



UNIVERSIDADE FEDERAL DE SANTA MARIA
CENTRO DE CIÊNCIAS NATURAIS E EXATAS
PROGRAMA DE PÓS-GRADUAÇÃO
EM BIODIVERSIDADE ANIMAL



Arymathéia Santos Franco

**MORFOLOGIA DA CAVIDADE NASAL DE CINODONTES
TRAVERSODONTIDAE (EUCYNODONTIA: GOMPHODONTIA) DO
TRIÁSSICO SUPERIOR DO RIO GRANDE DO SUL**

Santa Maria, RS

2021

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(EUCYNODONTIA: GOMPHODONTIA) DO TRIÁSSICO SUPERIOR DO RIO
GRANDE DO SUL**

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

Santa Maria, RS

2021

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001

Franco, Arymathéia Santos
Morfologia da cavidade nasal de cinodontes
Traversodontidae (Eucynodontia: Gomphodontia) do
Triássico superior do Rio Grande do Sul / Arymathéia
Santos Franco.- 2021.
46 p.; 30 cm

Orientador: Leonardo Kerber
Dissertação (mestrado) - Universidade Federal de Santa
Maria, Centro de Ciências Naturais e Exatas, Programa de
Pós-Graduação em Biodiversidade Animal, RS, 2021

1. Therapsida 2. Tomografia Computadorizada 3.
Morfologia Endocraniana 4. Anatomia Comparada 5.
Cinodontes I. Kerber, Leonardo II. Título.

Sistema de geração automática de ficha catalográfica da UFSM. Dados fornecidos pelo autor(a). Sob supervisão da Direção da Divisão de Processos Técnicos da Biblioteca Central. Bibliotecária responsável Paula Schoenfeldt Patta CRB 10/1728.

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Aprovado em 20 de Março de 2020

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Santa Maria, RS
2021

AGRADECIMENTOS

- Aos meus familiares, pais, Margarida Rosa dos Santos e José de Arimatéia Franco pelo amor e apoio incondicional e principalmente pelo incentivo e apoio o tempo inteiro, minha irmã Amanda Santos Franco, e minha amada avó Maria Rosa dos Santos;
- Ao meu orientador Leonardo Kerber, por todo tempo dedicado a me ensinar e guiar nessa jornada;
- Aos amigos de longa data e aos novos que conheci neste período que me mudei para o Rio Grande do Sul desde 2017, que sempre me ajudaram e apoiaram, e em especial Fernando Borges, Matheus Marcos, Bruno Vinicius, Christian Felipe, Carlos Vinicius, Matheus Scherer, André OCG, Guilherme Mota meus irmãos de coração, muito obrigado pela amizade, por acreditar na minha capacidade e pelo grande incentivo durante o processo seletivo e ao longo da pós-graduação;
- Aos meus professores^a Rafaela Nazário, Natália Romão, Jéssica Silva, Carlos, Marcos Machado e Diego Jung, que foram essenciais da minha caminhada como aluno e ser humano;
- Ao doutor Sérgio Cabreira que me guiou nesta caminhada, pessoa a qual tive a oportunidade de trabalhar junto por um ano
- Aos colegas do Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia (CAPPA), em especial Rodrigo Müller pela ajuda, sugestões e discussões ao longo do mestrado;
- Aos coautores do trabalho bem como os membros da banca que prontamente aceitaram o convite;
- À Coordenação e Secretaria do Programa de Pós-Graduação em Biodiversidade Animal da UFSM, pela disponibilidade de infraestrutura para preparação e estudo dos materiais desta dissertação, em especial o secretário Sidnei pela orientação e ajuda relacionadas ao PPG;
- À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela bolsa de estudo (001); Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul (FAPERGS 17/2551-0000816-2) e Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 422568/2018-0), pelo financiamento concedido para o desenvolvimento do projeto.

RESUMO

MORFOLOGIA DA CAVIDADE NASAL DE CINODONTES TRAVERSODONTIDAE (EUCYNODONTIA: GOMPHODONTIA) DO TRIÁSSICO SUPERIOR DO RIO GRANDE DO SUL

AUTOR: Arymathéia Santos Franco

ORIENTADOR: Leonardo Kerber

Traversodontidae é um grupo de cinodontes não-Mammaliaformes herbívoros/onívoros que viveram durante o período Triássico. Esses animais compõem a linhagem mais diversificada dentro do clado Cynognathia. No sul do Brasil, um registro muito diversificado de fósseis de cinodontes do final do Triássico Médio e Superior tem sido documentado, onde *Exaeretodon riograndensis* e *Siriusgnathus niemeyerorum* representam dois traversodontídeos abundantes e bem documentados. A presente dissertação fornece uma análise comparativa da morfologia da cavidade nasal, recessos, ducto nasolacrimal e canais maxilares de ambas as espécies por meio da utilização de tomografia computadorizada, destacando as modificações que ocorreram paralelamente à origem dos mamíferos. Para isso, três crânios dos espécimes melhor preservados foram tomografados e posteriormente os tomogramas foram analisados, modelos tridimensionais foram gerados e comparados com outros cinognátios e probainognátios. Os resultados demonstram que não haviam turbinas ossificadas ou placa cribiforme delimitando a extremidade posterior da cavidade nasal, sugerindo que essas estruturas eram provavelmente cartilaginosas, assim como nos demais cinodontes não-Mammaliaformes. Ambas as espécies apresentam cristas laterais na superfície interna do teto da cavidade nasal, mas a crista mediana para a inserção de um septo nasal está ausente. Ambos os táxons apresentam recessos na região dorsal da cavidade nasal, que aumentam o volume da cavidade nasal, potencializando o tamanho da câmara olfatória, possivelmente contribuindo para o olfato desses animais. Na região lateral da cavidade nasal, os táxons analisados apresentam recesso maxilar bem desenvolvido. Embora *E. riograndensis* e *S. niemeyerorum* tenham uma cavidade nasal aproximadamente semelhante, no primeiro táxon, o espaço entre os recessos dorsais esquerdo e direito da cavidade nasal é uniforme em toda a sua extensão, ao passo que esse espaço se estreita posteriormente em *S. niemeyerorum*. Finalmente, o ducto nasolacrimal de *S. niemeyerorum* é mais inclinado ântero-posteriormente do que em *E. riograndensis*.

Palavras-Chave: Therapsida, tomografia Computadorizada, morfologia endocraniana, anatomia comparada.

ABSTRACT

THE NASAL CAVITY OF TWO TRAVERSODONTID CYNODONTS (EUCYNODONTIA: GOMPHODONTIA) FROM THE UPPER TRIASSIC OF BRAZIL

AUTHOR: Arymathéia Santos Franco

ADVISOR: Leonardo Kerber

Traversodontidae is a group of Triassic herbivorous/omnivorous cynodonts that represents the most diversified lineage within Cynognathia. In southern Brazil, a rich fossil record of late Middle/mid-Late Triassic cynodonts has been documented, with *Exaeretodon riograndensis* and *Siriusgnathus niemeyerorum* representing two abundant and well-documented traversodontids. The present master's dissertation provides a comparative analysis of the morphology of the nasal cavity, recesses, nasolacrimal duct, and maxillary canals of both species using computed tomography, highlighting the changes that occurred in parallel to the origin of mammaliaforms. Three crania that represent the best-preserved specimens of these species were scanned, the tomograms were analyzed, and three-dimensional models were generated. After these procedures, the nasal morphology was compared to other representatives of Cynognathia and Probainognathia. Our results show that there were no ossified turbinals or a cribriform plate delimiting the posterior end of the nasal cavity, suggesting these structures were probably cartilaginous as in other non-mammaliaform cynodonts. Both species show lateral ridges on the internal surface of the roof of the nasal cavity, but the median ridge for the attachment of a nasal septum is absent. *Exaeretodon riograndensis* and *S. niemeyerorum* show recesses on the dorsal region of the nasal cavity, which increase the volume of the nasal cavity, potentially enhancing the olfactory chamber and contributing to the sense of smell. On the lateral sides of the nasal cavity, the analyzed taxa show a well-developed maxillary recess. Although *E. riograndensis* and *S. niemeyerorum* have a roughly similar nasal cavity, in the former taxon, the space between the left and right dorsal recesses of the nasal cavity is uniform along its entire extension, whereas this space narrows posteriorly in *S. niemeyerorum*. Finally, the nasolacrimal duct of *S. niemeyerorum* is more inclined anteroposteriorly than in *E. riograndensis*.

Keywords: Therapsida, computed tomography, endocranial morphology, comparative anatomy.

Abreviaturas institucionais

CAPPA/UFSM, Centro de Apoio à Pesquisa Paleontológica da Universidade Federal de Santa Maria, São João do Polêsine, Brasil;

MACN-Pv, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” colección de Paleontología de Vertebrados, Buenos Aires, Argentina;

MCP, Museu de Ciência e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brasil;

PVSJ, Universidad Nacional de San Juan, San Juan, Argentina;

TMM, Texas Memorial Museum, Austin, Texas, USA;

UCMP, University of California Museum of Paleontology, Berkeley, California, Estados Unidos;

UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil

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APRESENTAÇÃO DA ESTRUTURA DA DISSERTAÇÃO

A presente dissertação de mestrado objetiva descrever a morfologia endocraniana da cavidade nasal de dois cinodontes Traversodontidae do Triássico Superior do sul do Brasil, e analisar suas implicações paleobiológicas. A dissertação foi elaborada em forma de artigo científico de acordo com as normas do Manual de Dissertações e Teses da UFSM (MDT), e integra os requisitos necessários para a obtenção do título de Mestre em Biodiversidade Animal, pelo Programa de Pós-Graduação em Biodiversidade Animal da Universidade Federal de Santa Maria.

O **capítulo 1** é composto por uma contextualização sobre o tema de estudo, os cinodontes não-Mammaliaformes e o estudo da cavidade nasal no grupo e a relevância da tomografia computadorizada neste tipo de abordagem. Detalhes metodológicos estão descritos no artigo científico, e por questões de brevidade, não são mencionados no texto integrador.

O **capítulo 2** inclui o artigo científico, já publicado no *Journal of Paleontology*.

No **capítulo 3** são apresentadas as considerações finais bem como as referências referentes ao introdutório.

CAPITULO 1 – *ASPECTOS INTRODUTÓRIOS*

1.1 INTRODUÇÃO

1.1.1 Cinodontes não-Mammaliaformes do sul do Brasil

Durante Permiano, o clado Therapsida, que por sua vez é incluído em Synapsida, foi representado por ampla variedade de formas que são inclusas em seis clados menos inclusivos: Biarmosuchia, Gorgonopsia, Therocephalia, Dinocephalia, Anomodontia e Cynodontia (ANGIELCZYK, 2009). Essa diversidade de grupos perdurou até o final da Era Paleozoica, no intervalo de tempo da transição Permo-Triássica, onde crises bióticas levaram a uma das maiores transições faunísticas já registradas. Entre os fatores que levaram a essa grande extinção em massa, destaca-se a atividade tectônica e vulcanismo com emissão de gases tóxicos para a atmosfera resultando na alteração no ciclo de carbono e redução do oxigênio livre, gerando efeito estufa e precipitação do carbono nos oceanos, transformando-os em ambientes anóxicos (BENTON, 2016; BUTTON et al., 2017; EZCURRA et al., 2017; SONG et al., 2020). Com uma ampla gama de “nichos vazios” durante os primeiros estágios do Triássico Inferior, Olenekiano e Induano, alguns representantes dos anomodontes, terocefálios e cinodontes sobreviveram a essa extinção e passaram a se diversificar. Entretanto, terocefálios foram extintos ao início do Triássico Médio (ABDALA E RIBEIRO, 2012).

Particularmente, o clado Cynodontia, de maior interesse aqui, se diversificou durante o Triássico, e ao final desse intervalo de tempo, deu origem ao clado Mammaliaformes, que por sua vez inclui Mammalia (CROMPTON et al., 2017; ABDALA et al., 2020). Logo, a compreensão da evolução morfológica dos mamíferos está fundamentada no estudo das formas triássicas que precedem a origem do grupo (FRÖBISCH 2008; ABDALA e RIBEIRO, 2012). Entre as principais características morfológicas que emergiram nesses animais, destaca-se a diferenciação da morfologia pós-canina, a presença de dois côndilos occipitais para articulação com a coluna vertebral, o desenvolvimento de um palato secundário ósseo, e o surgimento de uma fossa massetérica mandibular, caracteres que surgiram logo após a origem do grupo (ABDALA e RIBEIRO, 2012; ABDALA e GAETANO, 2018).

O clado Cynodontia (Figura 1) inclui o grupo Eucynodontia, que possui duas maiores divisões - Cynognathia e Probainognathia (LIU e OLSEN, 2010; WALLACE et al., 2019), sendo que os cinognatios evoluíram paralelamente aos probainognátios

e se extinguíram durante o final do Triássico. Fósseis dos cinodontes não-Mammaliaformes (isto é, formas que não incluem o clado Mammaliaformes) são abundantes em rochas triássicas da Bacia do Paraná no Estado do Rio Grande do Sul. Com grande diversidade no registro fóssil entre o Triássico Médio e Superior do Brasil, os cinodontes são encontrados em quatro diferentes zonas de associação (ZA) (vide abaixo) (ABDALA e RIBEIRO, 2012; ABDALA e GAETANO 2018; MARSOLA et al., 2018; MIRON et al., 2020; SCHULTZ et al., 2020).

