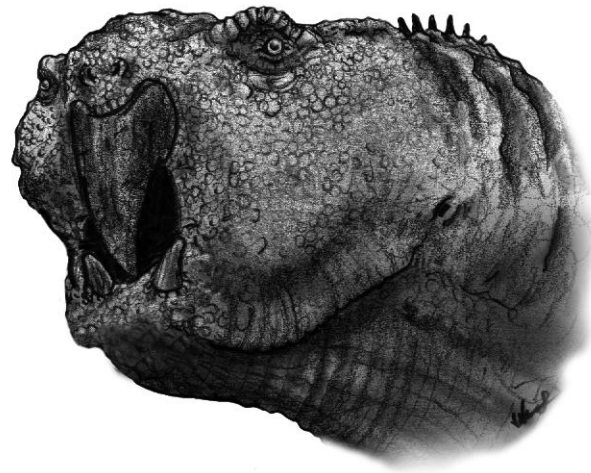


**UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE GEOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM GEOCIÊNCIAS**

**PALEOBIOLOGIA SENSORIAL DO RINCOSSAURO SUL-RIO-GRANDENSE
TEYUMBAITA SULCOGNATHUS (AZEVEDO E SCHULTZ, 1987)**

MARCOS ANDRÉ FONTENELE SALES



Porto Alegre – 2013

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ORIENTADOR – Cesar Leandro Schultz

BANCA EXAMINADORA

Prof. Dr. Alexandre Liparini Campos

Prof. Dr. Max Cardoso Langer

Prof. Dr. Sergio Alex Kugland de Azevedo

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À minha família.

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A Deus.

À minha família, que nunca disse “não” aos meus sonhos.

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A todos, o meu sincero muito obrigado.

“Nenhum problema pode ser solucionado a partir do mesmo nível de consciência que o criou.”

Albert Einstein

RESUMO

O crânio do espécime UFRGS-PV-0232-T, holótipo de *Teyumbaita sulcognathus*, foi avaliado no presente trabalho por meio de imagens de tomografia e com o uso do software InVesalius para se obter dados acerca da paleobiologia sensorial dessa espécie de rincossauro. Por meio dessa metodologia foi possível recriar digitalmente um molde da cavidade interna do neurocrânio, bem como de dois dos três canais semicirculares de cada orelha interna. Também foi possível constatar a presença de impressões da parte olfatória do encéfalo desse animal na superfície ventral dos ossos frontais, além de se realizar uma inspeção da morfologia da cavidade nasal. Todos os moldes, as impressões e os aspectos da cavidade nasal são semelhantes aos já figurados na literatura para outro rincossauro, *Hyperodapedon gordonii*. Para essa espécie, foi inferido um apurado sentido da olfação, o que também pode ser estendido para *T. sulcognathus*. No entanto, esse estudo julga como inconclusivo o teste da hipótese quanto à presença dos órgãos de Jacobson na cavidade nasal dos rincossauros. Ademais, foi inferido que o sentido da vomerolfação tenha sido pouco desenvolvido nesses animais, o que implica o fato de o comportamento social nesses animais ter requerido uma maior contribuição de outros sentidos, como a visão e o olfato, do que em outros arcossaumorfos basais.

ABSTRACT

The skull of UFRGS-PV-0232-T, the holotype of the rhynchosaur *Teyumbaita sulcognathus*, was restudied in order to gather informations about the sensory paleobiology of this animal. The material was subjected to CT scanning and the CT images obtained were imported into the free software InVesalius. It was possible to digitally reconstruct the cranial endocasts and the casts of two semicircular canals of each inner ear and to analyze the morphology of the nasal cavity. The data gathered was essentially similar to the ones already available in the literature for *Hyperodapedon gordonii*, and is probable that both taxa had a great sense of smell. In the other hand this work does not support the inferences about the presence of Jacobson's organs in the snout of these animals and considers this issue as uncertain. Actually, it was inferred that rhynchosaurs had a vomerolfaction sense poor developed, what suggests that the social behavior in these animals required a greater contribution of other senses like vision and olfaction than in other basal archosauromorphs.

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SOBRE A ESTRUTURA DESTA DISSERTAÇÃO

O presente trabalho versa sobre a paleobiologia sensorial do rincossauro sul-riograndense *Teyumbaita sulcognathus*, tema este abordado em dois artigos científicos já submetidos a periódicos (*Journal of Vertebrate Paleontology* e *Paleontologia Electronica*). Esses artigos constituem o corpo principal da dissertação, ao qual se somam as seguintes seções:

- a) Objetivos gerais e específicos que nortearam a execução do projeto;
- b) Estado da arte, na qual conceitos básicos para os temas abordados nos artigos científicos são sinteticamente revisados. Basicamente, a temática abrange os assuntos: paleoneurologia como ciência e paleobiologia dos rincossauros;
- c) Apresentação dos materiais e métodos utilizados para se alcançar os objetivos citados. Essa parte nada mais é do que a versão vernácula da metodologia descrita nos artigos científicos somada a uma contextualização estratigráfica dos fósseis utilizados.
- d) Anexo A, o qual consiste em um resumo sobre as chances de inferências enganosas a cerca do comportamento e de outros aspectos da paleobiologia de táxons extintos com base em dados paleoneurológicos. Esse trabalho foi apresentado no VIII Simpósio Brasileiro de Paleontologia de Vertebrados, realizado de 26 a 31 de agosto de 2012 em Recife.

1. INTRODUÇÃO

1.1 OBJETIVOS

Os objetivos gerais do presente trabalho são:

- 1) Analisar a morfologia intracraniana do crânio holotípico de *Teyumbaita sulcognathus*;
- 2) Inferir aspectos da paleobiologia desse táxon.

Os objetivos específicos, por sua vez, são:

- 1) Testar a hipótese quanto à presença dos órgãos vomeronasais na cavidade nasal dos rincossauros hiperodapedontíneos;
- 2) Analisar a morfologia da cavidade nasal de *T. sulcognathus* e, assim, delimitar as regiões identificadas nas cavidades nasais de táxons viventes;
- 3) Reportar a ocorrência de um molde intracraniano formado naturalmente e alojado internamente no neurocrânio e das impressões dos bulbos olfatórios na superfície ventral do teto craniano de *T. sulcognathus*;
- 4) Avaliar o significado dos dados paleobiológicos obtidos a fim de se compreender como os sentidos químicos contribuíam para a paleoautoecologia de *T. sulcognathus*.

1.2 ESTADO DA ARTE

1.2.1 Paleoneurologia e a investigação da paleobiologia de táxons extintos

Reconstruir o comportamento de organismos extintos, bem como outros aspectos paleobiológicos, é normalmente uma tarefa difícil e que provavelmente jamais decifrará o modo de vida deles em toda a sua extensão, devido à limitada capacidade de extrair dados dos fósseis e, em última análise, a impossibilidade de se investigar a

etologia desses seres conforme é feito atualmente com os vivos. Outro detalhe importante a ser considerado é que inferir o que um animal seria capaz de fazer é diferente de inferir o que ele de fato realizava, sendo o primeiro caso aquele em que os estudos paleobiológicos em sua maioria se enquadram e que, de qualquer forma, por si só já significa um grande avanço em torno da maior compreensão da vida pretérita (ver ANEXO A).

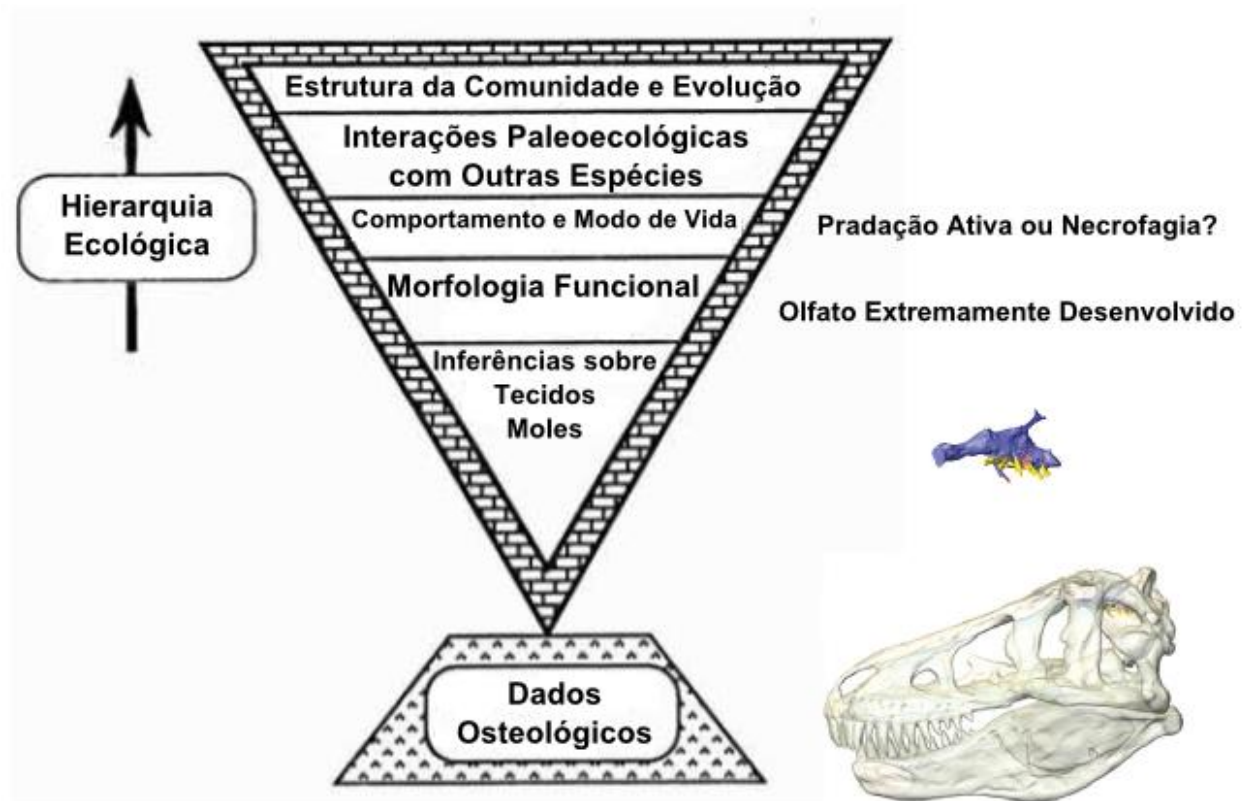


Figura 1 – Pirâmide de inferências paleobiológicas segundo a qual níveis superiores requerem considerações prévias sobre a natureza das estruturas moles, as quais são feitas baseadas em dados osteológicos. O exemplo utilizado é o da paleoneurologia de *Tyrannosaurus rex*, cujo encéfalo possuía grandes bulbos olfatórios, indicativos de olfação extremamente desenvolvida, sendo talvez utilizada durante o forrageamento. A paleoneurologia, portanto, se mostra uma importante evidência para a reconstrução do modo de vida de vertebrados extintos. Modificado de Witmer (1995) e Witmer e Ridgely (2009).

Benton (2010) listou três tipos de evidências fundamentais para a reconstrução do comportamento de formas de vida extintas: evidências empíricas, comparações com organismos vivos e modelagens biomecânicas. Entretanto, qualquer inferência paleobiológica trará consigo certo grau de inferência também a cerca das estruturas de

tecido mole, as quais, juntamente com o sistema esquelético, participaram da fisiologia dos seres extintos (WITMER, 1995). Dentro desse contexto, dados sobre a paleobiologia sensorial dos táxons fósseis, certamente, são de grande valia para inferências comportamentais e ecológicas, conforme esquematizado na Figura 1. A paleoneurologia é o ramo da paleobiologia devotado ao estudo dos “cérebros antigos”, isto é, dos encéfalos dos animais já extintos e, portanto, representa a interface entre a paleontologia e a neurologia. Ela também costuma ser definida como o estudo da evolução do cérebro, uma vez que essa é uma perspectiva por ela contemplada ao lidar com a variável tempo geológico (BUCHHOLTZ; SEYFARTH, 2000; BUTLER; HODOS, 2005; WITMER *et al.*, 2008; WITMER; RIDGELY, 2009).

Embora nunca tenha sido o foco principal dos paleontólogos, a paleoneurologia tem estado presente há muito tempo, tendo sido praticada inclusive por Othniel C. Marsh durante o século XIX (OSBORN, 1912; EDINGER, 1921, 1926, 1941, 1942; BUCHHOLTZ; SEYFARTH, 2000). Para Buchholtz e Seyfarth (2001), a moderna Paleoneurologia teve suas bases estabelecidas pela paleoneurologista Ottilie Edinger, a qual já investigou por meio dessa abordagem uma grande diversidade de táxons, que incluem sirênios, cavalos, “anfíbios” extintos, pterossauros e répteis marinhos. Ao longo da sua carreira, Edinger se concentrou em quatro questões principais que ainda norteiam os atuais estudos paleoneurológicos:

1. Com quanto de precisão os moldes intracranianos refletem a verdadeira anatomia dos encéfalos de organismos extintos?
2. A anatomia comparada é realmente adequada para responder questões sobre a evolução cerebral?
3. O modo de vida dos táxons fósseis pode ser inferido a partir dos moldes intracranianos?
4. O tamanho do cérebro tem aumentado ao longo do tempo geológico?

