com os cervídeos sul-americanos *Mazama nana*, *Mazama gouazoubira*, *Mazama americana*, *Ozotoceros bezoarticus*, *Blastocerus dichotomus*, e os cervídeos do hemisfério norte *Axis axis* e *Cervus elaphus*, utilizando tomografia computadorizada, coeficiente de encefalização e morfometria geométrica.

Dois espécimes de *A. ensenadensis* foram tomografados e seus moldes endocranianos foram gerados. O primeiro (U-4922) apresentou algumas deformações tafonômicas, mas ainda permitindo reconstruir todo modelo endocraniano, enquanto o segundo espécime (MCN-PV 943) estava sem deformações, mas não possuía a região dorsal preservada.

Constatou-se que o molde endocraniano cerebral de *Antifer ensenadensis* é girencefálico, assim como nos demais cervídeos. De uma forma geral, o molde endocraniano do espécime U-4922 é ântero-posteriormente alongado, assemelhando-se à *Axis axis* e diferenciando-se de *Ozotoceros bezoarticus*. Em relação ao formato, *A. ensenadensis* possui uma forma romboide; *O. bezoarticus* e *Mazama. nana* uma forma arredondada; e *A. axis*, *Blastocerus dichotomus* e *Cervus elaphus* uma forma subquadrangular. As áreas da superfície neocortical e do bulbo olfativo possuem pouca variação entre os espécimes analisados.

O rinencéfalo de *A. ensenadensis* é semelhante aos outros cervídeos, contudo, o lobo piriforme não é tão desenvolvido quanto a região temporal-occipital do hemisfério cerebral. Em ambos espécimes de *A. ensenadensis*, o pedúnculo olfatório

é robusto, sendo em MCN-PV 943 levemente mais alongado anteriormente. Os bulbos olfatórios apresentam-se individualizados, localizados ventralmente na região anterior do molde encefálico. Todos os espécimes analisados apresentaram os bulbos olfatórios orientados levemente em sentido lateral e ventralmente oblíquos em relação ao eixo horizontal que passa no molde encefálico.

Dorsalmente, o seio sagital superior é bem marcado, dividindo os hemisférios cerebrais. Dentro da amostra analisada, a presença de um seio sagital superior proeminente é compartilhada com *A. ensenadensis* e *Blastocerus dichotomus*. Na região mais posterior do molde está presente o sulco transversal. A fissura rinal forma um sulco ântero-posteriormente orientado e é bem marcada na região anterior dos moldes. O sulco cruciato também é visível e percorre o molde ântero-lateralmente. Dorsalmente posicionado na região anterior do molde, está presente o sulco ansato, sendo este confluente anteriormente com o sulco coronal. Em vista lateral, é visualizado o sulco diagonal paralelo ao sulco suprasilviano, o qual delimita o lobo temporal. Em vista dorsal, o sulco lateral é paralelo a linha medial do encéfalo.

Em todos os espécimes, o mesencéfalo é recoberto pelo neocórtex. A região cerebelar é parcialmente recoberta pelo neocórtex, sendo visível a região mais posterior do vermis – o qual se projeta mais dorsalmente. A fissura transversal é proeminente em todos os espécimes (exceto em U-4922) e o paraflóculos é visível, porém não é bem delimitado.

Na face ventral, as impressões foramens que transmitem os nervos cranianos estão presentes nos espécimes, sendo eles: forame óptico (saída do nervo cranial II), fissura esfenorbital (saída dos nervos craniais III (oculomotor), IV (troclear), V (trigêmeo) e seus ramos V_1 (oftálmico) e V_2 (maxilar), VI (abducente) em cetartiodáctilos terrestres), forame oval (saída do nervo V_3, ramo do nervo trigêmeo) e em alguns espécimes é possível ver o quiasma óptico. A glândula pituitária (hipófise) está localiza na linha medial, entre as impressões da fissura esfenorbital e forame oval. A menor e maior largura da hipófise está presente em *A. ensenadensis* e *Cervus elaphus*, respectivamente. Mais posteriormente, está a impressão do meato auditivo interno, saída do nervo cranial VII (facial) e VIII (vestibulococlear). A medula oblongata é longa, lateralmente a ela está a impressão do nervo craniano XII (hipoglosso).