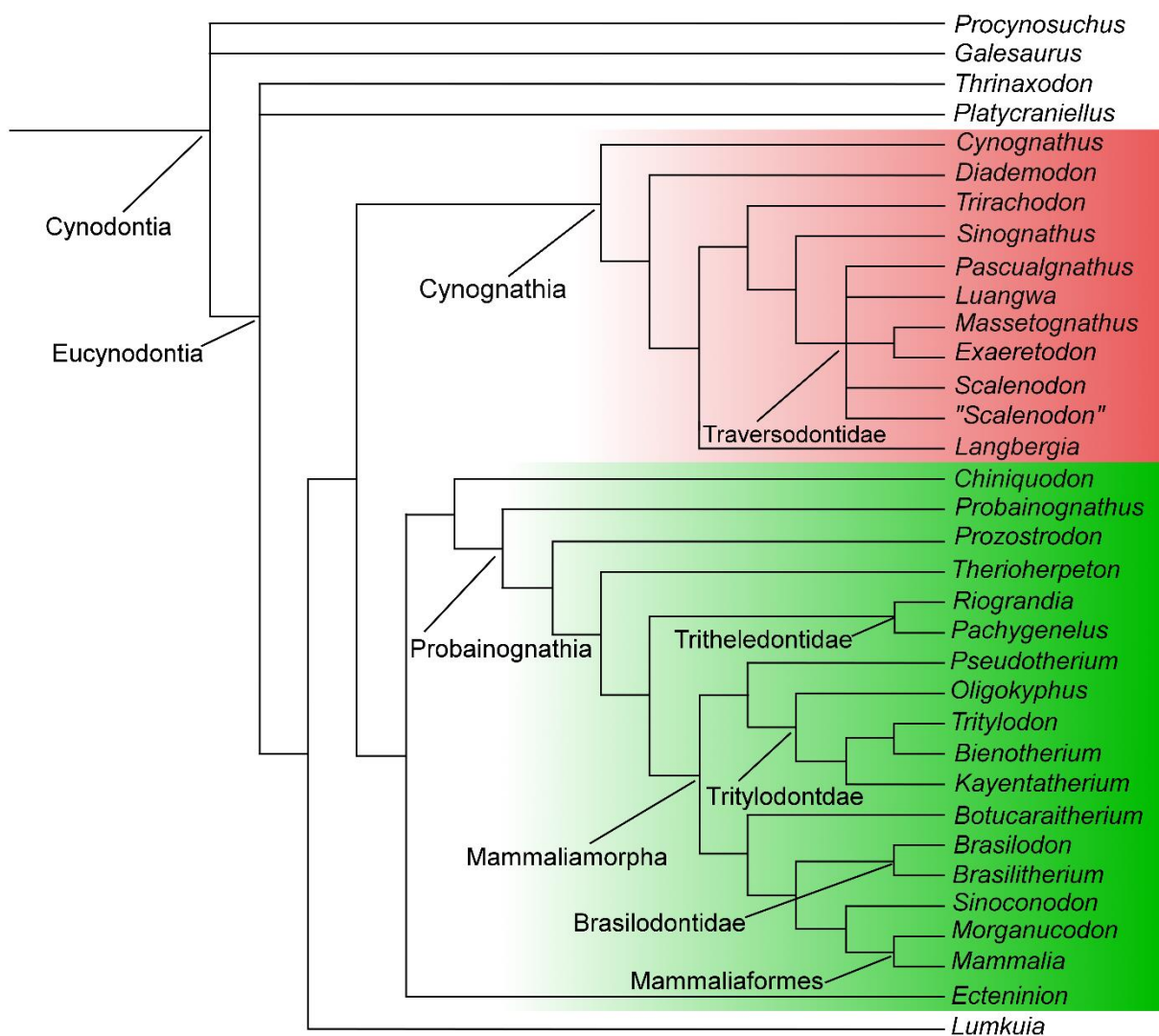


Figura 1. Relações filogenéticas de Eucynodontia evidenciando a dicotomia entre os clados Cynognathia (em verde) e Probainognathia (em vermelho). Modificado de WALLACE et al., (2019).

O clado Cynognathia, inclui Gomphodontia, composto por Diademodontidae, Trirachodontidae e Traversodontidae (Figura 2), que é o grupo mais diversificado de cinognátios e de distribuição cosmopolita. O clado surgiu no estágio Anisiano (Triássico Inferior) e se estendeu até o Noriano (MIRON et al., 2020). Dos 96 gêneros de cinodontes não-Mammaliaformes conhecidos deste período, 12 são traversodontídeos coletados na supersequência Santa Maria no Sul do Brasil (ABDALA et al., 2020). Uma das características mais peculiares dos Traversodontidae está em sua dentição pós-canina: seus dentes superiores são transversalmente expandidos com um contorno retangular e os inferiores têm formas quadrangulares em vista oclusal, o que sugere uma adaptação a herbivoria e onivoria (RAY, 2015; ABDALA, 2019; HENDRICKX et al., 2020).

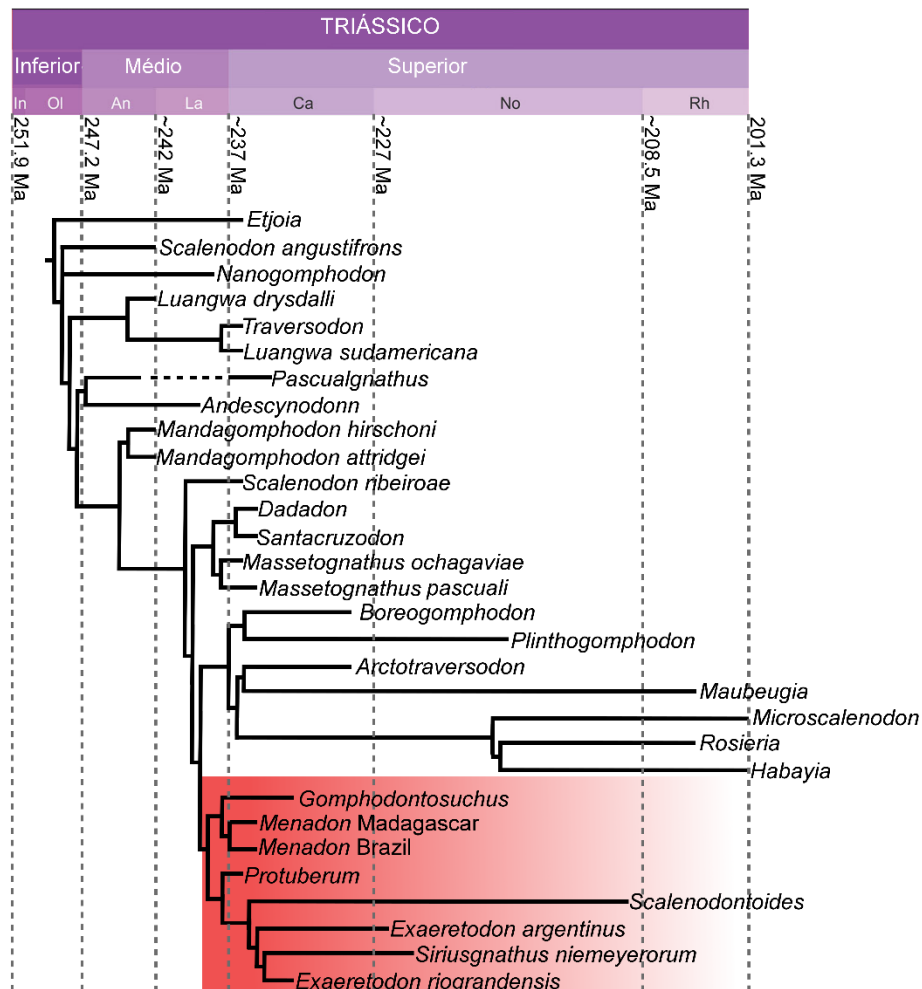


Figura 2. Relações filogenéticas e distribuição temporal de Traversodontidae. Em vermelho, o clado Gomphodontosuchinae, que inclui *Exaeretodon* e *Siriusgnathus*, táxons de interesse no presente trabalho. Modificado de HENDRICKX et al. (2020).

Como mencionado acima, no Rio Grande do Sul, fósseis de cinodontes são abundantes e os de traversodontídeos têm sido encontrados em zonas referentes ao Triássico Médio e Superior, da Supersequência Santa Maria (SCHULTZ et al., 2020). Na ZA *Dinodontosaurus* (Sequência Pinheiros-Chiniquá, Ladiniano/Carniano), foram registrados *Traversodon stahleckeri* HUENE, 1936 *Massetognathus ochagaviae* BARBERENA, 1981, *Protuberum cabralensis* REICHEL, SCHULTZ e SOARES, 2009, *Luangwa sudamericana* ABDALA e TEIXEIRA, 2004 e *Scalenodon ribeiroae* MELO et al., 2017. Na ZA *Santacruzodon* (Sequência Santa Cruz, Carniano) foram encontrados *Santacruzodon hopsoni* ABDALA e RIBEIRO, 2003, *Menadon besairiei* MELO et al., 2015 e *Massetognathus* sp. (SCHMITT et al., 2019). Na ZA *Hyperodapedon* (Sequência Candelária, Carniano), fósseis de *Gomphodontosuchus brasiliensis* HUENE, 1928 (vide HOPSON, 1985) e *Exaeretodon riograndensis* ABDALA et al., 2002. Recentemente, um novo traversodontídeo, *Siriusgnathus niemeyerorum* PAVANATTO et al., 2018, foi descrito para esta ZA. Inferências sobre a idade das camadas de onde os fósseis da espécie são provenientes tem sugerido que a mesmas seriam mais jovens do que as da ZA *Hyperodapedon*, podendo pertencer a ZA *Riograndia* (Sequência Candelária, Noriano), a zona de associação de vertebrados mais jovem das camadas sul-rio-grandenses, ou ainda a níveis intermediários entre a ZA *Hyperodapedon* e a ZA *Riograndia* (ver MIRON et al., 2019; MARTINELLI et al., 2020).

Na presente dissertação fósseis de *E. riograndensis* e *S. niemeyerorum* são analisados. Ambos táxons representam dois traversodontídeos abundantes e bem conhecidos, principalmente através de fósseis encontrados na região de Agudo, Rio Grande do Sul (Figura 3). Ambos traversodontídeos também representam as maiores formas encontradas no Brasil, com crânios adultos de até 25 cm de comprimento já relatados. A osteologia de *E. riograndensis* foi estudada por ABDALA et al. (2002), OLIVEIRA et al. (2007) e LIPARINI et al. (2013), e de *S. niemeyerorum* por PAVANATTO et al. (2018) e MIRON et al. (2019). Recentemente, a morfologia endocraniana da cavidade encefálica de ambos os cinodontes foi estudada por PAVANATTO et al. (2019).

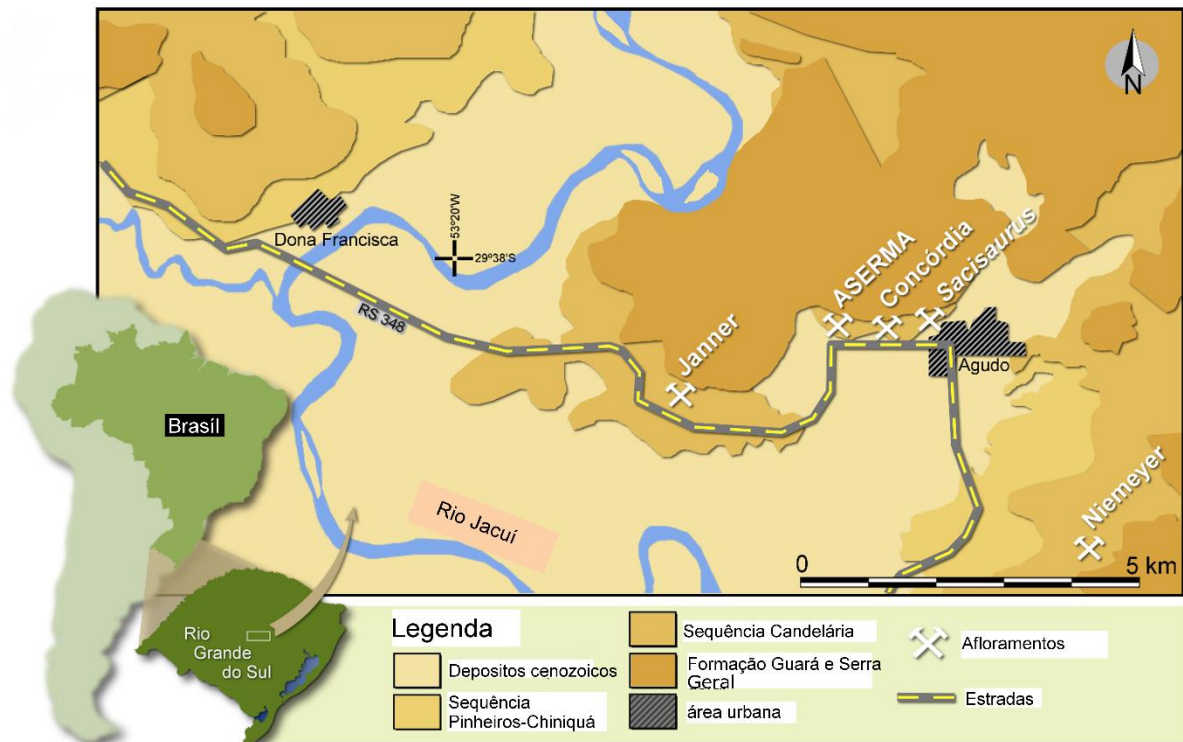


Figura 3. Afloramentos fossilíferos da região de Agudo, Rio Grande do Sul. Os fósseis aqui analisados são provenientes dos afloramentos Janner e Niemeyer. Modificado de MIRON et al. (2020).

1.1.2 A cavidade nasal cinodontes e a tomografia computadorizada

A cavidade nasal mamaliana fornece a porta para a troca de oxigênio e partículas de odor entre o ambiente e o organismo (CLARKE e PÖRTNER, 2010; LAAB et al., 2011; RODRIGUES et al., 2014; COMPTON et al., 2015, 2017). Como parte superior do sistema respiratório, fornece a passagem nasal para o ar inalado das narinas para o trato respiratório via nasofaringe. Essa cavidade possui duas funções primordiais: a respiração e o olfato. A respiração ocorre na região anterior da cavidade, onde estão localizados os maxiloturbinais. Essa região é recoberta pela mucosa, que reveste os maxiloturbinais e parte anterior dos nasoturbinais, além de uma grande parte do trato respiratório, estendendo-se da cavidade nasal até a passagem nasofaringeal. Além da respiração, a região é responsável pela filtração, aquecimento e umidificação do ar inspirado (HILLENIUS, 1994; RUF et al., 2015; PANG et al., 2016), realizando tais funções através de trocas contracorrentes temporais (CROMPTON et al., 2015, 2017).