Para a primeira pergunta, a resposta varia de táxon para táxon (HOPSON, 1979; BUCHHOLTZ; SEYFARTH, 2000; WITMER *et al.*, 2008). Moldes intracranianos são preenchimentos naturais (por sedimento) ou artificiais (por materiais sintéticos ou reproduzidos digitalmente) da cavidade da caixa craniana, onde se alojava o encéfalo e as estruturas associadas. Em répteis, o encéfalo não preenche totalmente a cavidade intracraniana, sendo o espaço restante preenchido pelos seios venosos e meninges. Na prática, isso significa que o molde intracraniano desses animais só refletirá a

localização das principais estruturas encefálicas, dos nervos cranianos e de alguns vasos sanguíneos e seios venosos. Já mamíferos e aves apresentam um maior volume encefálico em relação ao espaço interno de suas caixas cranianas e, por isso, muitas vezes é possível adquirir também dados sobre a superfície cerebral, como a visualização de giros e sulcos (RADINSKY, 1969; DOMINGUEZ-ALONSO *et al.*, 2004; MACRINI; ROUGIER; ROWE, 2007; DONG, 2008).

Para as segunda e terceira questões a resposta é algo intermediário entre “sim” e “não”. Na realidade, elas precisam de um conjunto de dados que só podem ser fornecidos parcialmente pela paleoneurologia, o que já foi discutido para o comportamento nos dois primeiros parágrafos dessa seção. Quanto à evolução cerebral, ela só pode ser mais bem apreciada para aquelas regiões de fácil identificação nos moldes intracranianos como, os bulbos olfatórios (LARSSON; SERENO; WILSON, 2000; ZELNITSKY; THERRIEN; KOBAYASHI, 2009) e ainda assim a análise estará sujeita a uma série de restrições, inclusive de ordem prática. Vale lembrar que em estudos neurológicos, informações sobre a organização e a interação neural e suas implicações para o grau de complexidade comportamental são de suma importância, sendo esta uma sorte de dados não disponível aos paleoneurologistas. Esse fato se torna ainda mais digno de menção nos casos em que os estudos da evolução cerebral e do modo de vida dos organismos extintos trazem implicitamente a expectativa de inferências quanto às capacidades cognitivas desses animais (BUTLER; HODOS, 2005).

Finalmente, a quarta questão parece ter o “não” como resposta. A ideia de que o cérebro tem aumentado foi concebida por Marsh em seus estudos de mamíferos terciários da América do Norte. No entanto, duas ressalvas são importantes ao contexto em que se deram as conclusões de Marsh. A primeira é a falta de uma análise matemática e estatística rigorosa, uma vez que ele não levou em conta o efeito da alometria. A segunda é que o século XIX foi o momento em que a psicologia comparada estava desenvolvendo seus princípios, um dos quais preconizava que a evolução da capacidade cognitiva seguia um caminho ortogenético em sua essência, atingindo níveis progressivamente mais elevados até atingir o ápice da evolução cerebral, o qual seria o cérebro humano. Dentro dessa concepção de *scala naturae*, as ideias de Marsh encontraram apoio nos psicólogos e neuroanatomistas da época. No entanto, tentativas posteriores de se encontrar uma tendência de crescimento do

encéfalo se não obtiveram êxito e outros fatores mais se mostraram capazes de influenciar a razão tamanho cerebral/ tamanho corpóreo, como a taxa de crescimento corpóreo ao longo do tempo (BUCHHOLTZ; SEYFARTH, 2000; BUTLER; HODOS, 2005).

Metodologicamente, a paleoneurologia se baseia na maioria dos casos nos já mencionados moldes intracranianos, os quais inicialmente eram obtidos como artefatos naturais ou artificialmente por meio de emprego de resinas, o que requeria a secção dos crânios (OSBORN, 1912; RADINSKY, 1969; HOPSON, 1979). O emprego da tomografia computadorizada e de “softwares” para a manipulação e construção de imagens tridimensionais deu um novo impulso a essa ciência nas últimas duas décadas e permitiu que moldes intracranianos digitais fossem obtidos para espécimes raros (WITMER *et al.*, 2008). Além disso, algumas inferências paleoneurológicas puderam ser feitas mesmo sem os moldes. Nos casos em que a caixa craniana não se encontra totalmente ossificada ou em que somente parte do crânio foi encontrada, as impressões de algumas estruturas encefálicas e outras associadas na superfície ventral do teto craniano permitiram breves incursões sobre a paleobiologia sensorial desses animais (OSMÓLSKA, 2004; ALI *et al.*, 2008; ZELENIITSKY; THERRIEN; KOBAYASHI, 2009).

Como um ramo da Paleobiologia, a Paleoneurologia também se beneficiou da proposição do método do Extant Phylogenetic Bracket (EPB) por Witmer (1995). Em sua essência o método nada mais é do que uma forma de se extrair informações sobre a anatomia de estruturas frágeis a partir dos tecidos rijos preservados, que podem ser conchas ou ossos, por exemplo. Essas informações são adquiridas a partir do reconhecimento nos ossos, no caso dos vertebrados, de correlatos osteológicos, isto é, feições anatômicas indicativas da presença de uma estrutura mole e que apresenta uma relação de causalidade com a última. Assim, basicamente o que Witmer (1995) propôs é que fosse reconhecido nos espécimes fósseis correlatos osteológicos identificados previamente nos dois grupos viventes mais filogeneticamente relacionados ao táxon fóssil de interesse e que em termos heurísticos o enclausuram em cladogramas, limitando o grau de liberdade para inferências graças ao princípio da parcimônia (Figura 2).

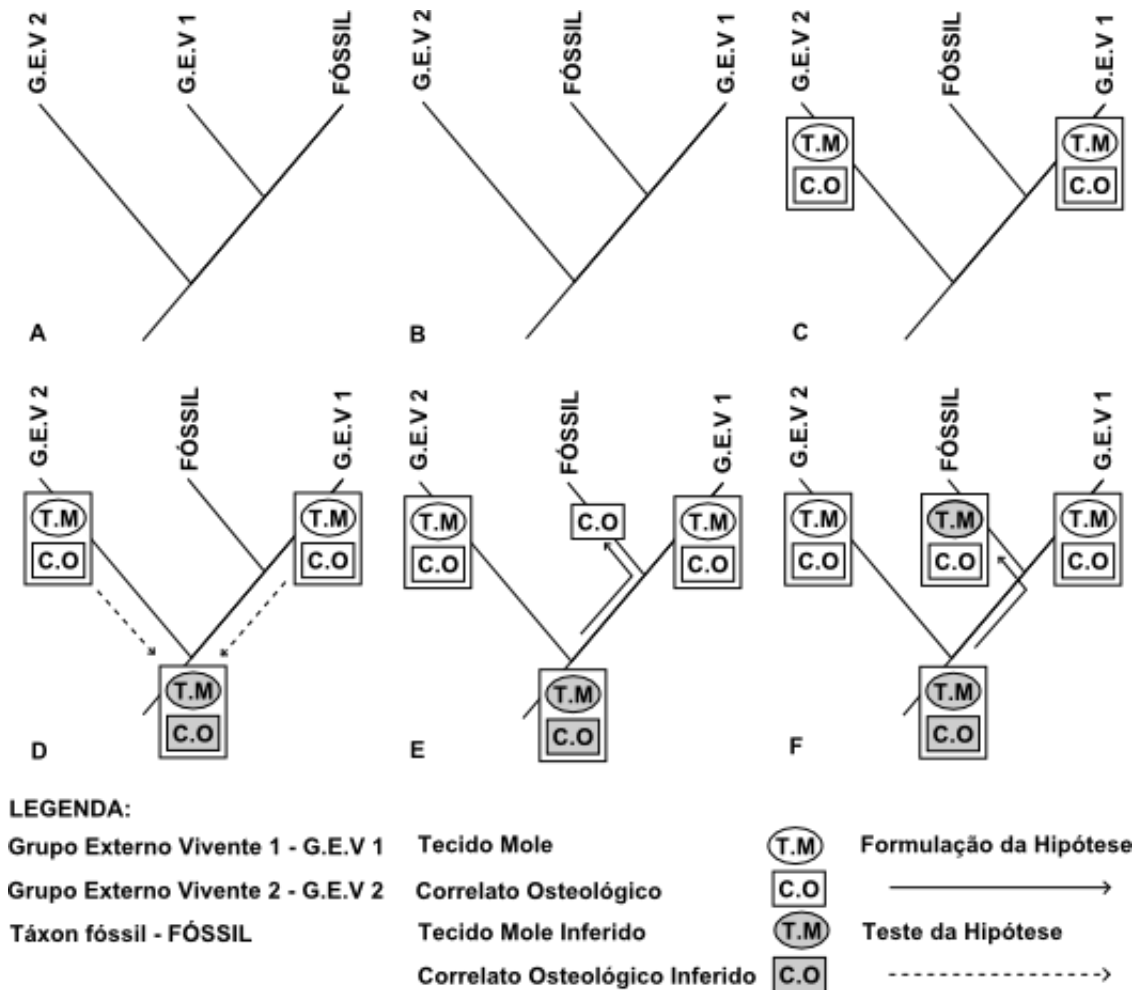


Figura 2 – Esquemática da metodologia do Extant Phylogenetic Bracket com a listagem a seguir dos passos básicos para inferências sobre tecidos moles em táxons extintos: (A) escolha dos grupos externos vivos mais relacionados filogeneticamente ao táxon fóssil de interesse; (B) rearranjo heurístico do cladograma em (A) de forma que o fóssil fique enclausurado pelos táxons vivos; (C) determinação da presença da estrutura tecidual mole em ambos os grupos vivos e de seus correlatos osteológicos; (D) formulação da hipótese quanto à presença dos tecidos moles em questão e dos correlatos osteológicos no último ancestral comum das formas vivas; (E) teste da hipótese por meio da busca do correlato osteológico no grupo fóssil, uma vez que por parcimônia ele deve estar presente nos demais descendentes do último ancestral comum dos táxons vivos; (F) inferência da presença do tecido mole no táxon fóssil quando do reconhecimento neste último do correlato osteológico do primeiro. Segundo Witmer (1995).

Os principais ganhos proporcionados pela utilização do EPB pela paleoneurologia foram a revisão e/ou a confirmação da identificação de algumas estruturas neurológicas feitas em estudos anteriores e até mesmo posteriores ao trabalho de Witmer (1995). Um exemplo clássico é o dos bulbos olfatórios do terópode

cretácico *Tyrannosaurus rex*. Brochu (2000) os reconstruiu como sendo maiores do que o próprio cérebro do animal. Trabalhos posteriores (WITMER *et al.*, 2008; WITMER; RIDGELY, 2009) aplicando a metodologia de Witmer (1995) redimensionaram os bulbos, atribuindo-lhes uma extensão menor e limitando-os às impressões na superfície ventral dos frontais. Aparentemente, Brochu (2000) incluiu parte da região olfatória da cavidade nasal de *T. rex* dentro da região ocupada pelos bulbos. Ainda assim, o tamanho relativo deles continuou maior do que o da maioria dos terópodes (Figura 3; WITMER; RIDGELY, 2009). Evans (2006) semelhantemente reavaliou as proposições feitas para a extensão anterior dos bulbos olfatórios de lambeossauríneos e os re-identificou como não se estendendo além dos frontais, dado este que o auxiliou na reavaliação das homologias das regiões das cristas cranianas.