Na amostra comparativa, também se observou a presença de variação ontogenética. O espécime jovem sem sexo definido de *Ozotoceros bezoarticus*

apresenta o lobo frontal projetado anteriormente e o sulco longitudinal pouco desenvolvido em comparação com o espécime adulto. Também é visível que a área dos bulbos olfatórios e do neocórtex é maior, em relação a área total.

3.2 MORFOMETRIA GEOMÉTRICA

Na análise de morfometria geométrica, concluiu-se que os componentes de variação (PC1, PC2, PC3 e PC4) explicam 73.43% da variação endocraniana, sendo *Antifer ensenadensis* a forma extrema. O encéfalo possui uma relação entre forma e tamanho (=alometria) forte e significante, sendo que o tamanho explica 28.5% da variação da forma. Os padrões alométricos dos moldes endocranianos demonstram que, a medida que o tamanho aumenta, há a expansão dos hemisférios cerebrais e os bulbos olfativos se posicionam mais lateralmente. Esse padrão é compartilhado entre os grandes cervídeos sul-americanos (*A. ensenadensis* e *Blastocerus dichotomus*) e os espécimes do grupo Cervini (*Axis axis* e *Cervus elaphus*).

3.3 MASSA CORPÓREA, ENCEFALIZAÇÃO E ECOLOGIA

Este estudo demonstrou que *Antifer ensenadensis* é um dos maiores cervídeos sul-americanos que já existiram, podendo ter atingido mais de 200 kg. Os coeficientes de encefalização (EQ) de *A. ensenadensis* foram de 0,68 (JERISON, 1973) e 0,63 (EISENBERG, 1981), e a variação dos cervídeos atuais foi de 0,60 a 1,06 (EISENBERG, 1981) e 0,64 a 1 (JERISON, 1973), sendo observado que os menores espécimes possuem os maiores EQs.

A pressão seletiva influencia na encefalização cerebral de mamíferos (JERISON, 1973, WOUTER, 2018). Espécies que sofrem maior predação e competição tendem a possuir coeficientes de encefalização maiores, enquanto em espécies com menor pressão seletiva, tende a ocorrer o oposto (JERISON, 1973). É conhecido que a pressão seletiva de predadores, competição, seleção neutra ou negativa, domesticação, hábitos fossoriais, procura de alimento entre outros, pode modificar o grau de encefalização ao longo do tempo em diversos grupos de mamíferos (BERTRAND et al., 2018; DUNBAR, 2009; JERISON, 1973; KÖHLER e MOYÀ-SOLÀ, 2004; KRUSKA, 2005; PALOMBO et al., 2008; WESTON e LISTER,

2009). Por exemplo, animais insulares e domésticos tendem a ter menores EQs do que seus parentes mais próximos que habitam regiões continentais ou parentes selvagens, no caso da domesticação (vide discussão em FERREIRA et al. 2020). Sabe-se que espécies de menor tamanho i) tendem a especializar-se em alimentos de melhor qualidade (DUNBAR, 2009) e consequentemente sofrem maior competição; ii) sofrem maior predação devido ao seu tamanho (JERISON, 1973, WOUTER, 2018). Logo, tais aspectos poderiam explicar a variação nos coeficientes de encefalização entre espécies menores (coeficientes maiores) e maiores (coeficientes menores) dentro da amostra analisada.

O grau de encefalização de *Antifer* está dentro da variação dos cervídeos sul-americanos atuais, sugerindo uma manutenção desse padrão dentro do clado desde pelo menos o final do Pleistoceno (últimos 120 mil anos). Essa hipótese pode ser explicada pela presença de um ambiente complexo e relações tróficas múltiplas durante o Pleistoceno, o que exige a presença estruturas neurológicas também complexas. Tem-se hipotetizado que a pressão evolutiva da predação sobre a encefalização dos herbívoros terrestres era reduzida até o Grande Intercâmbio Biótico Americano ocorrer, momento em que grandes predadores carnívoros dispersaram-se na América do Sul (FERNÁNDEZ-MONESCILLO et al., 2017; FERREIRA et al., 2020). Juntamente com esses carnívoros, os cervídeos e outros cetartiodáctilos terrestres ingressaram no nosso continente, evoluindo paralelamente pelos últimos 2 milhões de anos. Tais relações entre encefalização e predação durante o Pleistoceno sul-americano ainda necessitam ser estudadas.

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