Durante a inspiração do ar, o mesmo é aquecido e umidificado, enquanto os turbinais respiratórios são arrefecidos. Já na respiração o ar aquecido e umidificado vindo dos pulmões é condensado no epitélio dos turbinais. Desta maneira os turbinais respiratórios auxiliam recuperar boa parte do calor e umidade do ar expirado, também auxiliando no arrefecimento do trato respiratório superior.

A função olfativa ocorre na parte média e posterior cavidade nasal, onde se localizam os etmoturbinais e nasoturbinais (REZNIK, 1990; HILLENIOUS, 1992, 1994; VAN VALKENBURGH et al., 2004; WAGNER e RUF, 2019). A região olfativa é recoberta pelo epitélio olfatório, que é innervado pelo nervo craniano I, que transmite o sentido do olfato ao cérebro. Tal epitélio é dotado de células especializadas na captação de odores, mesmo em concentrações muito pequenas. Em mamíferos, há uma placa cribiforme ossificada formada pelo osso etmoide que separa a cavidade nasal da fossa olfatória da cavidade cerebral (REZNIK, 1990; HILLENIOUS, 1992, 1994; VAN VALKENBURGH et al., 2004; PIHLSTRÖM et al., 2005; CROMPTON et al., 2017).

A história evolutiva da cavidade nasal dos mamíferos, incluindo seu sistema complexo de turbinais ossificados e tecidos moles sensoriais e não sensoriais, pode ser rastreada em terápsidos, especialmente, em cinodontes não-Mammaliaformes (HILLENIOUS, 1992, 1994; RUF et al., 2014; CROMPTON et al., 2015, 2017; ROWE, 2020; ROWE et al., 2011). Mudanças morfológicas têm sido documentadas na cavidade nasal de cinodontes não-Mammaliaformes associadas a modificações fisiológicas que ocorreram durante o período Triássico (~251–201 Ma.) (HILLENIOUS, 1992, 1994; CROMPTON et al., 2015; ROWE, 2020). Grandes mudanças climáticas, ocorridas em um curto espaço de tempo durante o início do Mesozoico, resultaram em momentos de atmosfera hipóxica como resultado do efeito estufa gerado pelos gases liberados do vulcanismo. Essa condição atmosférica é conhecida por aumentar as taxas respiratórias dos animais que estão inseridos em tais ambientes, o que pode ter influenciado o surgimento de novas características, principalmente no trato respiratório dos cinodontes (HUEY e WARD, 2005; CROMPTON et al., 2017).

Contudo, o estudo anatômico da cavidade nasal dos cinodontes não-Mammaliaformes não é algo tão simples. Principalmente pelo fato de que estruturas internas, como os turbinais e a placa cribiforme eram cartilagosos (CROMPTON et al., 2015, 2017), e o limite entre as regiões respiratória e olfativa não é claro nos

fósseis. Consequentemente, nosso conhecimento repousa na interpretação da anatomia interna dos ossos rostrais e do molde da cavidade. Dessa forma, a análise anatômica da cavidade nasal de cinodontes não-mammaliaformes tem permitido a verificação de sulcos, cristas, e outras evidências que indicam a presença de estruturas turbinais cartilaginosas que não ossificavam (QUIROGA, 1979; SIGURDSEN, 2006; RODRIGUES et al., 2014; RUF et al., 2014; BENOIT et al., 2016; BENOIT et al., 2017; CROMPTON et al., 2017; PUSCH e FRÖBISCH, 2019).

Vários estudos examinaram a morfologia da cavidade nasal, recessos rostrais, ducto nasolacrimal e canal maxilar de cinodontes não-Mammaliaformes (e.g. WATSON, 1913; BRINK, 1955; KÜHNE, 1956; CROMPTON, 1958; BONAPARTE, 1966; FOURIE, 1974; KEMP, 1979, 1980, 2006; HILLENIUS, 1994, 2000; RUF et al., 2014; CROMPTON et al., 2015, 2017; BENOIT et al., 2016, 2019; KERBER et al., 2020; HENDRICKX et al., 2020), mas embora os traversodontídeos sejam taxonomicamente diversos como relatado acima, a cavidade nasal desses animais foi pouco estudada (e.g. BONAPARTE, 1966; KEMP, 1980; HILLENIUS, 1994; CROMPTON et al., 2017; HENDRICKX et al., 2020).

Antes da década de 1990, os estudos da cavidade nasal e de outras estruturas endocranianas de espécies extintas eram realizadas através de fósseis fragmentados, que apresentavam exposição de estruturas da cavidade, através de métodos destrutivos (cortes), ou através de moldes naturais da cavidade, formados por sedimento consolidado que preencheu a cavidade durante o processo de fossilização, que vinham a ser expostos quando os ossos se fragmentavam naturalmente (WATSON, 1913; BRINK, 1955; FOURIE, 1974; KEMP, 1980; BONAPARTE, 1966).

Nos últimos 30 anos, o uso de tomografia computadorizada tem se tornado cada vez mais frequente em empregado em estudos paleontológicos permitindo a visualização da anatomia interna de fósseis de maneira não destrutiva (e.g. PAULINA-CARABAJAL et al., 2016; LAAß et al., 2017; NAPOLI et al., 2018; PUSCH et al., 2019). A técnica utiliza raios-x para gerar centenas e até milhares de cortes virtuais (tomogramas), e no caso estudo do crânio, a partir desses cortes, é possível gerar moldes internos endocranianos (*endocasts*) (TATE e CANN, 1982; RAHMAN et al., 2012; ABEL et al., 2012; CUNNINGHAM et al., 2014; BRONZATI et al., 2017; BALANOFF e BEVER, 2020). A utilização de moldes endocranianos tem auxiliado no estudo da morfologia comparativa de grupos extintos, auxiliando nas análises que

buscam verificar as diferenças estruturais e modificações que ocorreram no grupo ao longo do tempo (HILLENIOUS, 1994; CUNNINGHAM et al., 2014; RODRIGUES et al., 2014; BALANOFF e BEVER, 2020; CROMPTON et al., 2017).

1.2 OBJETIVOS

2.1 Objetivo Geral




Estudar a morfologia da cavidade nasal de cinodontes não-Mammaliaformes Traversodontidae do Triássico Superior do sul do Brasil.

2.2 Objetivos específicos

- i) Realizar descrição comparativa da morfologia da cavidade nasal, recessos cranianos, ducto nasolacrimal e canal maxilar de *Exaeretodon riograndensis* e *Siriusgnathus niemeyerorum* do Triássico Superior, utilizando tomografia computadorizada e modelagem tridimensional;
- ii) Discutir as implicações paleobiológicas oriundas da interpretação funcional da cavidade e estruturas.

CAPÍTULO 2 – *ARTIGO CIENTÍFICO*

The nasal cavity of two traversodontid cynodonts (Eucynodontia, Gomphodontia) from the Upper Triassic of Brazil

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Abstract.—Traversodontidae is a group of Triassic herbivorous/omnivorous cynodonts that represents the most diversified lineage within Cynognathia. In southern Brazil, a rich fossil record of late Middle/mid-Late Triassic cynodonts has been documented, with *Exaeretodon riograndensis* Abdala, Barberena, and Dornelles, 2002 and *Siriusgnathus niemeyerorum* Pavanatto et al., 2018 representing two abundant and well-documented traversodontids. The present study provides a comparative analysis of the morphology of the nasal cavity, nasal recesses, nasolacrimal duct, and maxillary canals of both species using computed tomography, highlighting the changes that occurred in parallel to the origin of mammaliaforms. Our results show that there were no ossified turbinals or a cribriform plate delimiting the posterior end of the nasal cavity, suggesting these structures were probably cartilaginous as in nonmammaliaform cynodonts. Both species show lateral ridges on the internal surface of the roof of the nasal cavity, but the median ridge for the attachment of a nasal septum is absent. *Exaeretodon riograndensis* and *S. niemeyerorum* show recesses on the dorsal region of the nasal cavity, which increase the volume of the nasal cavity, potentially enhancing the olfactory chamber and contributing to the sense of smell. On the lateral sides of the nasal cavity, the analyzed taxa show a well-developed maxillary recess. Although *E. riograndensis* and *S. niemeyerorum* have roughly similar nasal cavities, in the former taxon, the space between the left and right dorsal recesses of the nasal cavity is uniform along its entire extension, whereas this space narrows posteriorly in *S. niemeyerorum*. Finally, the nasolacrimal duct of *S. niemeyerorum* is more inclined anteroposteriorly than in *E. riograndensis*.

Introduction

The mammalian nasal cavity has two primary functional divisions: olfactory and respiratory (Moore, 1981; Hillenius, 1992, 1994; Novacek, 1993; Rowe et al., 2005; Clarke and Pörtner, 2010; Laaß et al., 2011; Crompton et al., 2015, 2017). The respiratory region, related to air filtration and conservation of heat and water, includes the maxilloturbinal ossifications and is located mostly in the anteriormost part of this cavity. The olfactory region is located in the middle and posterior portions of the nasal cavity and contains the ethmoturbinals and nasoturbinals covered by olfactory epithelium, which is innervated by the olfactory nerve (cranial nerve I) that transmits the sense of smell to the brain. In crown mammals, an ossified cribriform plate formed by the ethmoid bone separates the nasal cavity

from the olfactory fossa of the brain cavity (Reznik, 1990; Hillenius, 1992, 1994; Van Valkenburgh et al., 2004; Crompton et al., 2017).

The evolutionary history of the complex mammalian nasal region, including its complex system of ossified turbinals and sensory and nonsensory soft tissues, can be traced in nonmammaliaform therapsids, and especially in nonmammaliaform cynodonts (Hillenius, 1992, 1994; Ruf et al., 2014; Crompton et al., 2015, 2017; Rowe, 2017; Rowe et al., 2011). Significant morphological changes have been documented in the nasal cavity of nonmammaliaform cynodonts associated with physiological modifications that occurred during the Triassic Period (ca. 251–201 Ma) (Hillenius, 1992, 1994; Crompton et al., 2015; Rowe, 2017). In these forms, the turbinals and cribriform plate were cartilaginous (Crompton et al., 2015, 2017), and the limit between the respiratory and olfactory regions is not clear in the fossils. Consequently, our knowledge rests on the interpretation of the internal anatomy of the rostral bones and the mold of the cavity.

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Table 1. Scanning parameters of the analyzed specimens.

Taxon/specimen	Number of slices	Slice thickness/ increment (mm)	Voltage (kV)	Dose (mAs)
<i>Exaeretodon riograndensis</i> (CAPPA/UFSM 0030)	890	0.67/0.33	120	150.52
<i>Exaeretodon riograndensis</i> (CAPPA/UFSM 0227)	492	0.90/0.45	120	150.52
<i>Siriusgnathus niemeyerorum</i> (CAPPA/UFSM 0032)	687	0.80/0.40	140	280

Traversodontidae is a clade of Triassic cynodonts included within Cynognathia, which together with Probainognathia forms the Eucynodontia clade (Hopson and Kitching, 2001; Abdala and Gaetano, 2018; Abdala, 2019). Cynognathia comprises the carnivorous cynognathids plus gomphodonts (diademodontids, trirachodontids, and traversodontids), characterized by their labiolingually expanded postcanine teeth related to an herbivorous/omnivorous diet (Chinsamy and Abdala, 2008; Liu and Abdala, 2014; Abdala and Gaetano, 2018; Hendrickx et al., 2020). Several studies have examined the morphology of the nasal cavity, rostral recesses, nasolacrimal duct, and maxillary canal of nonmammaliaform cynodonts (e.g., Watson, 1913; Brink, 1955; Kühne, 1956; Crompton, 1958; Bonaparte, 1966; Fourie, 1974; Kemp, 1979, 1980, 2006; Hillenius, 1994, 2000; Ruf et al., 2014; Crompton et al., 2015, 2017; Benoit et al., 2016, 2019; Hendrickx et al., 2020; Kerber et al., 2020), but although traversodontids are taxonomically diverse, the nasal cavity of these animals has been poorly studied (e.g., Bonaparte, 1966; Kemp, 1980; Hillenius, 1994; Crompton et al., 2017; Hendrickx et al., 2020).

In southern Brazil, a rich fossil record of Late Triassic cynodonts has been documented (Abdala and Ribeiro, 2010; Martinelli and Soares, 2016). *Exaeretodon riograndensis* Abdala, Barberena, and Dornelles, 2002 and *Siriusgnathus niemeyerorum* Pavanatto et al., 2018 represent two abundant and well-known traversodontids. Both taxa are the largest traversodontids found in Brazil, with adult skulls reported up to 25 cm long. The external osteology of *E. riograndensis* was studied by Abdala et al. (2002), Oliveira et al. (2007), and Liparini et al. (2013), and that of *S. niemeyerorum* by Pavanatto et al. (2018) and Miron et al. (2020). Recently, the brain endocast morphology of both cynodonts was studied by Pavanatto et al. (2019). In the present study, we aim to describe the morphology of the nasal cavities of *E. riograndensis* and *S. niemeyerorum* using computed tomography (CT) scanning and explore their paleobiological implications.

Materials and methods

Analyzed specimens.—*Exaeretodon riograndensis* (CAPPA/UFSM 0030 and 0227) and *Siriusgnathus niemeyerorum* (CAPPA/UFSM 0032) from the Upper Triassic of southern Brazil. The specimens are housed in the Paleontological Collection of the Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia/Universidade Federal de Santa Maria (CAPPA/UFSM), São João do Polêsine, Rio Grande do Sul, Brazil.