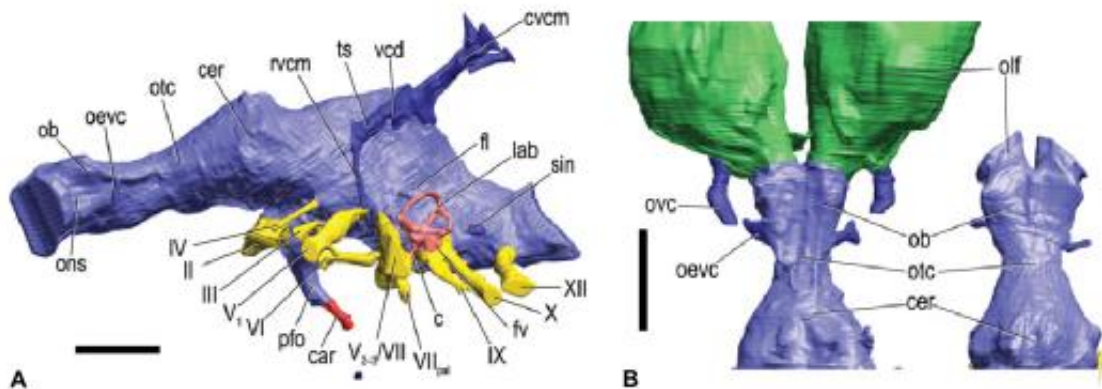


Figura 3 – Endocast digital de *Tyrannosaurus rex*. Em (A), vista lateral esquerda do endocast, artificialmente colorido de azul, enquanto nervos cranianos, vasos sanguíneos e a orelha interna estão coloridos de amarelo, vermelho e rosa, respectivamente. Em (B), bulbos olfatórios em detalhe mostrando duas diferentes reconstruções do mesmo: à esquerda, reconstrução de Brochu (2000), a qual incorporou parte da cavidade nasal (olf) aos bulbos olfatórios (ob), e à direita reconstrução de Witmer *et al.* (2008) e Witmer e Ridgely (2009), com os bulbos olfatórios re-identificados e redimensionados por meio da aplicação do EPB. Em (A), escala: 4 cm. Em (B), escala: 5 cm. Retirado de Witmer e Ridgely (2009).

De posse de uma nova abordagem metodológica e referendando as identificações das estruturas neurológicas dos moldes intracranianos nas homologias estabelecidas com os grupos vivos, a atual paleoneurologia necessitava, então, de um referencial teórico para corroborar as inferências paleobiológicas feitas principalmente com base em análises morfométricas. Se por um lado os fósseis não trazem nenhum tipo de informação sobre as interações nervosas e os neurônios, em

resumo, a fisiologia dos encéfalos de organismos extintos, por outro lado o “principle of proper mass” compensa parcialmente a ausência desse tipo de informação. Segundo esse princípio, a massa de uma determinada estrutura ou região neurológica é proporcional à quantidade de informações por ela processadas ou à importância relativa dela (BUTLER; HODOS, 2005). No caso de moldes intracranianos, em vez de massa se emprega comumente o volume e recentemente foi testada também a importância de dimensões lineares (LARSSON; SERENO; WILSON, 2000; MACRINI; ROUGIER; ROWE, 2007; ZELENITSKY; THERRIEN; KOBAYASHI, 2009). Com base nesse princípio, é possível inferir, por exemplo, que a olfação era mais desenvolvida ou mais importante para os tiranossaurídeos do que para a maioria dos terópodes (ZELENITSKY; THERRIEN; KOBAYASHI, 2009).

A Paleoneurologia, no entanto, pode não ser a única nem sequer a última palavra à cerca da paleobiologia sensorial dos organismos extintos. Os vertebrados se valem de um conjunto de sistemas sensoriais, compostos por órgãos sensoriais periféricos e por determinadas porções do sistema nervoso central, para realizar a percepção do meio ao seu redor e assim localizar alimento e parceiros sexuais e evitar predadores, entre outras funções. Entre os sentidos químicos, os principais são a gustação, a olfação e a vomerolfação, sendo eles mediados na maioria dos casos pela língua, cavidade nasal e órgãos vomeronasais ou de Jacobson, respectivamente. Quanto à sensibilidade à luz e à percepção visual do ambiente, a visão, mediada pelos olhos, é de longe o sentido mais significativo, embora o órgão pineal de alguns animais seja sensível também à luz e participe da regulação do ritmo circadiano deles. A audição, realizada pela porção coclear da orelha interna, é responsável pela percepção à propagação de ondas sonoras, enquanto a linha lateral dos vertebrados aquáticos é sensível à propagação de ondas mecânicas na água. A orientação do corpo do animal em três dimensões também é feita por uma porção da orelha interna, mais especificamente pelo aparelho vestibular. O tato é outro sentido extremamente importante dos organismos, sendo ele mediado pela superfície tegumentar e participando de comportamentos sociais e alimentares. Vertebrados aquáticos, como os condrictes por meio das ampolas de Lorenzini, costumam apresentar sensibilidade ao campo elétrico gerado por outros organismos e muitos deles, além de alguns terrestres, devem ser capazes de perceber o campo magnético terrestre (BUTLER; HODOS, 2005; KARDONG, 2009). Por fim, ainda há sentidos pouco estudados porque se restringem a

táxons pouco inclusivos e cujo papel na ecologia deles não é facilmente inferido. Um desses casos recentemente melhor estudado se trata dos pequenos órgãos mecanorreceptores localizados no rosto dos crocodilianos, responsável pela percepção da ondulação na superfície do corpo d'água onde eles se encontram (SOARES, 2002).

Nem todos os vertebrados possuem as habilidades sensoriais listadas acima e o grau de desenvolvimento de cada uma varia de grupo para grupo. No caso dos fósseis, reconhecer quais sentidos estavam presentes requer primeiramente a identificação dos correlatos osteológicos dos órgãos responsáveis por cada função sensorial por meio do EPB (Figuras 2 e 4; WITMER, 1995). Assim, é possível fazer inferências quanto à importância e o papel da visão levando em conta o tamanho e a posição das órbitas oculares e o tamanho do anel esclerótico, além, é claro, dos lobos visuais do encéfalo quando possível (WITMER *et al.*, 2003; STEVENS, 2006; SCHMITZ; MOTANI, 2011). Inferências quanto à olfação podem ser baseadas em características da cavidade nasal e no tamanho dos bulbos olfatórios como já mencionado (BENTON, 1983; WITMER; RIDGELY, 2009; ZELENITSKY; THERRIEN; KOBAYASHI, 2009). A audição, no que diz respeito à frequência à qual a cóclea seria mais sensível, pode ser analisada por meio da orelha interna que muitas vezes se encontra preservada dentro das paredes da caixa craniana (WALSH *et al.*, 2009). Também por meio da orelha interna, dessa vez graças aos canais semicirculares, é possível se ter uma ideia aproximada das capacidades locomotoras e/ou acrobáticas dos vertebrados, bem como da capacidade dos mesmos de manterem uma imagem em foco durante o deslocamento em grandes velocidades como em uma perseguição ou fuga (WITMER *et al.*, 2003; WITMER *et al.*, 2008; WITMER; RIDGELY, 2009). Outros sentidos como o tato e a gustação só podem ser considerados como presentes, já que eles fazem parte do aparato sensorial de todos os vertebrados (SCHWENK, 2008), seja em maior ou menor grau, mas qualquer tentativa de avaliar sua importância em grupos fósseis é impraticável. Já inferir a capacidade de perceber campos elétricos é um exemplo de habilidade sensorial difícil de ter sua presença demonstrada em grupos fósseis que não aqueles já inclusos em clados com formas viventes que a possuam, como os condrictes. Se algum “ostracodermo” ou qualquer outro grupo de vertebrado aquático inteiramente extinto possuía esse tipo de sentido é uma questão que dificilmente será satisfatoriamente respondida por qualquer tipo de abordagem, uma vez que os as ampolas de Lorenzini,

por exemplo, são estruturas sem correlatos osteológicos. O mesmo vale para os órgãos termossensíveis de algumas serpentes denominados de fosseta loreal.



Figura 4 – Correlatos osteológicos de órgãos sensoriais. Em (A), crânio do terópode jurássico *Juravenator starki* com o anel esclerótico (escl) preservado, o qual é um dos correlatos osteológicos do globo ocular. Por meio dele foi inferido que esse dinossauro deve ter sido mais ativo à noite. Em (B), orelha interna esquerda de *Tyrannosaurus rex*, na qual a cóclea (c) representa a parte auditiva, enquanto o vestíbulo (vest), por meio dos três canais semicirculares, é responsável pelo sentido do equilíbrio. O vestíbulo de *T. rex*, parece ter sido bem mais desenvolvido do que o de outros terópodes de grande porte, o que talvez deve ter implicado uma boa capacidade de manter a imagem focada na retina enquanto o animal se deslocava rapidamente. Escala para (B): 1 cm. (A) e (B) modificados de Schmitz e Motani (2011) e Witmer e Ridgely (2009), respectivamente.

A vomerolfacção é um sentido que requer uma consideração à parte com relação a táxons extintos. Como já fora dito, ela capta estímulos químicos, mas se distingue do olfato por normalmente requerer que as moléculas estejam dissolvidas em líquidos ou que sejam dispersas com ajuda deles (MEREDITH, 1998; SCHWENK, 2008). Assim, alguns autores (SENDER, 2002; KARDONG, 2009) preferem denominar os compostos químicos que estimulam o sistema vomerolfatório de vomodores. Os receptores próprios para vomodores estão no epitélio sensorial dos órgãos vomeronasais, situados na cavidade nasal de lepidossauros, quelônios, anfíbios e mamíferos e que devem se tratar de uma condição plesiomórfica de Tetrapoda (PARSONS, 1970; LIMAN, 1996; DØVING; TROTIER, 1998; BAXI; DORRIES; EISTHEN, 2006; HILLENIOUS, 2000; SENTER, 2002).

Em estudos descritivos que incluem a cavidade nasal de táxons extintos, a localização desses órgãos é feita tentativamente e algumas proposições chegaram a ser extremamente discrepantes, embora grande parte delas tenham se baseado na

Seguindo os passos de Hillenius (2000), Senter (2002) também testou a hipótese da presença dos órgãos vomeronasais em fitossauros, um grupo de arcossauros aquáticos. Aplicando mais uma vez os princípios do EPB, embora sem mencioná-lo explicitamente, Senter (2002) inferiu a ausência dos órgãos para Archosauria como um todo, uma vez que aves e crocodilos, que enclausuram filogeneticamente todos os arcossauros extintos, não possuem essas estruturas em fases pós-embrionárias. Ademais, os canais nasolacrimais só se estendem até a região anterior da cavidade nasal quando os órgãos estão presentes, determinando a presença da septomaxila como uma estrutura distinta e normalmente conspícua da região rostral do crânio. Arcossauros vivos e extintos geralmente não apresentam septomaxilas e nas exceções a essa regra, como nos fitossauros, elas dificilmente são estruturas ósseas homólogas às septomaxilas dos demais tetrápodes, se tratando, portanto, de neomorfos. Outra evidência para a provável ausência dessas estruturas em arcossauros extintos como os dinossauros é que, em táxons cujos canais nasolacrimais têm seus cursos passíveis de serem determinados, eles parecem não se dirigir para a região da cavidade nasal em que os órgãos vomeronasais deveriam estar presentes (EVANS, 2006).

Assim, os trabalhos de Hillenius (2000) e Senter (2002), referendados pelo EPB de Witmer (1995), ofereceram uma nova abordagem conceitual para a proposição da ausência ou presença da vomerolfacção em táxons extintos, embora ainda seja difícil, se não impossível, de mensurar com precisão a importância relativa desse sentido para esses táxons. No entanto, dada a usual relação entre os órgãos vomeronasais e aspectos sociais da biologia dos táxons que o possuem (ESTES, 1972, HALPERN, 1987; LIMAN, 1996; DØVING; TROTIER, 1998; BRENNAN; KEVERNE, 2004; BAXI; DORRIES; EISTHEN, 2006), é possível inferir, por exemplo, que a ausência dos órgãos vomeronasais em arcossauros extintos tenha implicado comportamentos sociais muito mais baseados nos sentidos da visão (e talvez do tato e da audição) do que das funções quimiossensoriais (SENER, 2002). Schwenk (2008), no entanto, relembra a possibilidade de o olfato, sendo outro sentido químico funcionalmente análogo à vomerolfacção, participar de alguma forma do comportamento social, compensando a ausência dos órgãos de Jacobson.

1.2.2 Paleobiologia dos rincossauros

Os Rhynchosauria ou, em sua forma aportuguesada mais utilizada, rincossauros estavam entre os muitos táxons de arcossaumorfos que floresceram durante o Triássico e cujas extinções se deram na fase final desse mesmo período (BENTON, 1983a). Eles dominaram a guilda de herbívoros durante o meio e o final do período, um papel desempenhado anteriormente por sinápsidos durante o Permiano e posteriormente pelos dinossauros por todo o restante do Mesozoico (Figura 6; LANGER; SCHULTZ, 2000). Alcançaram uma distribuição quase global no começo do Neotriássico e até agora só não foram encontrados nos continentes da Oceania e da Antártica (Tabela 1; CHATTERJEE, 1974).

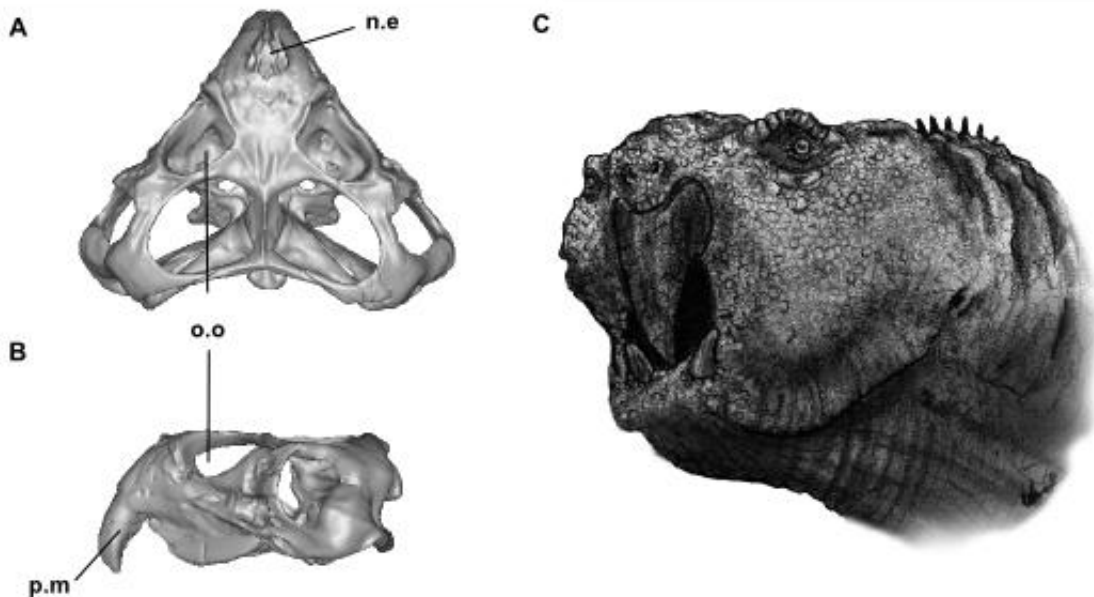


Figura 6 – Aspectos gerais da morfologia dos rincossauros. Em (A) e (B) crânio digitalizado do rincossauro hiperodapedontíneo brasileiro *Teyumbaita sulcognathus* em vista dorsal e lateral esquerda, respectivamente (ver seção Materiais e Métodos). Em (C) restauração feita pelo paleoartista Voltaire Paes da possível aparência de *T. sulcognathus* quando vivo. É possível visualizar nas três imagens duas características tipicamente rincossaurianas, as narinas externas mediais e as pré-maxilas modificadas em bico. Abreviaturas: n.e – narinas externas; o.o – órbita ocular; p.m – pré-maxila.

Tabela 1 – Classificação dos rincossauros baseado no cladograma de Hone e Benton (2008) e modificado segundo Langer e Schultz (2000a).

Táxon	Distribuição Estratigráfica e Geográfica	Distribuição Temporal	Referências Adicionais
<i>Mesosuchus browni</i> Watson, 1912	Zona Assembléia de Cynognathus, Bacia do Karoo, África do Sul	Neo-Scitiano	
<i>Howesia browni</i> Broom, 1905	Zona Assembléia de Cynognathus, Bacia do Karoo, África do Sul	Neo-Scitiano	
<i>Stenaulorhynchus stockleyi</i> Hughton, 1932	Formação Manda, Tanzânia	Amisiano	
<i>Mesodapedon kutuyi</i> Chatterjee, 1980	Formação Yerrapali, Índia	Amisiano	
<i>Rynchosaurus articeps</i> Owen, 1942	Formação Silito Tarporley, Reino Unido	Amisiano	
<i>Rynchosaurus broadiei</i> Benton, 1990	Formação Arenito Bromsgrove, Reino Unido	Amisiano	
<i>Otschalkia elderae</i> Hunt e Lucas, 1991	Grupo Dockum, Texas, Estados Unidos	Carniano	
<i>Ammorhynchus navajoi</i> Nesbitt e Whatley, 2004	Membro Holbrook, Formação Moenkopi, Arizona, Estados Unidos	Amisiano	Nesbitt e Whatley (2004)
<i>Fodonyx spenceri</i> (Benton, 1990)	Formação Arenito Otter, Reino Unido	Amisiano	
<i>Teyumbaita sulcognathus</i> (Azevedo e Schultz, 1987)	Zona Assembléia de <i>Hyperodapedon</i> , Formação Caturrita, Rio Grande do Sul, Brasil	Carniano	Langer <i>et al.</i> (2007), Montefeltro <i>et al.</i> (2010)
<i>Hyperodapedon huenei</i> Langer & Schultz, 2000	Zona Assembléia de <i>Hyperodapedon</i> , Formação Santa Maria, Rio Grande do Sul, Brasil	Carniano	Langer e Schultz (2000b), Langer <i>et al.</i> (2007)
<i>Hyperodapedon gordoni</i> Huxley, 1859	Formação Arenito Lossiemouth, Reino Unido	Carniano	
<i>Hyperodapedon genovefae</i> Buffetaut, 1983	Grupo Isalo II, Madagascar	?Carniano	
<i>Hyperodapedon huxleyi</i> Lydekker, 1881	Formação Maleri, Índia	Carniano	
<i>Hyperodapedon</i> do Zimbábue (Raath <i>et al.</i> , 1992)	Formação Pebbly Arkose, Zimbábue	Carniano	
<i>Supradapedon stockleyi</i> (Boonstra, 1953)	Horizonte indeterminado, Região de Ruhuhu, Tanzânia	?Carniano	
<i>Hyperodapedon mariensis</i> (Tupi-Caldas, 1933)	Formação Santa Maria, Rio Grande do Sul, Brasil; Formação Ischigualasto, Argentina	Carniano	Langer e Schultz (2000b), Langer <i>et al.</i> (2007)
"Rincossauro de Mariante" (Schultz e Azevedo, 1990)	Zona Assembléia de <i>Dimodontosaurus</i> , Formação Santa Maria, Rio Grande do Sul, Brasil	Ladiniano	Langer <i>et al.</i> (2007)
"Rincossauro da Nova Escócia"	Formação Wolfville, Nova Escócia, Canadá	Carniano	
<i>Hyperodapedon sarjuanensis</i> Sill, 1970	Zona Assembléia de <i>Hyperodapedon</i> , Formação Santa Maria e Formação Caturrita, Rio Grande do Sul, Brasil; Formação Ischigualasto, Argentina	Carniano	Langer e Schultz (2000b), Langer <i>et al.</i> (2007)
<i>Hyperodapedon</i> de Wyoming (Lucas <i>et al.</i> , 2002)	Formação Popo Agie, Wyoming, Estados Unidos	Carniano	Lucas <i>et al.</i> (2002)

RYNCHOSAURIA Osborn, 1903

†Rynchosauridae Huxley, 1859

‡Hyperodapedontinae Chatterjee, 1869

A diagnose para o grupo varia de autor para autor, mas normalmente as diferentes propostas incluem, entre outras, as seguintes características: (i) narinas externas como uma abertura única e medial, (ii) pré-maxilas orientadas verticalmente e assemelhando-se a bicos, (iii) contato entre as pré-maxilas e os pré-frontais, (iv) parietais fusionados, (v) dentição do tipo anquilotecodonte, (vi) depressão na superfície dorsal tanto dos frontais como dos pós-frontais, (vii) central intimamente associado ao astrágalo e compondo a série de tarsais proximais (BENTON, 1983b; DILKES, 1995; DILKES, 1998; LANGER; SCHULTZ, 2000; HONE; BENTON, 2008). Quanto às relações internas do grupo, elas se encontram brevemente sumarizada na Tabela 1, segundo o trabalho de Hone e Benton (2008). Depois desse trabalho, um novo gênero foi criado, *Bentonyx sidensis* (LANGER *et al.*, 2010), o qual não foi incorporado à tabela.

A maior parte do histórico das pesquisas sobre rincossauros compreendem descrições osteológicas de novos táxons, a revisão desses estudos e a investigação das relações filogenéticas dentro do grupo e entre rincossauros e os demais arcossaumorfos basais (ex.: OWEN, 1862; HUXLEY, 1869; HUENE, 1942; CHATTERJEE, 1974; BENTON, 1983b; AZEVEDO, 1982; SCHULTZ, 1986; BENTON, 1990; DILKES, 1995; WILKINSON; BENTON, 1995; DILKES, 1998; LANGER *et al.*, 2000; HONE; BENTON, 2008; LANGER *et al.*, 2010; MONTEFELTRO; LANGER; SCHULTZ, 2010). Inferências de natureza paleobiológica estão presentes tanto na forma de seções dentro das descrições mais abrangentes ou como estudos em que elas são o foco principal, com o espectro de temas incluindo a dentição, biomecânica mandibular e dos membros locomotores e a paleoecologia do táxon (CHATTERJEE, 1974; BENTON, 1983b; BENTON, 1984; AZEVEDO, 1987; FARIÑA, 1991; CABRERA, 2004). Dentre esses estudos, o de Benton (1983b) versando sobre a anatomia funcional do gênero *Hyperodapedon* é certamente o mais completo e audacioso, uma vez que tentou a reconstrução de várias estruturas moles da cabeça do animal como vasos e nervos. Ele também figura um molde da cavidade intracraniana e das orelhas internas, além das impressões dos bulbos olfatórios na superfície ventral dos frontais, sendo assim a principal, senão a única, abordagem paleoneurológica sobre rincossauros (Figura 7). Muito das reconstruções tentativamente propostas por Benton (1983b) se basearam em comparações com lagartos e tuataras. Embora nenhuma justificativa seja dada para esse fato, é possível especular que a diversidade de literatura disponível

sobre a descrição anatômica de lepidossauros, principalmente de lagartos, seja uma das explicações (PARSONS, 1970 e referências nele citadas). Outra possibilidade é a visão antes bastante arraigada de que os tuataras eram estruturalmente semelhantes aos rincossauros, motivo pelo qual os últimos já foram considerados grupo-irmão dos primeiros (ex.: HUXLEY, 1869; ROMER, 1956). Curiosamente, Benton (1983b) foi um dos primeiros a defenderem Rhynchosauria como membro de Archosauromorpha em vez de Lepidosauromorpha ou, mais especificamente, de Rhynchocephalia.

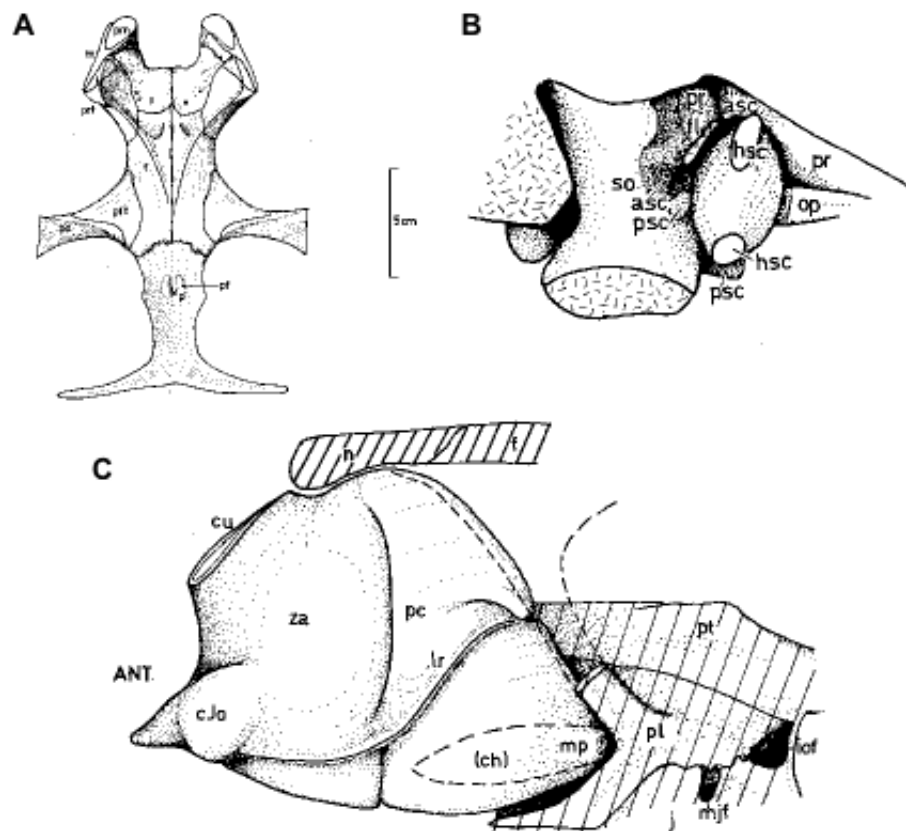


Figura 7 – Estudo paleobiológico de *Hyperodapedon gordonii*. Em (A), teto craniano em vista entral com as impressões dos bulbos olfatórios e possivelmente do órgão pineal (pf). Em (B), molde intracraniano e da orelha interna direita, com os canais semicirculares horizontal (hsc) e posterior (psc) preservados. Em (C), reconstrução da cápsula nasal cartilaginosa contendo os órgãos de Jacobson (cJo). Retirado de Benton (1983b).