Location and stratigraphic information.—The fossils were collected from Upper Triassic strata in southern Brazil. The specimens CAPPA/UFSM 0030 and 0227 of *E. riograndensis*

were excavated from the Janner site on the outskirts of Agudo, State of Rio Grande do Sul (29°39'10.89"S; 53°17'34.2"W), which is biostratigraphically positioned in the upper portion of the *Hyperodapedon* Assemblage Zone (i.e., *Exaeretodon* sub-AZ), Candelária Sequence, and is late Carnian in age (Oliveira et al., 2007; Pretto et al., 2015; Müller and Garcia, 2019). The specimens come from the reddish mudstone within the basal two-thirds of the outcrop; the upper levels are composed of massive sandstones, with no records of fossil vertebrates so far (Müller et al., 2015). In addition to *E. riograndensis*, the Janner site has yielded several other fossil vertebrates, such as the sauropodomorph dinosaurs *Pampadromaeus barberenai* Cabreira et al., 2011 and *Bagualosaurus agudoensis* Pretto et al., 2019, the probainognathian *Trucidocynodon riograndensis* Oliveira et al., 2010, and the pseudosuchian ornithosuchid *Dynamosuchus collisensis* Müller et al., 2020 (see Oliveira et al., 2010; Cabreira et al., 2011; Stefanello et al., 2018; Pretto et al., 2019; Müller et al., 2020).

The specimen assigned to *S. niemeyerorum* (CAPPA/UFSM 0032) was collected from the Niemeyer site, also located in Agudo (29°40'25"S; 53°14'4.20"W). The stratigraphic column comprises a 23 m thick lithological sequence of reddish mudstones, sandstones, and intraformational conglomerates, with carbonatic concretions and hydromorphic levels (Pavanatto et al., 2018). *Siriusgnathus niemeyerorum* is the most abundant fossil found at this site, which also contains remains of probainognathians, dinosaurs, and indeterminate archosauromorphs (Pavanatto et al., 2018; Müller, 2020; Stefanello et al., 2020). The strata exposed at this site are considered younger than those of the Janner site (for further details, see Martinelli et al., 2020; Miron et al., 2020).

Scanning procedures and three-dimensional modeling.—The three specimens were scanned at the DIX medical clinic (Diagnóstico por Imagem do Hospital de Caridade) in Santa Maria, Rio Grande do Sul, using a Philips Brilliance 16-slice CT scanner and a Philips Brilliance 64-slice CT scanner (see Pavanatto et al., 2019). The raw scanning data were exported from the scanner computer in DICOM format. The scanning parameters are available in Table 1.

The endocranial structures were observed through analysis of the tomographic slices and by using tridimensional reconstructions of the cavities. The slices were manually segmented using 3D Slicer 3.8 to generate three-dimensional (3D) models of the regions of interest. The same software was employed to measure the volumes of the nasal cavity and the dorsal recess of the nasal cavity. The dorsal recess of the nasal cavity was artificially extracted (the ventral limit of the structure is a straight plane, and its contour is delimited by the edges of the recess) from the rest of the nasal cavity endocast, and its volume was

estimated and compared with the total volume of the cavity. Design Spark Mechanical 2.0 was employed to render the models.

Comparison.—For comparison, we collected data from the literature (e.g., Watson, 1913; Brink, 1955; Fourie, 1974; Kemp, 1980; Hillenius, 1994; Ruf et al., 2014; Crompton et al., 2017; Kerber et al., 2020) and analyzed the specimen MACN-Pv 18114 of *Exaeretodon argentinus* Bonaparte, 1962 (Ischigualasto Formation, late Carnian, Argentina; Bonaparte, 1966) and CT scans of *Diademodon* cf. *D. tetragonus* Seeley, 1894 (UCMP 42446, *Cynognathus* Assemblage Zone, early Anisian, South Africa; Macrini, 2006) (http://digimorph.org/specimens/Diademodon_sp/); *Massetognathus pascuali* Romer, 1967 (UFRGS-PV-0968-T, Chañares Formation, early Carnian, Argentina; Rodrigues, 2005); *Massetognathus ochagaviae* Barberena, 1981 (MCP 3871 PV, Pinheiros-Chiniquá Sequence, late Ladian–early Carnian, Brazil; Hoffmann et al., 2019); *Ecteninion lunensis* Martínez et al., 1996 (PVSJ 422, Ischigualasto Formation, late Carnian, Argentina; Martínez et al., 1996) (http://digimorph.org/specimens/Ecteninion_lunensis/); *Trucidocynodon riograndensis* (CAPPA/UFSM 0029, Candelária Sequence, Carnian, Brazil; Stefanello et al., 2018); *Pseudotherium argentinus* Wallace et al., 2019 (PVSJ 882, Ischigualasto Formation, late Carnian, Argentina; Wallace et al., 2019) (http://digimorph.org/specimens/Pseudotherium_argentinus/); and *Didelphis virginiana* (Kerr, 1792) (TMM M-2517, Recent; Macrini et al., 2007) (http://digimorph.org/specimens/Didelphis_virginiana/).

Except for *T. riograndensis* (CAPPA/UFSM 0029), *M. pascuali* (UFRGS-PV-0968-T), and *M. ochagaviae* (MCP 3871 PV), the CT-scan data sets for the specimens are available on digimorph.com. The CT scan of *T. riograndensis* (CAPPA/UFSM 0029) was studied by Stefanello et al. (2018); the brain endocast morphology of *M. pascuali* (UFRGS-PV-0968-T) was described by Rodrigues (2005) and Rodrigues et al. (2013) and that of *M. ochagaviae* (MCP 3871 PV) by Hoffmann et al. (2019). Scan parameters for the comparative specimens are available at digimorph.com and in the respective studies mentioned, and for brevity, they are not repeated here.

Terminology.—The anatomical nomenclature follows Crompton et al. (2017) for the structures of the nasal cavity, Hillenius (2000) for the nasolacrimal duct, and Benoit et al. (2019) for the maxillary canal.

Repositories and institutional abbreviations.—CAPPA/UFSM, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia, Universidade Federal de Santa Maria, São João do Polêsine, Brazil; MACN-Pv, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Colección de Paleontología de Vertebrados, Buenos Aires, Argentina; MCP, Museu de Ciência e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; PVSJ, Museu de Ciências Naturais, Universidade Nacional de San Juan, San Juan, Argentina; TMM, Texas Memorial Museum, Austin, Texas, USA; UCMP, University of California Museum of Paleontology, Berkeley, California,

USA; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Results

Description of the nasal cavity.—The nasal cavities of *Exaeretodon riograndensis* and *Siriusgnathus niemeyerorum* (Figs. 1–8) are confluent with the brain cavity (Figs. 1.3, 2.3, 3.3), without an ossified cribriform plate, following the pattern found in all other nonmammaliaform cynodonts (Crompton, 1958; Crompton et al., 2017; Pavanatto et al., 2019). The estimated volumes of the nasal cavities of the analyzed specimens are 157.199 cm³ in CAPPA/UFSM 0030 (skull length: 22.4 cm), 103.304 cm³ in CAPPA/UFSM 0227 (skull length: 16.8 cm), and 137.710 cm³ in CAPPA/UFSM 0032 (skull length: 22.04 cm).

The external nasal opening of the nasal cavity is anteriorly delimited by the nasal and a portion of the premaxilla (dorsally) and by the premaxilla and septomaxilla (lateroventrally) (Figs. 1–3, 6.1, 7.1, 8.1). Anterodorsally, the nasal cavity is covered by the nasal and posterodorsally, by the prefrontal, frontal, and postorbital (Figs. 1–3, 6.1, 7.1, 8.1). The lateral wall of the nasal cavity is formed by the premaxilla (anteriorly), maxilla, and lacrimal (posteriorly). Ventrally, it is delimited by the premaxilla, maxilla, and palatine. The intranarial process is absent in *E. riograndensis* and *S. niemeyerorum* (Pavanatto et al., 2018) (Figs. 5.1, 7, 8). The vomer is preserved only in *E. riograndensis* (Figs. 1, 2, 4, 5.2) and is better preserved in CAPPA/UFSM 0030 than in CAPPA/UFSM 0227, which preserves only the posterior portion of this bone (Figs. 4.2, 5.2). It is a long and thin plate-like bone located in the middle region of the nasal cavity.

The transverse lamina is located in the posterior region of the nasal cavity. According to Crompton et al. (2017), it is formed by the vomerine plate and palatine flange (Fig. 5.2). This structure consists of an obliquely (dorsoventrally) oriented lamina that converges medially with its counterpart, forming the floor of the olfactory chamber and the roof of the nasopharyngeal passage, as in other nonmammaliaform cynodonts (Crompton et al., 2015, 2017). Lateral to the transverse lamina is a rounded opening (Fig. 5.2) that Crompton et al. (2017; figs. 7B, 8A) identified as the entrance of branch V₂ of the trigeminal nerve into the nasal cavity.

On the internal surface of the nasal and frontal, bones that form the roof of the nasal cavity in *E. riograndensis* and *S. niemeyerorum*, are two well-marked and convergent lateral ridges, anteroposteriorly oriented, which are almost as long as the entire extension of the cavity (Figs. 1–3, 5.3, 5.4). They are more evident in the posterior region of the nasal cavity. There is no median ridge on the internal surface of the nasal and frontal in both taxa (Figs. 1–3, 5.3, 5.4). The lateral ridges form sulci on the endocast of the nasal cavity (Figs. 6.4, 7.4, 8.4).

Lateral to the lateral ridge is a wide recess on the ventral surface of the bones of the roof of the nasal cavity (i.e., frontal, prefrontal, nasal, and maxilla) (Fig. 5.1). The recess forms a salient elevation on the dorsal aspect of the nasal cavity endocast, being wider in its middle portion and narrower posteriorly, similar to a scalene triangle. In one specimen of *E. riograndensis* (CAPPA/

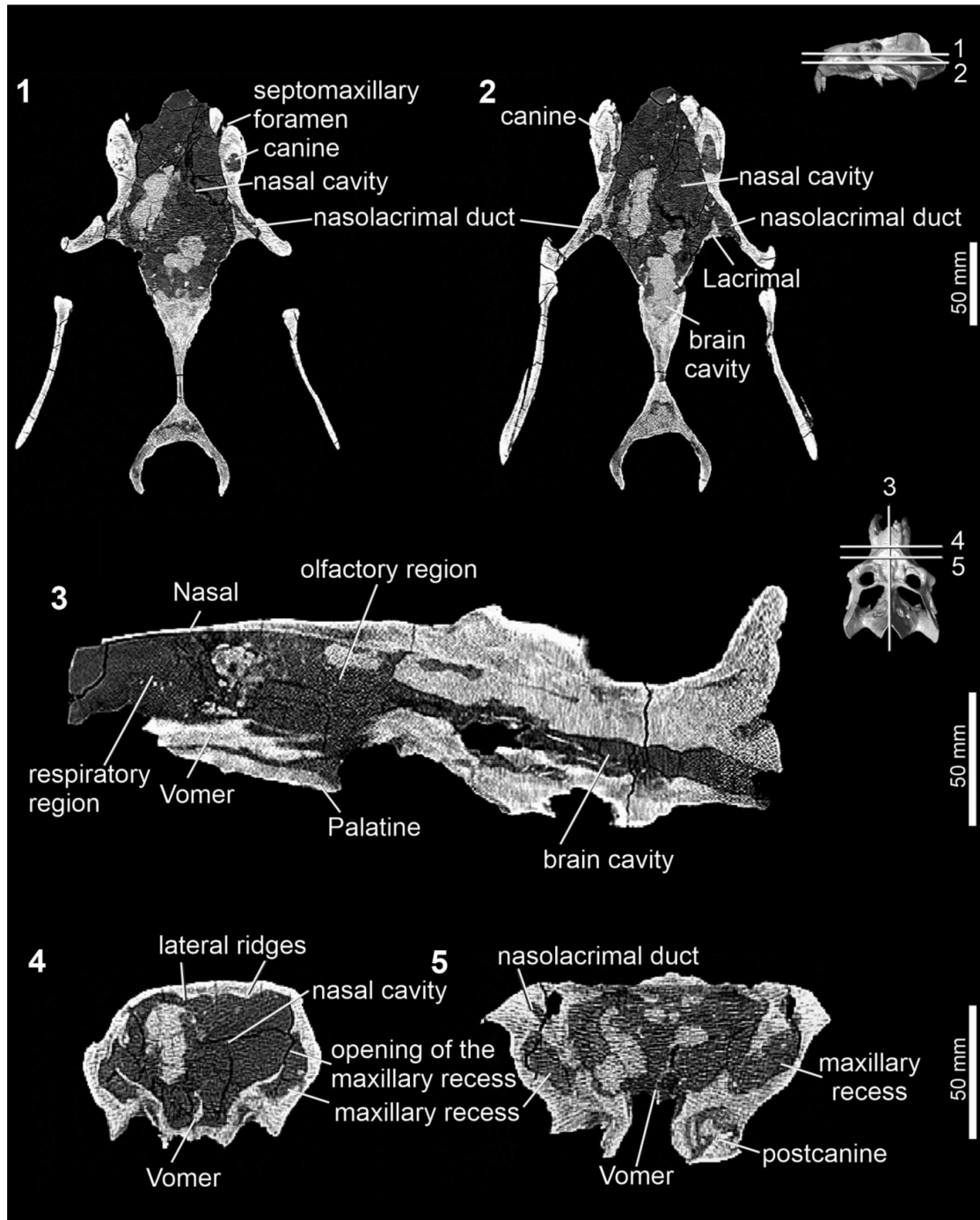


Figure 1. Computed tomography slices of the nasal cavity of *Exaeretodon riograndensis* (CAPPA/UFSM 0030). The 3D models of the cranium show the positions of the slices 1–5. (1, 2) Transverse slices; (3) sagittal slice; (4, 5) coronal slices.