Como resumo das principais investigações paleobiológicas, os rincossauros podem ser considerados animais bastante peculiares em uma série de aspectos. Sua dentição, por exemplo, é definida como anquilotecodonte por Chatterjee (1974) devido

aos dentes implantados profundamente nos alvéolos e a eles fixados por ossos de ligamento e aparentemente não havia substituição dentária, com o acréscimo posterior de novos dentes (BENTON, 1984). Esses dentes se organizavam em fileiras múltiplas de dentes que podiam se situar em uma ou duas cristas no dentário e em um ou dois sulcos nos maxilares. Esse aparato mandibular, que ainda contava com as pré-maxilas modificadas em bico, muito provavelmente apresentava oclusão perfeita e deve ter servido para processar oralmente alimento vegetal, os quais podem ter sido sementes ou estruturas reprodutivas de gimnospermas ou raízes e caules intumescidos enterrados no solo (BENTON, 1983b; BENTON, 1984; FARIÑA, 1991). Provavelmente a vegetação mais propensa a ser forrageada pelos rincossauros incluía majoritariamente as formas de menor porte, como aquelas componentes da flora de *Dicroidium*, pelo menos para os táxons da Gondwana. Parte do alimento talvez possa ter sido temporariamente acomodado em “bochechas”, caso as cristas *angulis oris* nos jugais desses animais realmente indiquem a presença de músculos faciais pelo menos nos hiperodapedontíneos (BENTON, 1983a; BENTON, 1990). A digestão deve ter sido processada por um tubo digestório relativamente volumoso, o que justificaria o formato em barril do tronco desses animais (BENTON, 1983b; BENTON, 1990; BENTON; HART; CLAREY, 1993).

Além da biomecânica mastigatória, a biomecânica locomotora também foi trabalhada por alguns autores. Foi sugerida uma postura parcialmente *sprawling* e eventualmente semi-ereta (CHATTERJEE, 1974; BENTON, 1983b). Além da locomoção, os membros, especialmente posteriores, também podem ter sido utilizados para escavar, uma vez que contavam com garras de morfologia semelhante às de alguns animais escavadores atuais. O hábito de escavar talvez estivesse relacionado à extração de tubérculos e rizomas enterrados no solo para a alimentação (BENTON, 1983b).

Benton (1983b) em suas considerações sobre a anatomia e a morfologia craniana de *Hyperodapedon gordonii*, verificou a presença de grandes impressões dos bulbos olfatórios na superfície ventral dos frontais e de uma ampla cavidade nasal, muito provavelmente maior do que a da maioria dos répteis mesmo em termos relativos. Para esse autor, esses dois dados eram evidências de que os rincossauros deviam ter possuído a olfação bastante desenvolvida. Benton (1983b) foi ainda mais longe quanto às inferências paleobiológicas sobre os sentidos dos rincossauros. Em um espécime de

H. gordonii, ele notou a presença de alguns elementos bastante conspícuos que compuseram o anel esclerótico de um dos olhos. Assim, Benton (1983b) propôs que os rincossauros possuísem grandes globos oculares, inferência que também encontrava suporte nas grandes dimensões das órbitas. Esses grandes olhos devem ter conferido a esses répteis triássicos uma aprimorada capacidade visual. Por fim, Benton (1983b) reconstruiu tentativamente a cavidade nasal desses animais alojando os órgãos vomeronasais (Figura 7), os quais de fato compunham a anatomia nasal dos lepdiossauros viventes utilizados por ele nas comparações com os rincossauros. Entretanto, assim como fora feito para a audição e a visão, Benton (1983b) não inferiu como deve ter se dado a contribuição dos órgãos vomeronasais para a paleoautoecologia dos rincossauros.

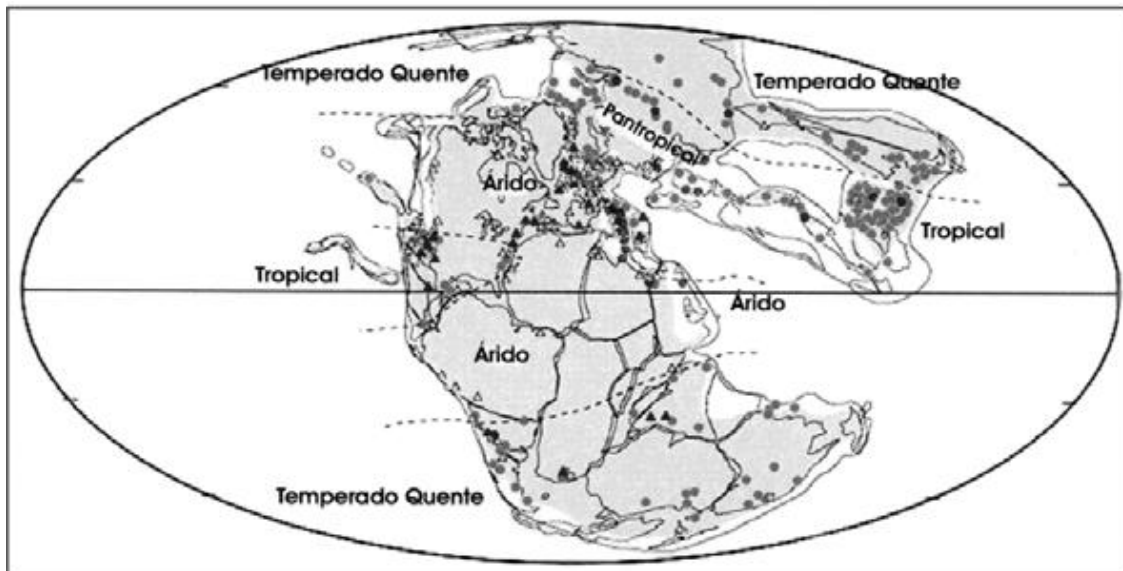


Figura 8 – Mapa paleogeográfico do Neotriássico, com as principais regiões climáticas delimitadas. Retirado de Bernardes-de-Oliveira *et al.* (2007).

Os rincossauros estavam entre os tetrápodes mais numerosos do começo do Neotriássico (BENTON, 1983a; ROGERS *et al.*, 1993; LANGER; SCHULTZ, 2000; LANGER *et al.*, 2007; SCHULTZ; LANGER, 2007), tornando-os provavelmente o principal item da dieta de muitos predadores, conforme evidenciado pelo achado de um esqueleto de juvenil dentro da caixa torácica de um fitossauro (CHATTERJEE, 1978). Essa teia cadeia alimentar ocorreu em um contexto paleoambiental, de temperaturas elevadas e grande aridez, e paleogeográfico, em que as principais massas continentais

estavam reunidas no supercontinente Pangea, bem diferente dos verificados atualmente (Figura 8; SCHULTZ, 2004; BENTON, 2005; BERNARDES-DE-OLIVEIRA *et al.*, 2007). A extinção dos rincossauros durante os eventos do final do Triássico talvez esteja de alguma forma relacionada à mudança florística que pôs fim ao domínio da flora *Dicroidium*, sendo esta sucedida pelas coníferas e bennettitales (BENTON, 2005; porém consultar ROGERS *et al.*, 1993).

Conforme é possível perceber pelas datas das referências, a maior parte dessas inferências antecedeu em mais de uma década dois avanços para a Paleobiologia: o emprego da modelagem tridimensional e a aplicação do Método do Enclausuramento Filogenético (WITMER, 1995; DARDON *et al.*, 2010). As reconstruções baseadas em lepidossauros, especialmente quando se fazia menção somente a lagartos, devem ter conferido um perfil quase lacertílio aos rincossauros, talvez longe de representar sequer a condição primitiva de Diapsida para uma série de atributos paleobiológicos. Na verdade, dentre os táxons vivos que os enclausuram em cladogramas, os rincossauros são filogeneticamente mais próximos dos crocodilianos e aves, o que reforça ainda mais a necessidade de se revisar uma série de asserções feitas sobre a paleobiologia desse táxon triássico. Nesse sentido, as formas sul-americanas podem desempenhar papel muito importante devido ao elevado número de espécimes já coletados e pela diversidade já amostrada (LANGER; SCHULTZ, 2000). De fato, os hiperodapedontíneos brasileiros já foram alvos de algumas abordagens paleobiológicas (FARIÑA, 1991; CABRERA, 2004) e alguns espécimes, como o holótipo da espécie *Teyumbaita sulcognathus* (AZEVEDO, 1982; AZEVEDO; SCHULTZ, 1987; MONTEFELTRO; LANGER; SCHULTZ, 2010), os tornam propensos a investigações paleoneurológicas, por exemplo.

1.3 MATERIAIS E MÉTODOS

1.3.1 Espécime UFRGS-PV-0232-T

O espécime UFRGS-PV-0232-T, pertencente à coleção paleontológica do setor de Paleovertebrados do Departamento de Paleontologia e Estratigrafia da Universidade Federal do Rio Grande do Sul, corresponde a material craniano e pós-craniano de um rincossauro escavado no ano de 1980, em um afloramento de corte de estrada na localidade Linha Facão. Essa localidade se situa no município gaúcho de Vera Cruz, próximo à divisa com Candelária, tendo como coordenadas geográficas 29°40'12"S e 52°43'30"W (AZEVEDO, 1982; MONTEFELTRO; LANGER; SCHULTZ, 2010). Ele provém de níveis estratigráficos considerados como pertencentes à Formação Caturrita devido à alternância de siltitos e níveis delgados, em sua maior parte lenticulares e com laminação planoparalela, embora esta se mostre pouco definida às vezes. O paleoambiente é interpretado como uma planície de inundação (AZEVEDO, 1982). Em termos de estratigrafia de sequências, o nível da Formação Caturrita de procedência do espécime é tido como parte de um trato de sistema de mar alto, dentro da Sequencia Santa Maria 2 (Figura 9; ZERFASS *et al.*, 2003; LANGER *et al.*, 2007). Já do ponto de vista bioestratigráfico, ele está inserido na Zona Assembléia de *Hyperodapedon*, embora esteja acima dos níveis estratigráficos de onde foram obtidos a maioria dos espécimes atribuídos ao gênero *Hyperodapedon*, denominada como Zona de Acme de *Hyperodapedon* por Langer *et al.* (2007). A idade é considerada como Neocarniana por alguns autores (LANGER; SCHULTZ, 2000; ZERFASS *et al.*, 2003; SCHULTZ; LANGER, 2007) e como Eonoriana por outros (LANGER *et al.*, 2007; MONTEFELTRO; LANGER; SCHULTZ, 2010), sendo a primeira mais concordante com o registro fóssil de rincossauros em outros países (LANGER; SCHULTZ, 2000).

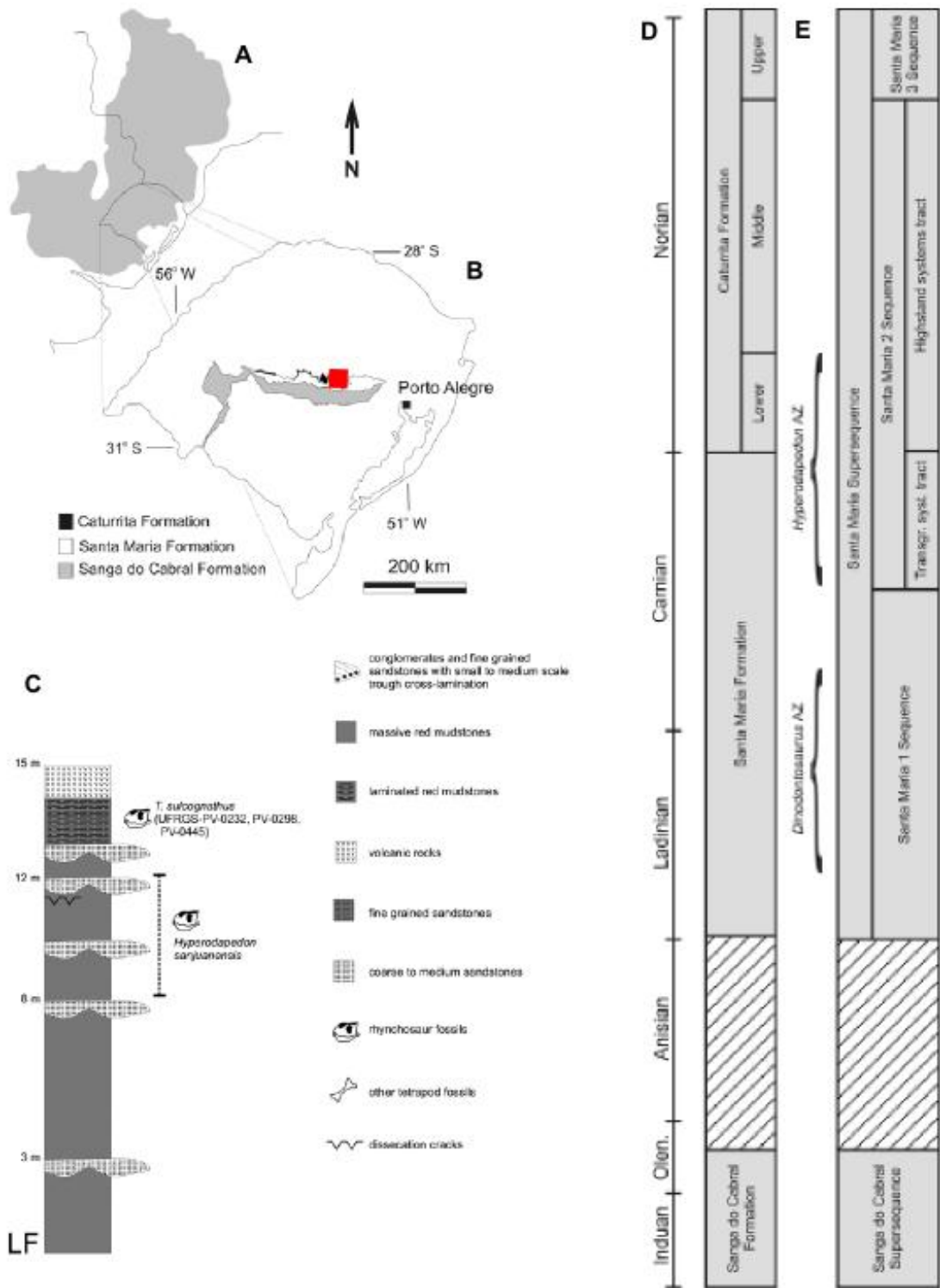


Figura 9 – Contextualização geográfica, litoestratigráfica e bioestratigráfica da localização tipo do holótipo de *Teyumbaita sulcognathus* (UFRGS-PV-0232-T). Em (A), extensão da Bacia do Paraná e, em (B), mapa do Rio Grande do Sul com as três formações triássicas encontradas no estado. A localidade Linha Facão está sinalizada em vermelho. Em (C), seção estratigráfica do afloramento da localidade Linha Facão indicando os níveis de procedência dos fósseis de rincossauros. Em (D) e (E), litoestratigrafia e

estratigrafia de sequencias do Grupo Rosário do Sul, ao qual pertencem as formações triássicas gaúchas. (A), (B), (D) e (E) retirados de Langer *et al.* (2007). (C) retirado de Montefeltro, Langer e Schultz (2010).

UFRGS-PV-O2322-T foi inicialmente alvo de estudos em duas dissertações de mestrado, as quais descreveram o crânio e o pós-crânio (AZEVEDO, 1982; SCHULTZ, 1986). Em sua totalidade ele inclui os seguintes elementos preservados: crânio praticamente completo, ambas as mandíbulas completamente preservadas, vértebras cervicais incluindo o atlas e o eixo, vértebras truncais e caudais, algumas gastrálias, escápulo-coracóide esquerdo e direito, mas somente o primeiro estando completo, úmero esquerdo, fêmur e tíbia direita e duas falanges (Figura 10 – elementos preservados do espécime; AZEVEDO, 1982; SCHULTZ, 1986; MONTEFELTRO; LANGER; SCHULTZ, 2010). A preservação do material é excelente e junto com a completude do sín-crânio possibilitou o estudo biomecânico da mastigação em mais uma dissertação de mestrado (FARIÑA, 1991).

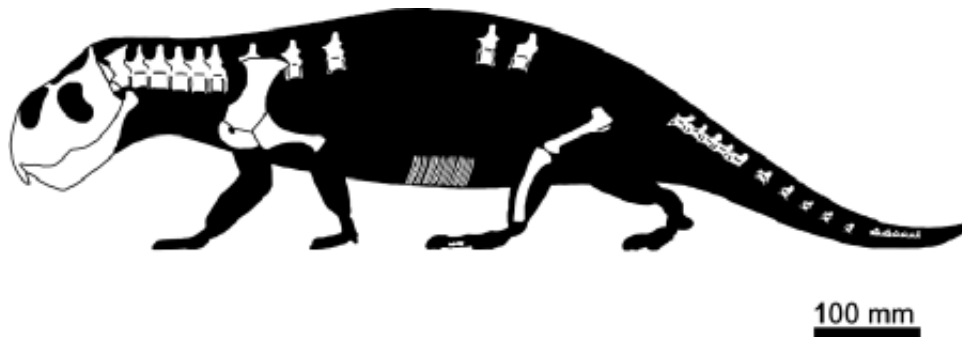


Figura 10 – Esquema ilustrando os elementos ósseos preservados de UFRGS-PV-0232-T. Retirado de Montefeltro, Langer e Schultz (2010).

Desde o início, ficou clara a importância taxonômica do espécime UFRGS-PV-0232-T, como um indivíduo pertencente a uma entidade taxonômica diferente das já descritas. Assim foi proposta uma nova espécie, *Scaphonyx sulcognathus*, tendo o espécime em questão como o holótipo (AZEVEDO, 1982; AZEVEDO; SCHULTZ, 1987). No entanto, posteriormente ficou claro que o gênero *Scaphonyx* havia sido erigido com base em características não diagnósticas, constituindo-se, portanto, em um *nomen dubium*, e requerendo a realocação das espécies e espécimes a ele atribuídos (LANGER; SCHULTZ, 2000; HONE; BENTON, 2008; MONTEFELTRO; LANGER;

SCHULTZ, 2010). Nesse contexto, foi criado o gênero *Teyumbaita*, sendo a espécie tipo *T. sulcognathus* (MONTEFELTRO; LANGER; SCHULTZ, 2010), a qual segue como membro da subfamília Hyperodapedontinae e provavelmente se trata do grupo-irmão do gênero *Hyperodapedon* (LANGER; SCHULTZ, 2000; HONE; BENTON, 2008; LANGER *et al.*, 2010; MONTEFELTRO; LANGER; SCHULTZ, 2010). Mesmo com toda essa revisão taxonômica, *T. sulcognathus* permanece como táxon endêmico do Triássico Superior do Rio Grande do Sul.

1.3.2 Escaneamento de UFRGS-PV-0232-T e manipulação digital das imagens

Em 2008, alguns espécimes da coleção de Paleovertebrados da UFRGS foram tomografados no Hospital das Clínicas de Porto Alegre. Entre esses espécimes estava o holótipo de *Teyumbaita sulcognathus*, o qual possui até agora o crânio melhor preservado de rincossauro achado em solo gaúcho. Na realidade, o crânio de UFRGS-PV-0232-T apresenta pouca ou nenhuma distorção significativa e tem como único elemento ósseo não preservado o epipteriгоide esquerdo (Figura 11 A e C; AZEVEDO, 1982; MONTEFELTRO. LANGER; SCHULTZ, 2010).

O procedimento foi realizado pelo tomógrafo Phillips Brilliance 16-Slice, com as seguintes especificações técnicas: voltagem de 140 kV, corrente de 275 mA, slices com espessura de 1 mm e com espaçamento entre si também de 1 mm e campo de visão de 341 mm. Ao fim do processo, foram obtidos 249 slices coronais do crânio em formato DICOM, cada um com as dimensões de 512x512 pixels e cada pixel medindo 0,666 cm.

A fim de visualizar e manipular as imagens tridimensionalmente, os slices foram importados para o *software* InVesalius (Centro de Tecnologia da Informação Renato Archer – CTI; Figura 12). Ele foi escolhido por ser gratuito, dispor das ferramentas básicas de outros softwares semelhantes e ter sido desenvolvido com tecnologia brasileira. Assim, foi possível recriar digitalmente tanto o crânio como o molde intracraniano formado naturalmente e presente no interior do neurocrânio de *T. sulcognathus* (seção 2 e Figura 11 B e D). Visto que o neurocrânio em rincossauros não reveste completamente o encéfalo, foi investigada a morfologia da superfície ventral do teto craniano em busca das impressões deixadas pela porção olfatória do encéfalo.

Além disso, aspectos da morfologia da cavidade nasal também foram avaliados digitalmente para se obter dados que permitissem inferências sobre os sentidos químicos dos rincossauros.

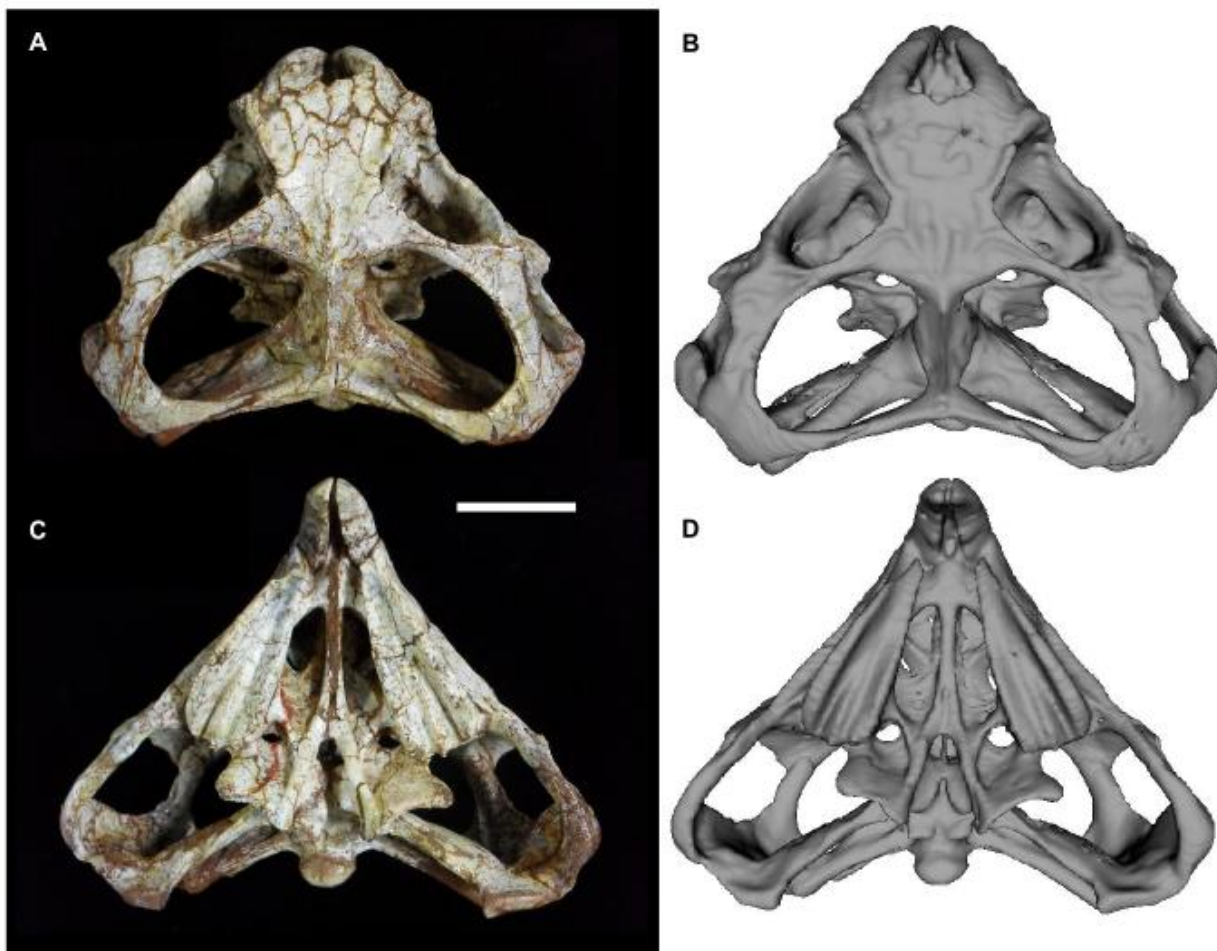


Figura 11 – Crânio holotípico de *Teyumbaita sulcognathus* (UFRGS-PV-0232-T). Em (A) e (C), espécime em vista dorsal e palatal, respectivamente. Em (B) e (D), reconstrução digital do espécime por meio do software InVesalius em vista dorsal e palatal, respectivamente. Escala: 5 cm.