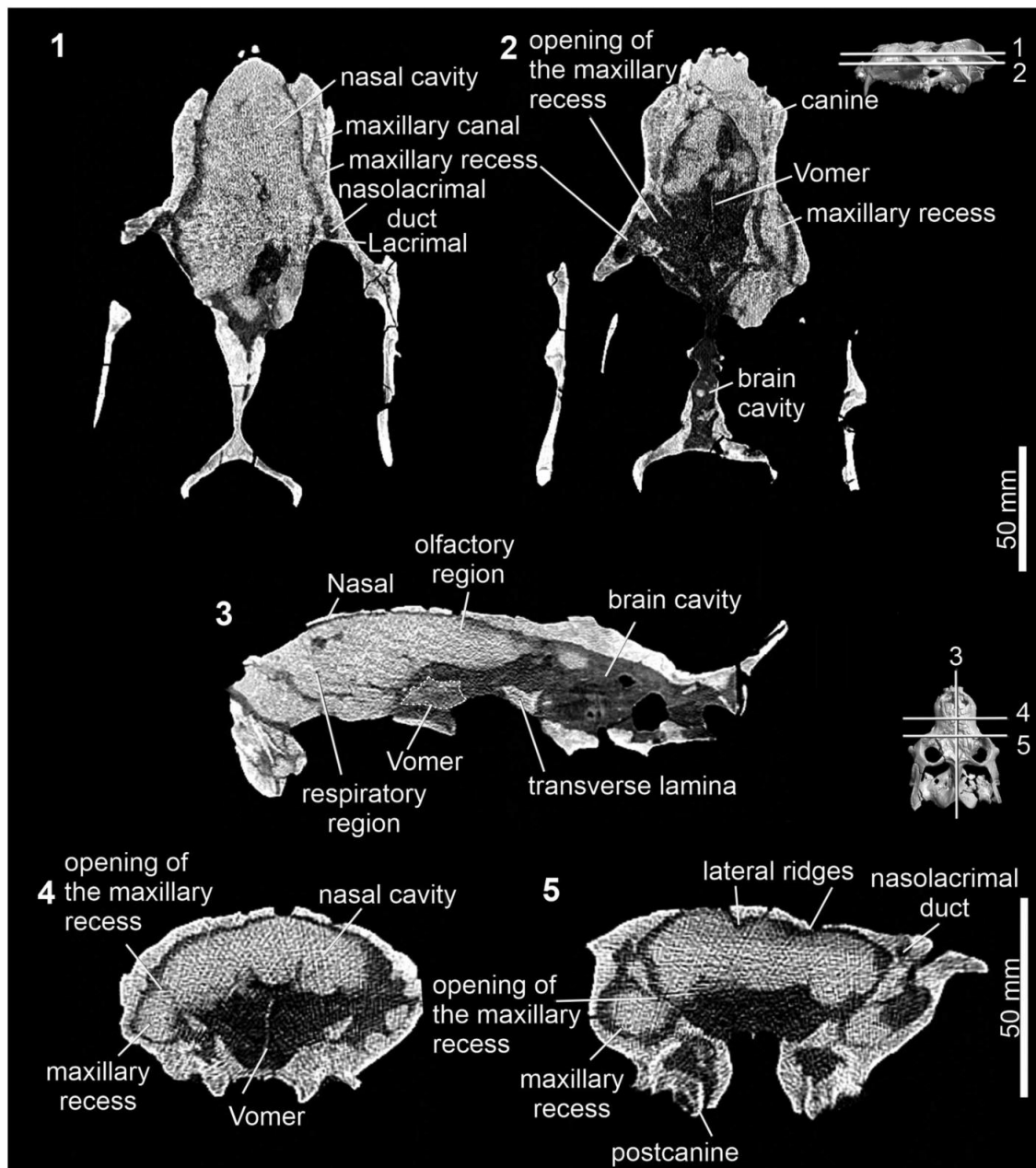


Figure 2. Computed tomography slices of the nasal cavity of *Exaeretodon riograndensis* (CAPPA/UFSM 0227). The 3D models of the cranium show the positions of the slices 1–5. (1, 2) Transverse slices; (3) sagittal slice; (4, 5) coronal slices.

UFSM 0030) (length: 55 mm; width: 19 mm; volume: 9.99 cm³) (Fig. 6.4) and in *S. niemeyerorum* (CAPPA/UFSM 0032) (length: 49 mm; width: 21.6 mm; volume: 8.95 cm³) (Fig. 8.4), the recess is more marked than in the other specimen of *E. riograndensis* (CAPPA/UFSM 0227) (length: 40 mm;

width: 20 mm; volume: 6.45 cm³) (Fig. 7.4), which is smaller in cranial size (and thus probably represents an ontogenetic difference).

In *E. riograndensis*, the width between the right and left recesses is the same along the entire extension of the structure

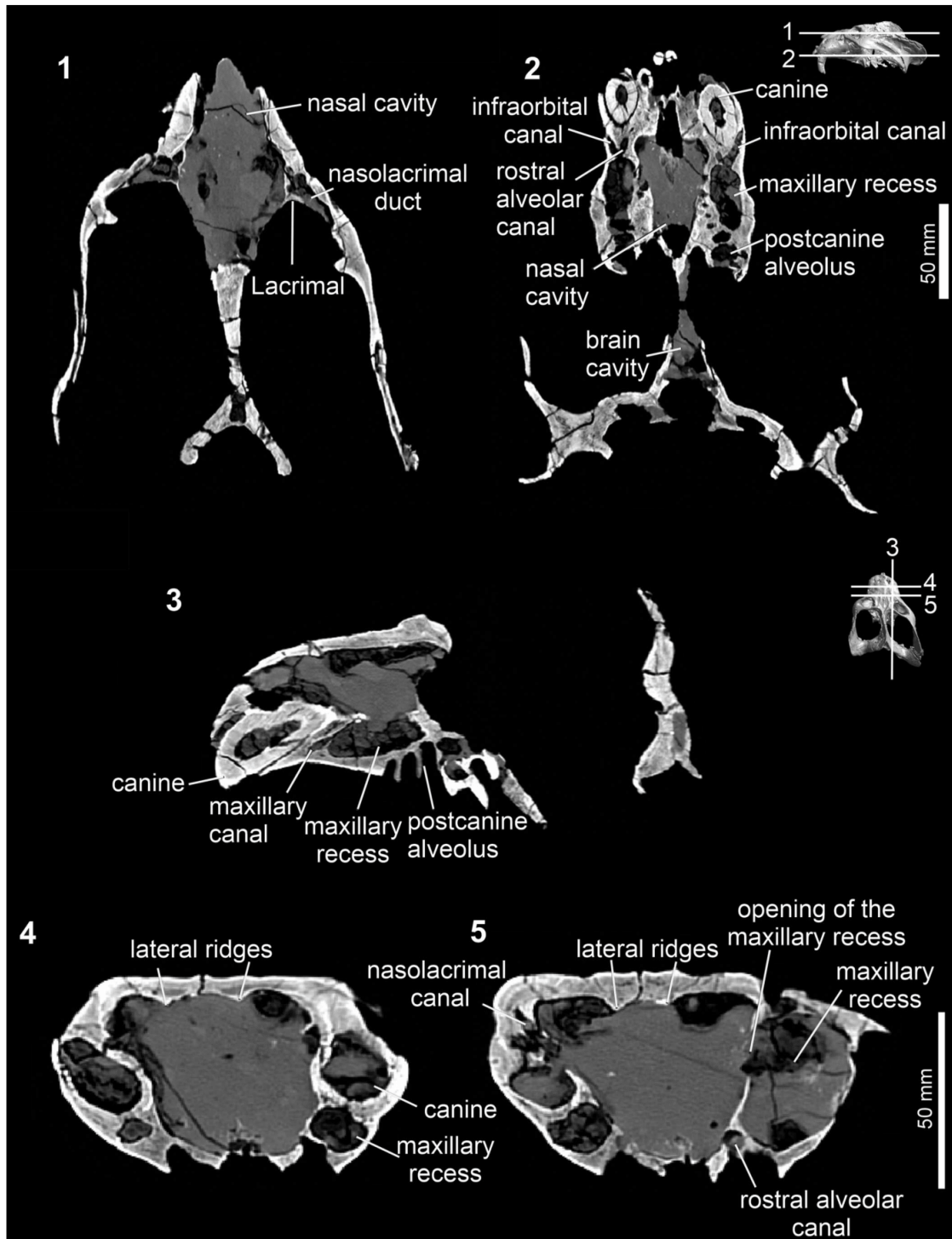


Figure 3. Computed tomography slices of the nasal cavity of *Siriusgnathus niemeyerorum* (CAPPA/UFSM 0032). The 3D models of the cranium show the positions of the slices 1–5. (1, 2) Transverse slices; (3) parasagittal slice; (4, 5) coronal slices.

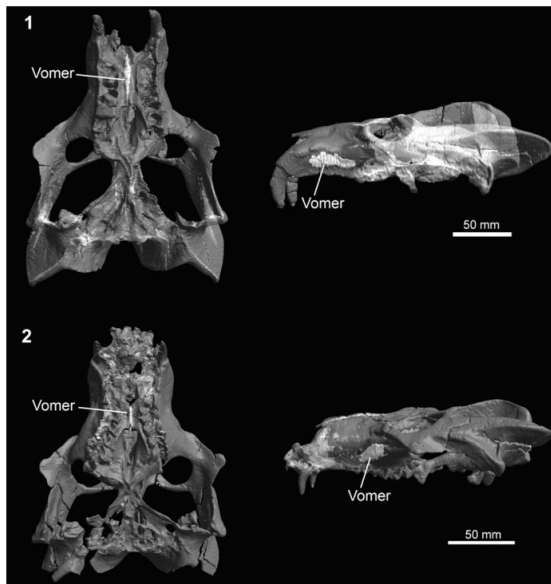


Figure 4. Translucent cranium of *Exaeretodon riograndensis* highlighting the vomer, in ventral and lateral views, respectively. (1) CAPPA/UFSM 0030; (2) CAPPA/UFSM 0227.

(Figs. 5.3, 7.4) (24 mm in the anteriormost region and 25 mm in the posteriormost in CAPPA/UFSM 0030; 14 mm and 16 mm, respectively, in CAPPA/UFSM 0227). By contrast, the width between the two recesses becomes narrower posteriorly in *S. niemeyerorum* (Figs. 5.4, 8.4) (23 mm in the anteriormost region and 10 mm in the posteriormost).

On the internal surface of the maxilla is a groove for the nasolacrimal duct (sensu Hillenius, 2000) extending anteroposteriorly from the point where the lacrimal duct enters the nasal cavity up to the septomaxillary foramen (Fig. 5.1). This groove is more clearly visible in CAPPA/UFSM 0032 (Fig. 5.1) and CAPPA/UFSM 0227 and is reflected on the surface of the endocast of CAPPA/UFSM 0032 (Fig. 8.5).

Located ventrally is the nasopharyngeal passage, which opens into the secondary choana. The 3D reconstruction of the nasopharyngeal passage reveals a posteroventrally oriented duct (Figs. 6.5, 7.5, 8.5).

Maxillary recess.—All specimens have a well-developed maxillary recess. In *E. riograndensis*, the recess is similar in both CAPPA/UFSM 0030 and CAPPA/UFSM 0227 (Figs. 6, 7). It is less dorsoventrally extended than in *S. niemeyerorum* (Figs. 3.5, 8.5) but anteroposteriorly longer. In *S. niemeyerorum*, this recess is pyramidal, transversally thin, and dorsoventrally elongated (Fig. 8). In all specimens, the recess is connected to the nasal cavity by a wide opening (Figs. 1–3, 5.1).

Nasolacrimal duct and maxillary canal.—In the studied taxa, the opening of the nasolacrimal duct, the lacrimal foramen, is located in the anterolateral region of the orbit, within the

lacrimal bone (Figs. 1–3, 5.1). In *E. riograndensis*, the nasolacrimal duct is longer and less obliquely oriented than in *S. niemeyerorum*. It is longer in the largest *E. riograndensis* specimen CAPPA/UFSM 0030 than in CAPPA/UFSM 0227, probably reflecting an ontogenetic difference. In CAPPA/UFSM 0227, it is bifurcated posteriorly (Fig. 7.5).

In *S. niemeyerorum*, the nasolacrimal duct is posterodorsally oblique (Fig. 8.5). This canal is located dorsally to the maxillary recess and anterolaterally to the region of the dorsal recess of the nasal cavity (Fig. 8.5). The nasolacrimal duct is anteriorly continuous with a groove on the internal face of the maxilla, which is extended up to the septomaxillary foramen (Fig. 5.1).

The maxillary canal is the passage for the maxillary branch of the trigeminal nerve (V_2) (Benoit et al., 2019). In our sample, it was possible to reconstruct the maxillary canal only in *S. niemeyerorum*. This canal leaves the maxillary recess and extends anteriorly in parallel and dorsolaterally to the postcanine dental series (Fig. 8.4, 8.5). At the level of the first postcanine, this canal splits into two separate canals, the rostral alveolar canal and the infraorbital canal (Figs. 3.2, 8.5) (Benoit et al., 2019). The rostral alveolar canal extends ventromedially, almost reaching the canine alveolus (posterior to this alveolus; Fig. 8.5), and the longer infraorbital canal is directed dorsolaterally up to one of the infraorbital foramina (there are at least two infraorbital foramina; see Pavanatto et al., 2018, fig. 5, where the authors identified these openings as “maxillary foramina”) located on the lateral surface of the maxilla. Other ramifications of the maxillary canal are possibly obliterated by the low resolution of the CT scans.

Discussion

Comparative morphology of the nasal cavity.—In comparison with other nonmammaliaform cynodonts (Fig. 9), the external morphology of the nasal cavities of the gomphodontosuchines *Exaeretodon riograndensis* and *Siriusgnathus niemeyerorum* is characterized by the absence of the internal process, differing from probainognathians (e.g., Kühne, 1956; Hopson and Kitching, 2001; Ruf et al., 2014; Crompton et al., 2017; Stefanello et al., 2018) and nongomphodontosuchine traversodontids (e.g., *Massetognathus ochagaviae*, MCP 3871 PV). The absence of this process is a synapomorphy of gomphodontosuchines (Liu and Olsen, 2010; Liu and Abdala, 2014).

There is no evidence of an ossified cribriform plate in *E. riograndensis* and *S. niemeyerorum*, as in other nonmammaliaform cynodonts in which the internal nasal cavity is known. The ossified condition of this structure is formed by the ethmoid bone in the crown Mammalia (Crompton et al., 2017). On the internal surface of the bones of the roof of the nasal cavity, in *E. riograndensis*, *E. argentinus* (Bonaparte, 1966), and *S. niemeyerorum*, are two lateral ridges that could have supported the cartilaginous turbinates (see Hillenius, 1994; Crompton et al., 2015, 2017). No median ridge was observed in the studied specimens (Fig. 5.3, 5.4). A median ridge, probably for the attachment of a cartilaginous nasal septum, is present in most cynodonts and is reflected on the

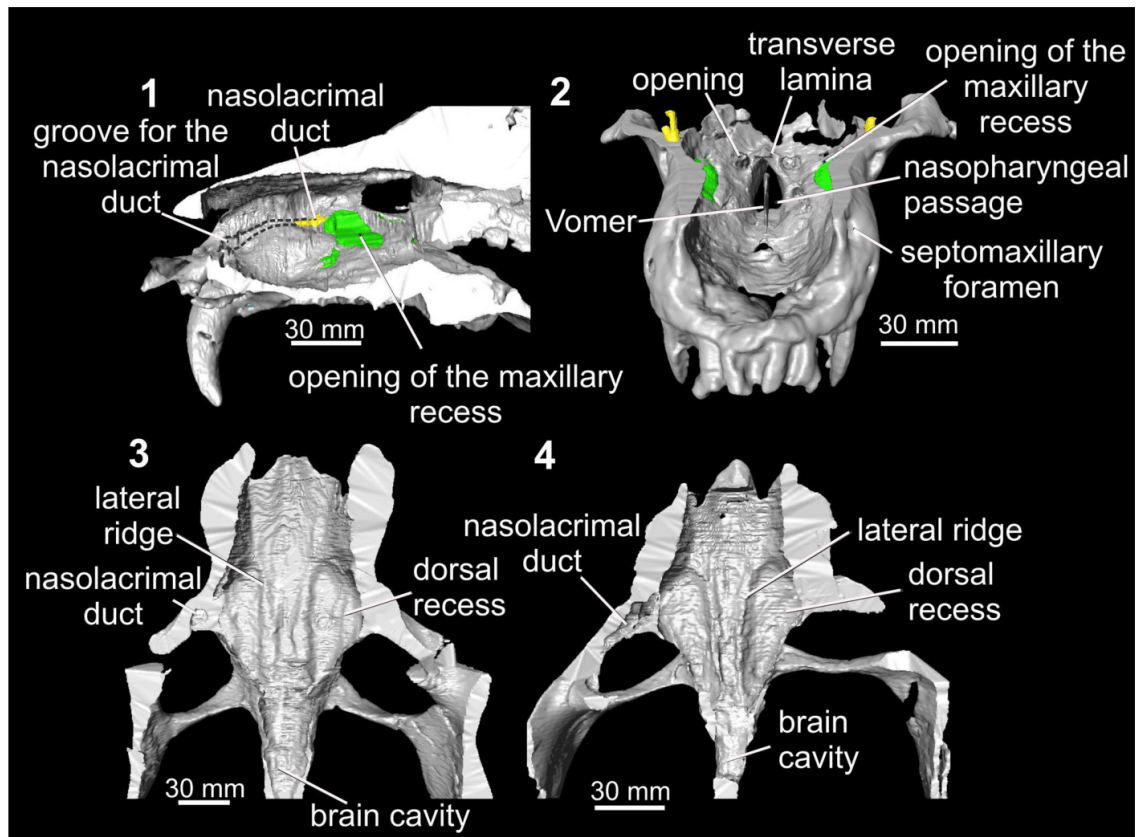


Figure 5. Sectioned crania of Traversodontidae evidencing the internal morphology of the nasal cavity. (1, 4) *Siriusgnathus niemeyerorum* (CAPPA/UFSM 0032); (2, 3) *Exaeretodon riograndensis*: (2) CAPPA/UFSM 0227; (3) CAPPA/UFSM 0030). (1) Cranium sagittally sectioned; (2) cranium transversally sectioned in anterior view; (3, 4) cranium transversally sectioned, evidencing the internal surface of the roof of the nasal cavity.

endocast of the nasal cavity, as seen in early epicynodonts *Galesaurus planiceps*, Owen, 1859 and *Thrinaxodon liorhinus* Seeley, 1894, the gomphodonts *Diademodon tetragonus*, *Massetognathus pascuali*, and *Eiyoia dentitransitus* Hendrickx et al., 2020 (Watson, 1913; Fourie, 1974; Crompton et al., 2015; Pusch et al., 2019a; Hendrickx et al., 2020), and the probainognathians *Oligokyphus major* Kühne, 1956, *Probainognathus jenseni* Romer, 1970, *Elliotherium kersteni* Sidor and Hancox, 2006, *Prozostrodon brasiliensis* (Barberena et al., 1987), and *Brasilodon quadrangularis* Bonaparte et al., 2003 (Kühne, 1956; Ruf et al., 2014; Crompton et al., 2017; Kerber et al., 2020). In the specimen CAPPA/UFSM 0029 assigned to *Trucidocynodon riograndensis*, the median ridge is not visible, and neither is its impression on the endocast surface. However, this condition could be related to the poor preservation of the internal cavities of the specimen. The nasal cavity of *Brasilodon quadrangularis*, the sister group of Mammaliaformes (Bonaparte et al., 2003, 2005), was studied by Ruf et al. (2014), and among other features, the authors inferred the presence of partially ossified turbinals identified as the remnants of the nasoturbinial and first ethmoturbinial, on the basis of thin

bone fragments, as well as a ridge on the ventral surface of the frontal identified as the mesethmoid. Crompton et al. (2017), however, argued that without having a more complete documentation of these bones, it is not possible to confirm whether the interpreted elements are indeed ossified turbinals. They also argued that the ridge that Ruf et al. (2014) described as the mesethmoid is quite similar to the median ridge found in other nonmammaliaform cynodonts and may not represent an independent ossification. The earliest mammaliaform *Morganucodon* has ridges on the internal surface of the nasal cavity, which would support turbinals (Kermack et al., 1981; Kielan-Jaworowska et al., 2004), but no unequivocal evidence of ossification of these structures exists (Crompton et al., 2017). The oldest fossil with signs of ossification of the internal structures of the nasal cavity is *Haldanodon expectatus* Kühne and Krusat, 1972 from the Upper Jurassic of Portugal (Lillegraven and Krusat, 1991). However, as noted by Crompton et al. (2017), these structures were not figured in detail.

The vomer of *E. riograndensis* is thin and tall, similar to that of *M. pascuali* (MCZ 3798; Crompton et al., 2017). In some probainognathians, the vomer is lower and robust

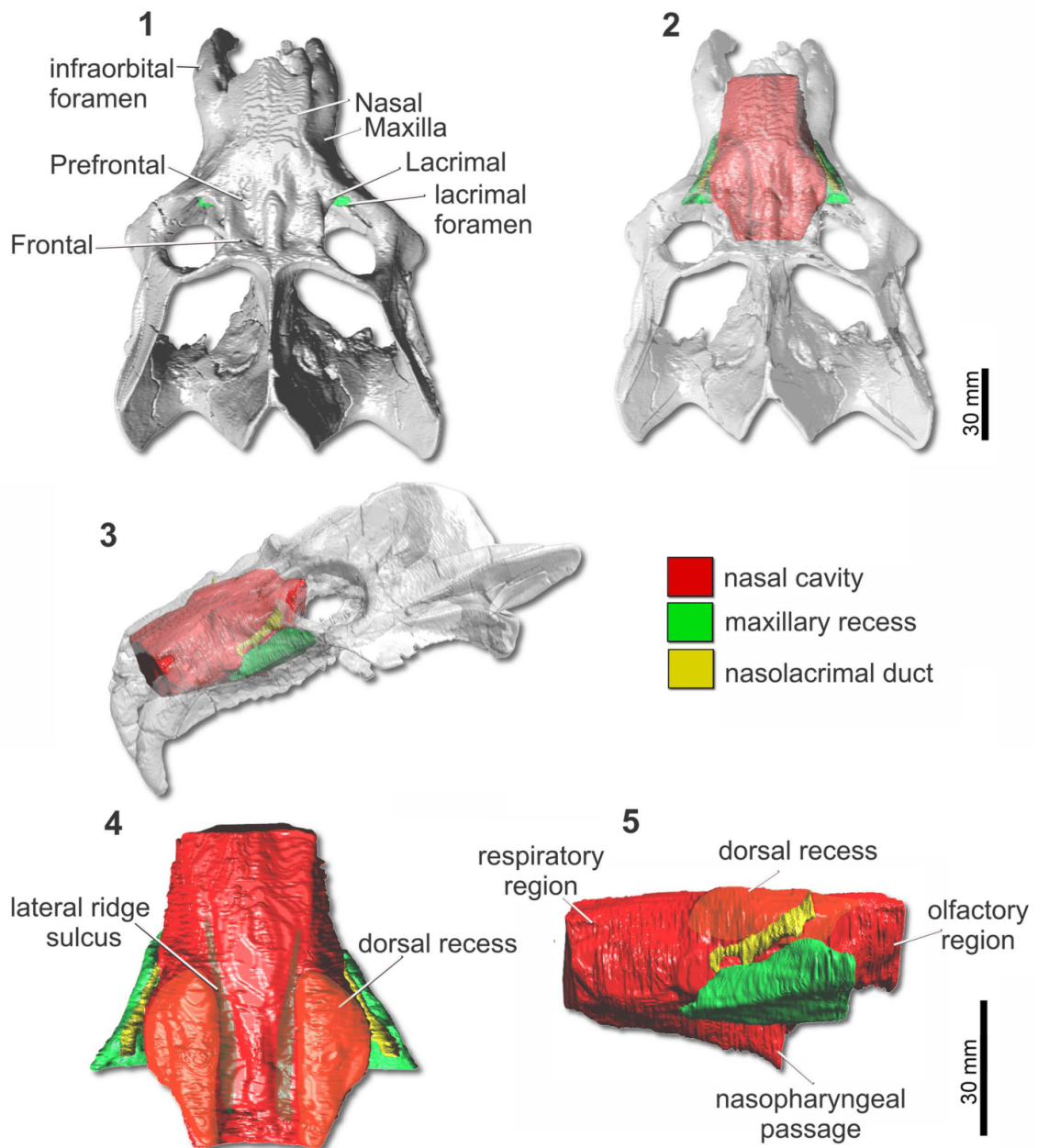


Figure 6. (1–3) Cranium and (4, 5) endocranial casts of the nasal cavity, maxillary recess, and nasolacrimal duct of *Exaeretodon riograndensis* (CAPPA/UFSM 0030). (1, 2, 4) Dorsal views; (3) lateral oblique view; (5) lateral view.

(Y-shaped), showing a well-marked dorsal sulcus, probably for the insertion of a cartilaginous septum, as seen in *P. brasiliensis*, *P. argentinus*, and *B. quadrangularis* (Ruf et al., 2014; Wallace et al., 2019; Kerber et al., 2020).

In the description of the nasal cavity of *E. argentinus*, Bonaparte (1966) pointed out the presence of globular longitudinal elevations on the dorsal region of a natural endocast, close to the orbital edges (Fig. 10), which he interpreted as cranial

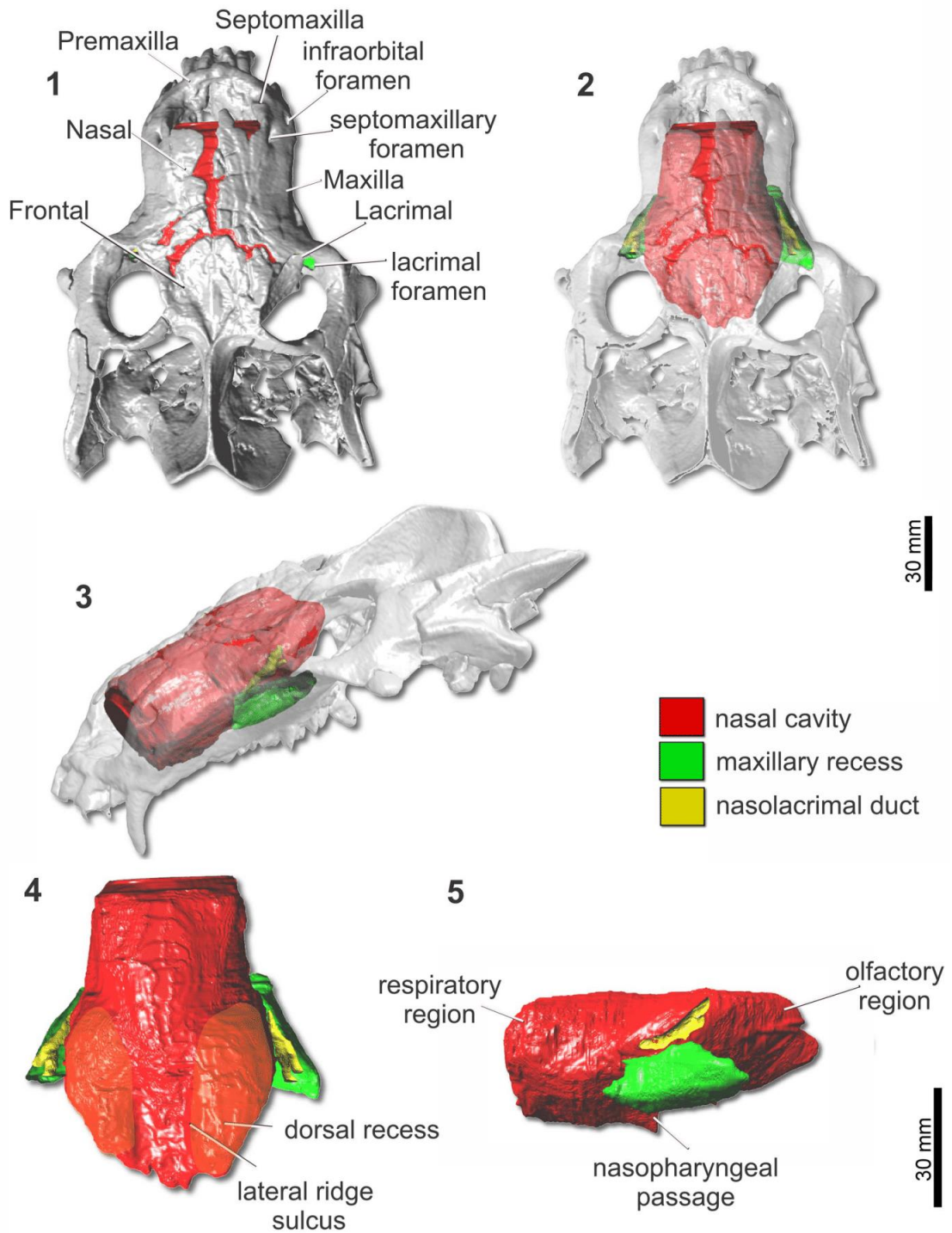


Figure 7. (1–3) Cranium and (4, 5) endocranial casts of the nasal cavity, maxillary recess, and nasolacrimal duct of *Exaeretodon riograndensis* (CAPP/UFMS 0227). (1, 2, 4) Dorsal views; (3) lateral oblique view; (5) lateral view.