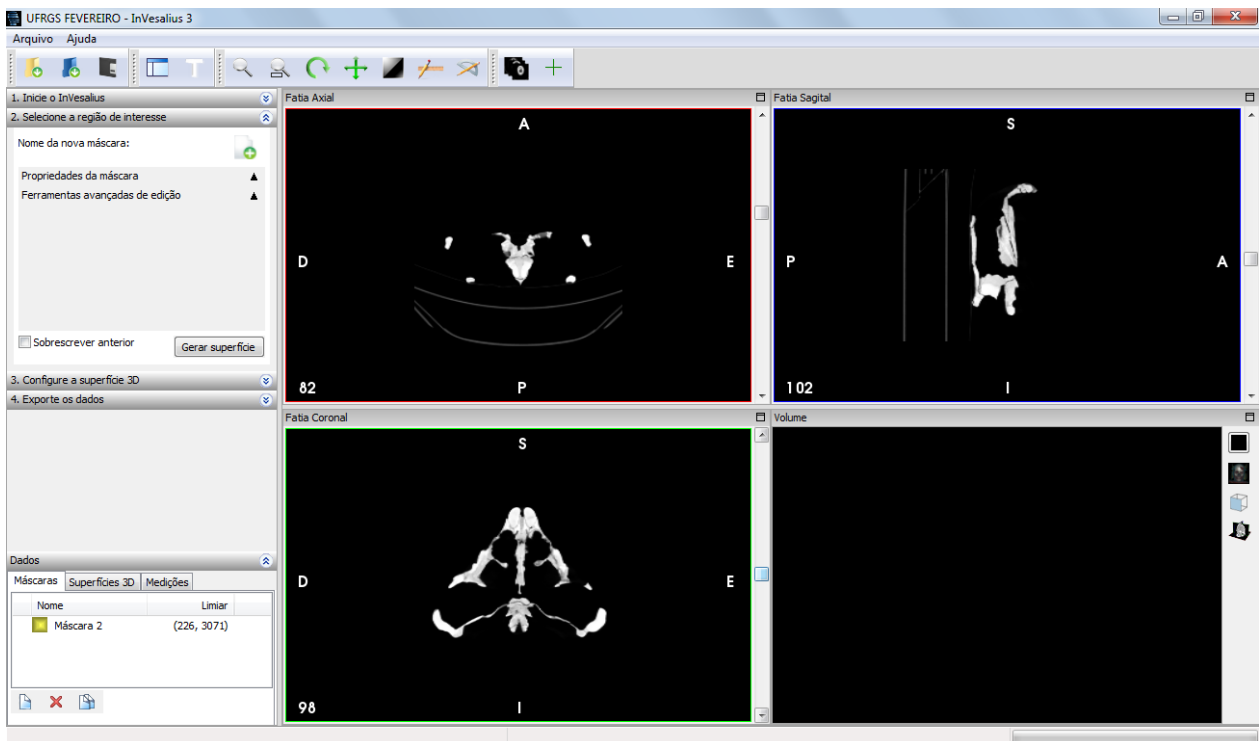


FIGURA 11 – Visualização das imagens de tomografia computadorizada de UFRGS-PV-0232-T no software InVesalius.

1.4 ANÁLISE INTEGRADORA

Imagens de tomografia computadorizada permitiram a análise da morfologia intracraniana das regiões da cavidade nasal e do neurocrânio do espécime UFRGS-PV-0232-T, holótipo do rincossauro hiperodapedontíneo sul-rio-grandense *Teyumbaita sulcognathus*. Essas imagens revelaram a morfologia geral do molde intracraniano alojado no neurocrânio, bem como de moldes dos canais semicirculares das orelhas internas desse táxon. Devido ao neurocrânio só circundar a metade posterior do encéfalo, pouco foi discutido sobre o molde intracraniano, sendo possível somente a localização do cerebelo e a identificação de uma proeminência dorsal no molde, o qual deve se tratar de um seio venoso ou de uma expansão dural, isto é, uma intumescência de alguma das meninges que revestia e protegia o encéfalo.

Por outro lado, também foi possível reconhecer na superfície ventral dos ossos frontais do crânio a ocorrência de sulcos delimitados pela estrutura chamada *crista*

cranii. Esses sulcos, na verdade, são impressões dos bulbos olfatórios e assim representam a única sorte de dado sobre a metade anterior do encéfalo. Devido ao tamanho dos sulcos, foi possível inferir que os bulbos olfatórios foram grandes em *T. sulcognathus*, mesmo sem poder realizar uma análise alométrica e estatística. Esses bulbos também parecem ter se comunicado com os hemisférios cerebrais por meio de um trato olfatório, sendo este mais um dado que indica a pouca redução ou até mesmo o maior desenvolvimento da porção encefálica do sistema olfatório.

Quanto à cavidade nasal, esta era profunda e amplamente larga, a despeito do comprimento relativamente curto do rostro. Assim, aparentemente havia muita área disponível para o revestimento da cavidade nasal por epitélio olfatório, sugerindo uma grande importância da olfação para a autoecologia de *T. sulcognathus*. Essas mesmas inferências já haviam sido feitas para *Hyperodapedon gordonii* e em parte devem refletir semelhanças paleobiológicas entre esses dois táxons que compõem a subfamília Hyperodapedontinae.

No entanto, a importância da olfação deve ter sido ainda mais dramática no contexto, aqui defendido, da redução da vomerolfação em rincossauros hiperodapedontíneos. Em uma reconstrução da cavidade nasal de *H. gordonii*, foi proposta a presença dos órgãos vomeronasais. A metodologia aqui adotada não foi capaz de comprovar ou rejeitar a presença dos órgãos, no entanto, a discussão feita sobre a provável ausência de comunicação entre os canais nasolacrimais e os órgãos vomeronasais indica uma redução da funcionalidade dos últimos. Estando a vomerolfação relacionada a comportamentos sociais, é provável que sua redução tenha implicado em alterações comportamentais nos rincossauros hiperodapedontíneos em relação ao que seria esperado para arcossaumorfos basais. Sendo um sentido químico assim como a vomerolfação, é possível que a olfação tenha assumido parcialmente os papéis antes desempenhados pelos órgãos vomeronasais, enquanto outros aspectos comportamentais devem ter recebido maior contribuição da visão, que também parece ter sido bastante desenvolvida em rincossauros.

Quanto à proposição dos aspectos pontuais da autoecologia dos rincossauros hiperodapedontíneos para os quais a olfação possuía maior importância, é difícil de testar as hipóteses levantadas. Na realidade, o processo de falseamento de algumas delas requer novas evidências fósseis, enquanto outras não são passíveis de testes. Outra questão importante está relacionada ao pouco conhecimento da variação

interespecífica encontrada nos rincossauros, o que também requer a realização de investigações semelhantes às aquelas aqui realizadas com outras espécies.

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2. CORPO PRINCIPAL DA DISSERTAÇÃO

2.1 ARTIGO SUBMETIDO À REVISTA *JOURNAL OF VERTEBRATE PALEONTOLOGY*

Rhynchosaurs and the evolution of Jacobson's organs

MARCOS A. F. SALES*,¹ and CESAR L. SCHULTZ²

¹Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 9500, Agronomia, 91501-970, Porto Alegre, Rio

Grande do Sul, Brazil, marcos.paleo@yahoo.com.br;

²Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 9500, Agronomia, 91501-970, Porto Alegre, Rio

Grande do Sul, Brazil, cesar.schultz@ufrgs.br

RH: SALES AND SCHULTZ—RHYNCHOSAURS AND VOMEROLFACTION

*Corresponding author

ABSTRACT— Jacobson's organs, also known as vomeronasal organs, are chemosensory structures found in most tetrapods. They are secondarily absent or reduced in some squamates and mammals and all living archosaurs, i.e., crocodylians and birds. Their absence has been inferred for extinct archosaurs based on the lack of anatomical, osteological and phylogenetic evidences. Using these same criteria, here we analyzed the possibilities of these organs also have been present in rhynchosaurs, a group of basal archosauromorphs that flourished in Triassic times. None of the features analyzed is conclusive, but in this taxon, the absence of nasolacrimal ducts in the anterior region of the nasal cavity suggests that Harderian glands were functionally dissociated from vomeronasal organs (if present). This fact, along with the lack of ecological, anatomical and physiological adaptations to compensate the change in the course of the nasolacrimal ducts, indicates that the vomeronasal organs were at least reduced and almost non-functional in rhynchosaurs. Behaviorally it means that social behaviors in rhynchosaurs relied more on other senses, probably olfaction and vision. Evolutionarily it means that reduction of the relative importance of vomerolfaction for social behavior occurred at least twice within Archosauromorpha, one represented by rhynchosaurs and other that probably initiated in some phylogenetic level between *Proterosuchus* and Archosauria.

INTRODUCTION

Jacobson's organs are a pair of chemosensory structures with important roles in the ecology and behavior of many tetrapods (Døving and Trotier, 1998; Brennan and Keverne, 2004; Baxi et al., 2006). They are located dorsally in the palate, in the anterior part of the nasal cavity, and are also known as vomeronasal organs (VNOs) because of their frequent association with the vomers (Parsons, 1970; Døving and Trotier, 1998; Trotier and Døving, 1998; Hillenius, 2000; Butler and Hodos, 2005). Originally described in anatomical studies about domestic mammals (Jacobson, 1813 apud Trotier and Døving, 1998), VNOs are also found in amphibians, *Sphenodon* (tuatara), squamates, and turtles, indicating that their presence is a tetrapod plesiomorphy (Parsons, 1970; Liman, 1996; Døving and Trotier, 1998; Baxi et al., 2006) and that vomerolfaction, as a structurally distinct sensory system, complementary to olfaction (Liman, 1996; Brennan and Keverne, 2004), have a shorter evolutionary history than this latter (Liman, 1996; for a better discussion concerning the emergence of vomerolfaction see also Eisthen, 2004, and Schwenk, 2008). The absence or reduction of VNOs in some mammals and squamates and all crocodylians and birds must represent a derived condition independently attained by each lineage (Senter, 2002). The chemosensory roles of the VNOs are related to the sense of molecules called vomodors by Kardong (2009) and Senter (2002) in order to distinguish them from the ones sensed by olfaction, the general odorants or odors. The stimuli provided by vomodors are transmitted to vomeronasal bulbs, also known as accessory olfactory bulbs, via vomeronasal nerves, which are branches of the cranial nerve I (Liman, 1996; Døving and Trotier, 1998; Brennan and Keverne, 2004), with mechanisms of transduction of stimuli rather different from the olfactory system (Liman, 1996; Døving and Trotier, 1998; Brennan and Keverne, 2004). Vomerolfaction is primarily related to detection and processing of vomodors called pheromones, which are employed in signaling and communication between conspecifics (Døving and Trotier,

1998; Brennan and Keverne, 2004; Butler and Hodos, 2005; but see Baxi et al., 2006). Thus, it usually conveys and stimulates behaviors associated to individual recognition, signalization of sexual readiness, and demarcation of territorial boundaries (Liman, 1996; Døving and Trotier, 1998; Brennan and Keverne, 2004). In these cases, pheromone releasing usually occurs via saliva, urine, feces and secretion from specialized glands, being deposited in a myriad of substrates and body surface (Brennan and Keverne, 2004).

With respect to fossil taxa, supposed evidences of the presence of VNOs in dinosaurs and other archosaurs (Maryanska, 1970; Chatterjee, 1985) have been rejected (Senter, 2002; Evans, 2006; Witmer and Ridgely, 2009; Weinbaum, 2010) and, based on the lack of possible osteological and anatomical evidences of these organs in those taxa, Senter (2002) proposes that their absence in living archosaurs should be extended to Archosauria as a whole and the reduction and loss of vomerolfaction occurred in some phylogenetic level between *Proterosuchus* and Archosauria. Nevertheless, the history of the loss of VNOs in the archosaurian lineage may have been more complicated than this. Rhynchosaurs, a basal group within Archosauromorpha, were described by Benton (1983) as bearing VNOs, but apparently do not have some features considered by Senter (2002) as evidences of the presence of these organs. Beyond the obvious behavioral and ecological implications of the presence (or absence) of vomerolfaction in this taxon, this question has also a great evolutionary relevance, because rhynchosaurs diverge within the archosauromorph lineage in a phylogenetic level more basal than the one proposed by Senter (2002) as the interval for the secondary loss of vomerolfaction.

MATERIAL AND METHODS

In order to investigate the presence or not of the VNOs in rhynchosaurs, the specimen UFRGS-PV-0232-T (Universidade Federal do Rio Grande do Sul, PaleoVertebrates Triassic collection),

which is the holotype of the hyperodapentinae rhynchosaur *Teyumbaita sulcognathus* (Azevedo and Schultz, 1987), was restudied (Azevedo and Schultz, 1987; Montefeltro et al., 2010). This specimen was chosen because it includes a nearly complete and very well preserved skull for which computed tomographic (CT) images are available (Fig. 1 and 2). Inferences for other species were made based on specimens of the genus *Hyperodapedon* from UFRGS collection and information gathered from the literature. We also made some observations about the features analyzed by Senter (2002).