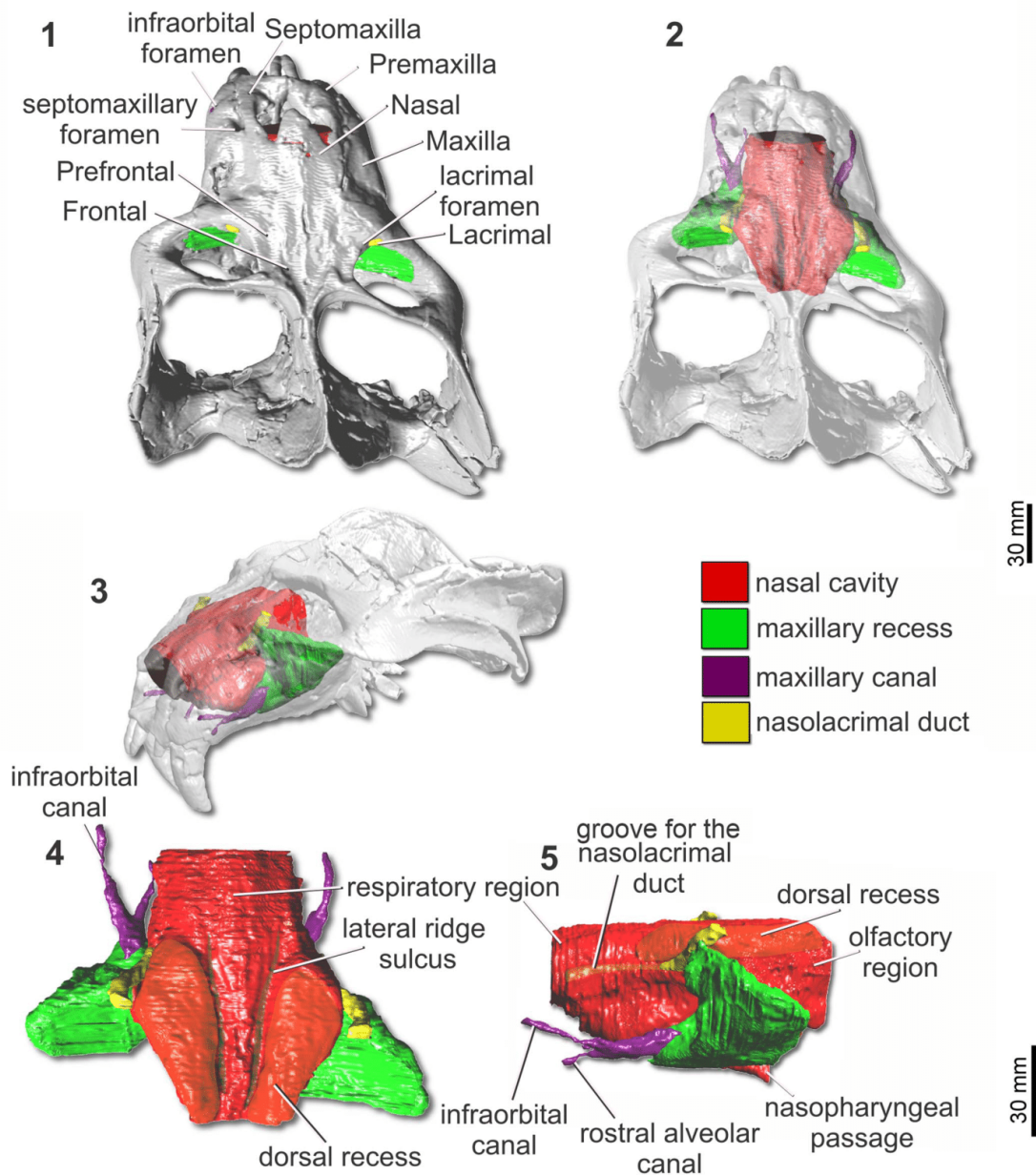


Figure 8. (1–3) Cranium and (4, 5) endocranial casts of the nasal cavity, maxillary recess, maxillary canal, and nasolacrimal duct of *Siriusgnathus niemeyerorum* (CAPP/UFMS 0032). (1, 2, 4) Dorsal views; (3) lateral oblique view; (5) lateral view.

sinuses. The anterior region of the elevation was interpreted as the cast of a “maxillary sinus” (not the same cavity present in the lateral of the nasal cavity, i.e., maxillary recess) and the

posterior region as the “frontal sinus” although there is no indication of bone separation between these regions. This cavity, which is reflected on the endocast of the nasal cavity as a

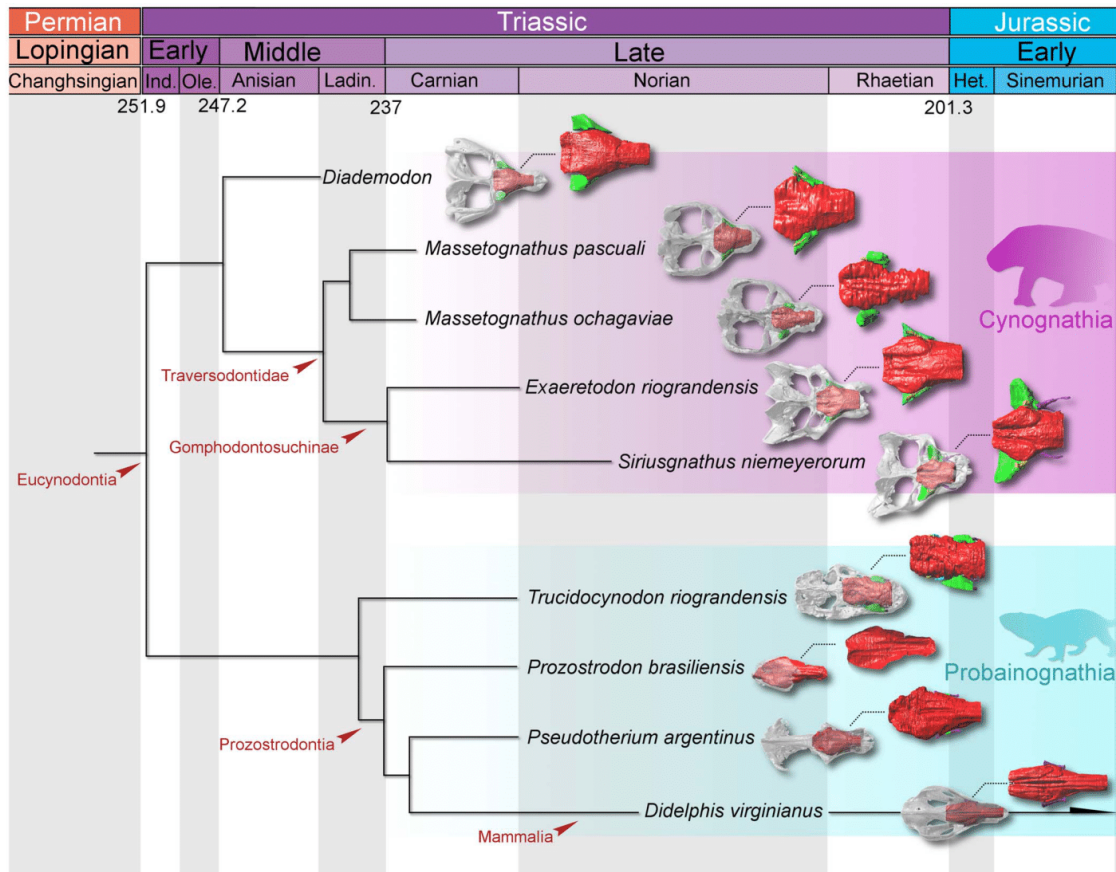


Figure 9. Phylogenetic relationships of selected cynodonts (based on Liu and Olsen, 2010; Pavanatto et al., 2018; Wallace et al., 2019). Cynognathia: *Diademodon* cf. *D. tetragonus* (UCMP 42446); *Massetognathus pascuali* (UFRGS-PV-0968-T); *Massetognathus ochagaviae* (MCP 3871 PV); *Exaeretodon riograndensis* (CAPP/UFMS 0030); *Siriusgnathus niemeyerorum* (CAPP/UFMS 0032). Probainognathia: *Trucidocynodon riograndensis* (CAPP/UFMS 0029); *Prozostronodon brasiliensis* (UFRGS-PV-0543-T; after Kerber et al., 2020); *Pseudothierium argentinus* (PVSJ 882); *Didelphis virginiana* (TMM M-2517). Not to scale.

globular longitudinal elevation, is also present in *E. riograndensis* and *S. niemeyerorum*. Notwithstanding, sinuses are cavities resulting from bone remodeling during ontogeny between two layers of bones, whereas recesses are cavities that do not necessarily form between bony layers or relate to the removal of bone tissue (Farke, 2010a; Sharp, 2016; Billet et al., 2017). In addition, sinuses and recesses are named according to the bones they excavate although they may invade adjacent elements (Novacek, 1993). However, as this cavity excavates more than a single bone, and the homology with other structures is not clear, we opted to identify it generically as a dorsal recess of the nasal cavity, at least until further studies are conducted.

Except for *Massetognathus*, which also shows a recess on the dorsal region of the nasal cavity, but less marked than in *Exaeretodon* spp. and *S. niemeyerorum* (see Crompton et al., 2015, fig. 11.4, identified as part of the olfactory chamber), other cynodonts in which the nasal cavity has been studied (Watson, 1913; Brink, 1955; Fourie, 1974; Kemp, 1979, 1980; Ruf et al., 2014; Kerber et al., 2020) do not show this structure

(Fig. 9), at least not as developed as in traversodontids, especially the gomphodontosuchines here studied. By comparing specimens of different cranial sizes, and probably ontogenetic stages, of *E. riograndensis* (CAPP/UFMS 0030 and CAPP/UFMS 0227) (as well as in the small-sized specimen MACN-Pv 18114 of *E. argentinus*), it is possible to observe that the dorsal recess of the nasal cavity increases in size during ontogenetic maturation. In this region, it is also possible to observe interspecific variation between the two traversodontids. The space between the right and left dorsal recesses of the nasal cavity in *E. riograndensis* is the same along the entire length of the structure, whereas it becomes narrower posteriorly in *S. niemeyerorum*.

Both analyzed species show well-developed maxillary recesses in the lateral region of the nasal cavity within the maxilla. Such structures are present in most nonmammaliaform cynodonts (Crompton et al., 2017). This structure has been identified as a sinus (Fourie, 1974; Kemp, 1979, 1980), atrium (Crompton et al., 2015), or antrum (Benoit et al., 2016), but

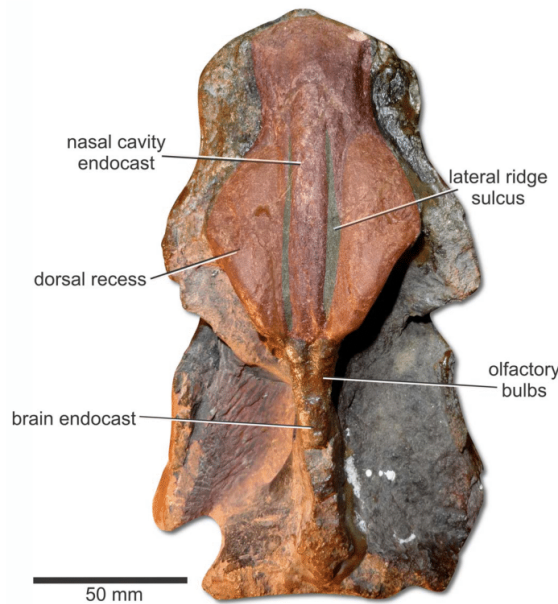


Figure 10. Specimen MACN-Pv 18114 of a small-sized specimen of *Exaeretodon argentinus* (Ischigualasto Formation, Ischigualasto-Villa Unión Basin, Argentina) with cranial bones detached, showing the natural endocasts of the brain and nasal cavity. It was originally described by Bonaparte (1966).

according to Crompton et al. (2017), it is better defined as a recess (see preceding discussion).

The nasolacrimal duct of both *E. riograndensis* and *S. niemeyerorum* is long and inclined dorsoposteriorly. In *S. niemeyerorum*, the duct is more inclined than in *E. riograndensis*, similar to *Massetognathus pascuali*. As observed in the taxa here studied, the nasolacrimal duct is connected by a groove to the septomaxillary foramen, which is close to the place where the vomeronasal organ was located (Hillenius, 2000). In this sense, the nasolacrimal duct supplied orbital fluids to the vomeronasal organ, increasing its function (i.e., chemosensory system) (Hillenius, 2000).

The maxillary canal found in *S. niemeyerorum* displays the plesiomorphic pattern of cynodonts, consisting of a long canal enclosed within the facial process of the maxilla, with two to three external openings (Benoit et al., 2019). By contrast, mammaliaforms have a shorter canal, and the innervations of the trigeminal nerve (V_2) are not distributed within the bone. This 3D reconstruction does not show a high degree of ramification inside the maxilla like other therapsids and nonprobainognathian cynodonts (Benoit et al., 2016, 2019; Pusch et al., 2019a, b). However, the existence of small branches cannot be excluded, their absence being perhaps a result of the resolution of the tomography.

Functional inferences.—The delimitation of the space for the respiratory and olfactory chambers in the nasal cavity of nonmammaliaform cynodonts is not clear, and only some speculations can be made about the limits of both areas (see

Crompton et al., 2015, fig. 11.4). The transverse lamina is considered the ventral limit of the olfactory chamber, and the space anterior to this lamina is occupied by the respiratory chamber, which was probably filled by cartilaginous turbinates attached on the ventral surface of the nasal and frontal bones (Hillenius, 1994; Crompton et al., 2015, 2017).

Due to the similarity of the nasal cavities of *E. riograndensis*, *S. niemeyerorum*, and *Massetognathus* (with the gross anatomy fairly similar among eucynodonts), it is possible that breathing in these animals was similar to that inferred for *Massetognathus* by Crompton et al. (2017; see also Hillenius, 1992, 1994). According to Crompton et al. (2017), the route taken by the airflow during the respiratory process could have been either directly into the nasopharyngeal passage or through the respiratory chamber, flowing into the maxillary recess before exiting the chamber. The path that most air takes to reach the lungs depends on the respiratory state. When in a state of low activity (resting phase), the air is inhaled through the nostrils, travels through the nasal cavity (passing through the recesses), and is exhaled through the nostrils. During periods of high activity (e.g., running phase), most of the air enters through the nostrils but is exhaled through the mouth, resulting in wheezing, which also has the purpose of reducing body temperature.

As discussed in the preceding, gomphodontosuchines show a recess in the dorsal region of the nasal cavity and a well-developed maxillary recess. The presence of sinuses/recesses around the nasal cavity (i.e., paranasal sinuses) has been found in other vertebrate groups, especially mammals (Witmer, 1999; Rossie, 2006; Farke, 2010a; Curtis and Van Valkenburgh, 2014; Ranslow et al., 2014; Mori et al., 2015; Ruf et al., 2015; Sharp, 2016; Kerber et al., 2019), but sinuses/recesses are rare in nonmammaliaform cynodonts (with the exception of the maxillary recess present in most forms). These structures could originate, opportunistically, through the pneumatization of areas where the bone is not mechanically necessary during ontogenetic development (epithelial hypothesis; Witmer, 1997). In parallel, possible particular functions of these structures could be the reduction of the mass of the cranium; an increase in the volume of the nasal cavity, increasing olfaction and immune defenses in the nasal cavity; the dissipation of stress across the skull during mastication and shock absorption from some behaviors such as head-butting; a heat-regulating effect and thermal insulation; an increase in the surface area for the attachment of muscles; and as vocal resonators, among others (Moore, 1981; Novacek, 1993; Witmer, 1999; Farke, 2008, 2010a, b; Márquez, 2008; Keir, 2009; Fericola et al., 2012; Curtis et al., 2015; Sharp, 2016; Crompton et al., 2017). Hence, it is plausible that potential functions for such structures are particular to each taxonomic group.

Analogous to the distribution of the paranasal sinuses in other vertebrates, which are more common in large animals, in nonmammaliaform cynodonts, the recess in the dorsal region of the nasal cavity is present in large-sized traversodontids and the maxillary recess is not present or is quite reduced in small forms, such as prozostrodonts (Ruf et al., 2014; Benoit et al., 2016, 2019). Although these endocranial cavities in traversodontids are quite simple when compared with those of large mammals, for example, they can be useful in reducing the weight of the head. However, the extreme size variation of

these forms is not the only explanation for the presence of these structures, since *Diademodon* is also a large cynodont but does not have an well-developed dorsal recess of the nasal cavity. Nevertheless, it is possible that it evolved subsequently in the lineage, appearing in traversodontids (Fig. 9).

Although it is not possible to know precisely the function of the dorsal recess of the nasal cavity, or whether it had functions, it is here inferred that it probably expanded the volume of the nasal cavity, especially the olfactory chamber, as the recess is located closer to this region. Comparing the estimated volume of the left and right recesses and the total volume of the nasal cavity (see values in the description section), it is suggested that these structures correspond to ~12.5% in *E. riograndensis* (12.7% in CAPP/UFMS 0030 and 12.4% in CAPP/UFMS 0227) and ~13% in *S. niemeyerorum* of the total volume of the nasal cavity. In *Massetognathus ochagaviae* (total volume of the nasal cavity: 29.595 cm³; recess volume: 1.97 cm³), both recesses also represent ~13% of the total volume of the nasal cavity. In living tetrapods, the olfactory chamber is covered by olfactory epithelium (Moore, 1981; Hillenius, 1992; Novacek, 1993; Rowe et al., 2005), and a posterior expansion of the nasal cavity has been interpreted as indicative of a possible increase in the sense of smell in vertebrates (Witmer and Ridgely, 2009; Fonseca et al., 2020). Concerning the biological role of the maxillary recess, Crompton et al. (2017) suggested it was involved in the respiration of cynodonts, increasing the area of the respiratory chamber.

Final remarks

As in all known nonmammaliaform cynodonts, the internal structures of the nasal cavities of *Exaeretodon riograndensis* and *Siriusgnathus niemeyerorum* were probably cartilaginous, without ossified turbinates and a cribriform plate separating them from the olfactory fossa of the brain cavity. These traversodontids lack a median ridge on the ventral surface of the roof of the nasal cavity. Interspecific differences in the nasal cavities of *E. riograndensis* and *S. niemeyerorum* are observed, such as the space between the right and left recesses, which is uniform in *E. riograndensis*, and the nasolacrimal canal, which is less inclined anteroposteriorly in this taxon.

The traversodontids *E. riograndensis*, *E. argentinus*, and *S. niemeyerorum* (as well as *Massetognathus*) show a dorsal recess located on the dorsal region of the nasal cavity. This recess could have increased the volume of the nasal cavity, and as it is located in the posterior portion where the olfactory chamber was probably located; it is suggested that it could have improved the olfactory systems of these omnivorous animals. Furthermore, the plesiomorphic condition of the maxillary canals of *S. niemeyerorum* indicates lower facial sensibility compared with probainognathians.

Acknowledgments

We thank the Niemeyer family for kindly allowing the paleontological prospection and field work at their property; CAPP/UFMS team for the support in the field work; Digimorph.org, UTCT, T. Rowe, J. Rodgers for access to the CT scans of

comparative specimens; A.E.B. Pavanatto and L.R. Miron, who prepared the specimens; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) scholarship for A.S.F.; Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul (FAPERGS 17/2551-0000816-2) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 422568/2018-0; research grant 309414/2019-9) to L.K. Finally, we thank F. Abdala and J. Schultz for their useful comments that greatly improved the manuscript.

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Accepted: 26 January 2021

CAPÍTULO 3 – *CONSIDERAÇÕES FINAIS*

CONSIDERAÇÕES FINAIS

Na presente dissertação, estudou-se a morfologia da cavidade nasal, recessos cranianos, recessos, ducto nasolacrimal e canal maxilar dos cinodontes Traversodontidae *Exaeretodon riograndensis* e *Siriusgnathus niemeyerorum*, provenientes de camadas do Triássico Superior do Rio Grande do Sul. Para isso, crânios foram tomografados e posteriormente, os tomogramas foram analisados e também modelos tridimensionais foram gerados e comparados com cinognátios e probainognátios. Em suma, as principais conclusões oriundas desse estudo são:

- i) Observou-se que como em todos os cinodontes não-mammaliaformes conhecidos, as estruturas internas da cavidade nasal desses animais eram provavelmente cartilagenosas, sem turbinas ossificadas e placa cribiforme separando tal cavidade da fossa olfatória da cavidade cerebral. Ambos os traversodontídeos não possuem uma crista mediana para a inserção de um septo cartilagenoso na superfície ventral do teto da cavidade nasal, o que os difere da maior parte das espécies com que foram comparadas. Entretanto, as cristas laterais para turbinas cartilagenosas estão presentes.
- ii) Os traversodontídeos *E. riograndensis* e *S. niemeyerorum* (bem como em *E. argentinus* e *Massetognathus*) apresentam um recesso localizado na região dorsal da cavidade nasal. Esse recesso aumenta o volume da cavidade nasal e, por se localizar na porção posterior onde provavelmente se localizava a região olfativa, sugere-se que o mesmo poderia incrementar o sistema olfatório desses animais (Figura 4), que possuíam provavelmente hábitos onívoros.
- iii) Na região lateral da cavidade nasal, os táxons analisados apresentam recesso maxilar bem desenvolvido, que embora não foi possível de ser quantificado em táxons comparativos devido a preservação dos espécimes, parece ser proporcionalmente maior do que em outros táxons.
- iii) A condição plesiomórfica do canal maxilar de *S. niemeyerorum* indica menor sensibilidade facial em comparação aos Probainognathia.
- iv) Embora *E. riograndensis* e *S. niemeyerorum* tenham uma cavidade nasal aproximadamente semelhante, diferenças interespecíficas são observadas, como o espaço entre os recessos direito e esquerdo, que é uniforme em *E. riograndensis*, e o canal nasolacrimal, que é menos inclinado ântero-posteriormente neste táxon.

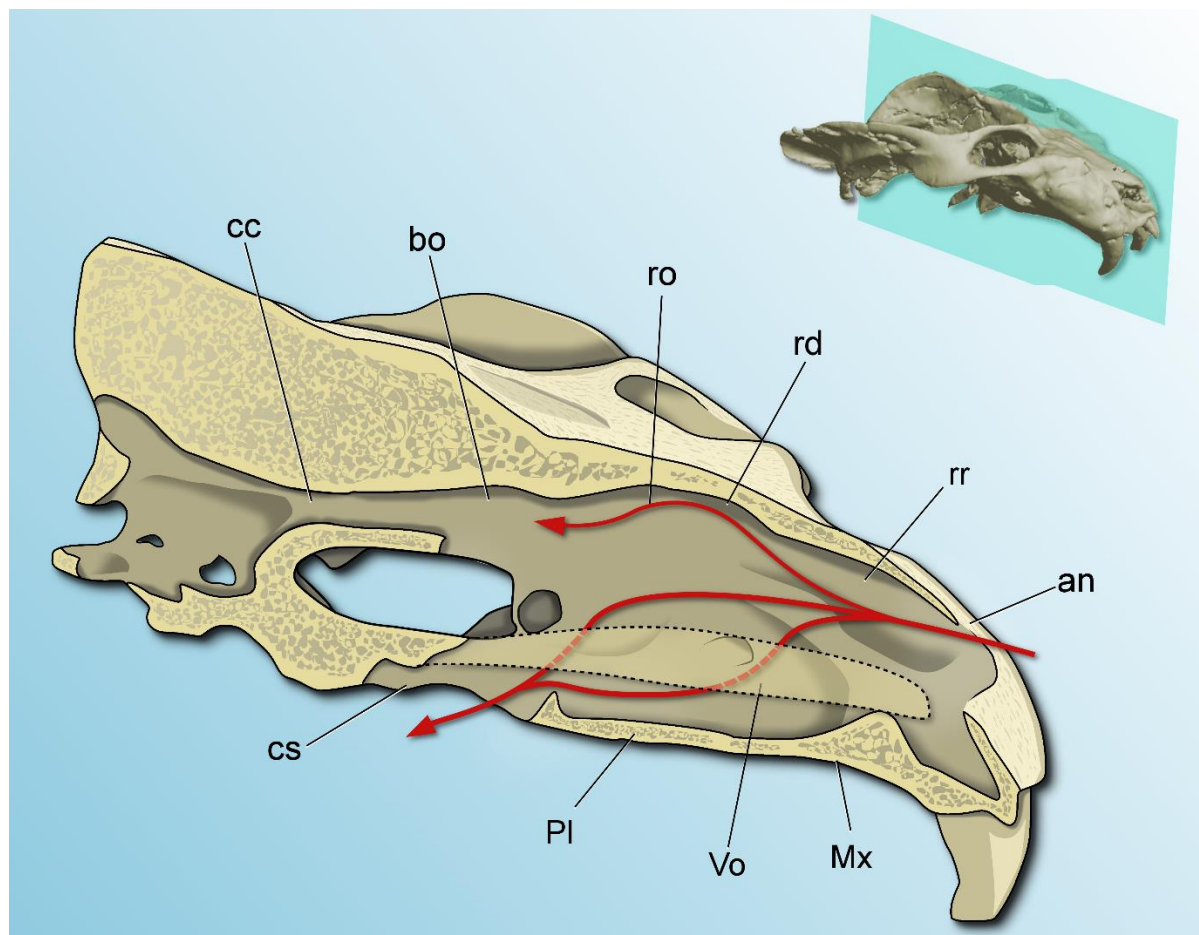


Figura 4. Crânio de *Siriognathus niemeyerorum* seccionado parasagitalmente mostrando as vias de entrada do ar na cavidade nasal (seta). As bifurcações ventrais indicam as vias respiratórias direto para a passagem nasofaríngea ou passando pela câmara respiratória, e a bifurcação dorsal indica a via aérea olfatória, passando pelo recesso dorsal da cavidade nasal. **Abreviaturas:** **cc**, cavidade craniana (que aloja o encéfalo); **rd**, recesso dorsal da cavidade nasal; **ne**, narina externa; **bo**, localização dos bulbos olfatórios (equivalente a fossa etmoidal em mamíferos); **ro** = região olfativa; **Mx** = maxila; **PI** = palatino; **rr** = região respiratória; **cs** = coana secundária; **Vo** = vômer (reconstruído). Fonte: Imagem elaborada Rodrigo Temp Müller.

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