The specimen UFRGS-PV-0232-T was collected in 1980 at Linha Facão locality (29°40'12"S; 52°43'30"W), close to the boundary between Candelária e Vera Cruz towns, Rio Grande do Sul State, Brazil. It comes from the lower part of the stratigraphic unit known as Caturrita Formation (Azevedo, 1982; Schultz, 1986, Azevedo and Schultz, 1987; Montefeltro et al., 2010). In terms of sequence stratigraphy, these layers integrate the upper part of Santa Maria Sequence 2, a highstand system tract, and are probably late Carnian in age (Azevedo and Schultz, 1987; Zeffass et al., 2003; Langer et al., 2007). Regarding to biostratigraphy, the fossils here mentioned are included in the *Hyperodapedon* Assemblage Zone (Langer et al., 2007). UFRGS-PV-0232-T is composed by cranial and post-cranial elements. The skull is nearly complete and well preserved, but it shows some degree of dorsoventral compression. Only the left epipterygoid is missing, whereas the right one was found disarticulated (Azevedo, 1982; Azevedo and Schultz, 1987; Montefeltro et al., 2010).

The skull was CT scanned at Hospital das Clínicas de Porto Alegre, Porto Alegre, Brazil, using a Phillips Brilliance 16-Slice CT Scanner. It was scanned with a slice thickness of 1 mm, slice increment (interslice spacing) of 1 mm, field of view of 341 mm, 140 kV, and 275 mA. The scanning yielded 249 slices in coronal slice plan with dimensions of 512x512 pixels, each pixel with a dimension of 0,666 mm. Data were output from the scanner in DICOM format and then

imported into the free software InVesalius 3.0 - Beta 2 (Centro de Tecnologia da Informação Renato Archer -CTI, Brazil) to enable visualization and analyze of the images.

EVIDENCES CONCERNING THE PRESENCE OR ABSENCE OF VNOS IN RHYNCHOSAURS

To investigate the presence or absence of VNOs in rhynchosaurs we analyzed the following features: (1) morphology of the dorsal surface of the vomers; (2) the possible areas for pheromone collection; (3) the course of the nasolacrimal ducts; and (4) the living outgroups, following the basis of the Extant Phylogenetic Bracket (Witmer, 1995).

Vomer Morphology

According to Hillenius (2000), the best osteological correlates of the VNOS in fossils are the vomers, once that the pattern observed in living taxa—the probable plesiomorphic condition for tetrapods—is the location of VNOs in the dorsal surface of the vomers, lateral to their dorsal expansions. In UFRGS-PV-0232-T, one sulcus was found in the dorsal surface of the anteriormost portion of each vomer, near to the suture with the maxilla (Fig. 2). These sulci are around 25 mm in length, from the contact between vomers and pre-maxillae until approximately the anterior outline of the choanae. Thus, inferring that these grooves housed the VNOs, if present, is compatible with the inference about the primitive condition for amniotes and with the condition observed in embryos of living archosaurs (Parsons, 1970; Hillenius, 2000).

Benton (1983:621), based on a mould of the nasal cavity of *Hyperodapedon gordonii*, hypothesized the location of VNOs in this taxon near to two notches, close to the contacts between vomers and premaxillae, identified by him as “fenestra vomeronasalis externa”, being possibly homologous to the ones found in lizards like the genus *Ctenosaura* (Oelrich, 1956).

However, the fenestrae vomeronasalis of extant lepidosaurs correspond to the openings in the palate through which the VNO ducts communicate with the oral cavity (Oelrich, 1956; Parsons, 1970; Kubie and Halpern, 1979; Halpern, 1987; Miller and Gutzke, 1999) and are considered as unique for Squamata, not being observed in *Sphenodon*, turtles, and crocodylians (Parsons, 1970; Hillenius, 2000). They emerge as the result of a constriction in the anterior portion of each choana during the late ontogeny of the palate and nasal cavity of lizards (Parsons, 1970). Thus, the notches found in rhynchosaurus by Benton (1983) must not be homologous to the fenestrae seen in squamates and not necessarily functional and structurally related to the VNOs.

In fact, it is not clear for us what is exactly the fenestra vomeronasalis externa of rhynchosaurus in the manner figured by Benton (1983:figs. 5b, 6b and 9d), but the morphology of the palate of UFRGS-PV-0232-T—as well as of all the other hyperodapedontine skulls available for this analysis—in dorsal view and the relationships with nasal cavity walls are identical to those of *H. gordonii* (Benton, 1983) and *H. huxleyi* (Chatterjee, 1974), which indicates that this feature must have been also present in the Brazilian species. Anyway, the location for VNOs proposed by Benton (1983) based on the location of the fenestra vomeronasalis externa seems to be near, if not coincident, with the one proposed here based on the sulci in the vomers of *Teyumbaita sulcognathus*.

Possible Areas for Collection of Pheromones

Vomodor molecules reach the VNO inside the nasal cavity via external nares, choanae, and incisive foramina in living animals (Hillenius, 2000). In the case of squamates, vomodors reach the VNOs through fenestrae vomeronasalis in the palate (see above). The palate of hyperodapedontine rhynchosaurus did not have incisive foramina; therefore nostrils and choanae are the remaining candidates for areas for collection of pheromones. The external nares of rhynchosaurus were located in the anterior-most portion of the snout, medial to the pre-maxillae,

resulting in a single external opening (Fig. 1 and 2; Romer, 1956; Benton, 1983; Langer and Schultz, 2000). Septomaxillae are absent. If the VNOs were present, the location of external nares certainly would facilitate the investigation of the substrate in search for vomodors.

However, the selective pressure responsible for their dislocation from a more posterior position, as in other diapsids, to their actual location, could have been more related to olfaction than vomerolfaction (Witmer, 2001).

In the other hand, the abbreviated snout of rhynchosaurs would have made also possible the use of choanae to transfer vomodors to the VNOs. In this case, the tongue probably would have to collect and transfer them to the choanae. Due to the size of some preserved elements of the hyoid apparatus, it was inferred that the tongue of rhynchosaurs was relatively large and powerful (Benton, 1983; Benton, 1990; Benton et al., 1993), being used to manipulate the food gathered by the pre-maxillae and conducting them throughout the length of the mouth (Benton, 1983).

However, it is worth to emphasize that the fact of the location of both the nostrils and the choanae be appropriate to receive vomodors—that could be transferred by the tongue—is far from being conclusive about the presence of vomerolfaction. These features are only compatible with the VNOs if they were present.

Nasolacrimal Ducts

In rhynchosaurs, each lacrimal has two lacrimal foramina (Chatterjee, 1974; Benton, 1983; Benton, 1990; Dilkes, 1998). Benton (1983) reconstructed the nasolacrimal ducts as being formed by the confluence of the ducts coming from these foramina and passing to the anterior region of the nasal cavity. Benton (1983) suggested two hypothetical routes for this passage of the nasolacrimal ducts because there are no impressions of these channels in the inner wall of the nasal cavity.

Two lacrimal foramina are readily recognized in *Teyumbaita sulcognathus* (Azevedo, 1982; Montefeltro et al., 2010), but the course of the ducts inside the bones could not be determined in CT images due to the impossibility of distinguishing permineralizing carbonatic infilling from the bone. Nevertheless it is possible to follow the course of the left upper nasolacrimal duct through the left lacrimal until it opens internally to the skull. Although the left lower nasolacrimal duct may extend towards the left upper nasolacrimal duct and then join it, the fact that the course of the upper nasolacrimal duct inside the lacrimal is straight, without great deviations, and that the lacrimal bone is relatively thin suggest that the ducts from the lower and upper foramina fuse out of the lacrimal. It was not possible to recognize any sort of groove that could be attributed to the nasolacrimal ducts in the nasal cavity of UFRGS-PV-0232-T, which corroborates the observation made by Benton (1983) to *H. gordonii* and indicates that there are no impressions of these channels in the nasal cavity at least in hyperodapedontine rhynchosaurs.

The lack of impression of the channels may be explained by two different ways. The first one is that the ducts extend throughout the nasal cavity, but they simply did not leave any impression in the inner surface of maxillae or they were located inside them. This hypothesis was adopted by Benton (1983) mainly because of its assumption of the presence of VNOs in rhynchosaurs. The second one is that the nasolacrimal ducts did not leave impressions just because they were absent in the nasal cavity. Although there is the possibility of the ducts extending inside the maxillae and their course being undistinguishable in CT images in a manner similar to what is suggested for them inside the lacrimals, we favor the second explanation because (1) many fossil *taxa* that possessed nasolacrimal ducts have also their impressions in the inner surface of the skull independently of their courses (Hillenius, 2000; Evans, 2006), (2) turtles have VNOs but lack nasolacrimal ducts (Parsons, 1970), and (3) the absence of nasolacrimal ducts or the non-anteriorization of their courses is concordant with the absence of septomaxillae in rhynchosaurs, as it is observed in most tetrapods (Hillenius, 2000).

Extant Outgroups

The methods of the Extant Phylogenetic Bracket (EPB; Witmer, 1995) rely on the comparison of extinct taxa with the two living outgroups attempting to determine the presence of anatomical and physiological features in the formers based on osteological correlates identified in the last ones.

Osteological correlates are features recognized in bones causally related to a soft-tissue structure.

In the case of VNOs, they are associated with the vomers, but it is not possible to establish a strict causal relation between them, because their association varies among animals and the lack of

VNOs does not imply the lack of vomers (or vice-versa). Thus, the comparison between

rhynchosaurs and living outgroups can only rely in a simple parsimony analysis.

In this case, the two living outgroups closer to rhynchosaurs are living archosaurs, i.e.,

crocodilians and birds, and living lepidosaurs, including *Sphenodon*, snakes and lizards (Benton,

1983; Gauthier et al., 1988). Extant archosaurs do not possess VNOs, whereas most of

lepidosaurs possess them, which is probably a diapsid plesiomorphy (Parsons, 1970; Hillenius,

2000; Senter, 2002). Thus, the condition in the last common ancestor of rhynchosaurs and living

archosaurs, located in the node called “outgroup node” by Witmer (1995:23), is dubious or

equivocal (Fig. 3). In other words, without the previous knowledge if rhynchosaurs had or not

vomerolfaction or at least the recognition of osteological features attributable to VNOs, inferring

the presence or the absence of these organs in the last common ancestor of rhynchosaurs and

living archosaurs is equally parsimonious. So the EPB did not clarify this issue.

Nevertheless, the phylogenetic relationships of turtles deserve a brief mention here. They have

been classically classified as anapsids due to the absence of fenestrae in their skull similar to the

temporal fenestrae found in mammals and other reptiles (Romer, 1956). Different hypotheses

concerning the relationships between turtles and other amniotes, i.e., diapsids and synapsids, have

been proposed (Rieppel, 2000), but in general they are considered members of Sauropsida, being

closer to diapsids (Gauthier et al., 1988). Furthermore, some modern works suggest their placement within Diapsida (Rieppel, 2000) and molecular data supports a turtle + archosaur clade (Crawford et al., 2012). If turtles, which have VNOs, are really modified diapsids closer to crocodylians and birds, there are two possible scenarios when applying the EPB for rhynchosaurs. In the first one, the most probable, turtles diverge in a phylogenetic level prior to rhynchosaurs. Once that the formers possess VNOs, they would have the same role of lepidosaurs in the EPB and thus the presence or absence of these organs in rhynchosaurs would remain equivocal. In the second one, turtles diverge in a level after rhynchosaurs. In this case, the hypothesis most parsimonious is that rhynchosaurs possessed VNOs.

DISCUSSION

In a similar way that we are doing here, Senter (2002) discussed the presence/absence of VNOs in phytosaurs based on anatomical parameters and phylogenetic relationships. Among the anatomical features analyzed were the course of the nasolacrimal ducts, the presence or absence of septomaxillae, and possible areas for collection of pheromones. The course of the nasolacrimal ducts tends to extend forward from the lacrimals to the vicinities of the VNOs when these are present. This fact is explained by the functional relationship between VNOs and Harderian glands, whose secretions are conducted to the formers via the mentioned ducts (Hillenius and Rehorek, 1997; Hillenius, 2000; see also Hillenius and Rehorek, 2005). In the case of phytosaurs, Senter (2002) considered the course of the nasolacrimal ducts towards the anterior palate as lacking fossil evidence.

Without knowing the course of nasolacrimal ducts, Senter (2002) considered septomaxillae the osteological correlates of these ducts, which was previously observed by Hillenius (2000). Because these bones tend to be missing in the skull of archosauriforms since the phylogenetic

levels above *Proterosuchus*, the author proposed that the loss of vomerolfaction occurred in some level after that genus. With regards to phytosaurs, these animals have bony elements identified as septomaxillae (Chatterjee, 1978), but considered by Senter (2002) as neomorphs instead of homologous to the septomaxillae of other tetrapods. The lack of a true septomaxillae was considered as an evidence of the absence of VNOs in phytosaurs.

Possible areas for collection of pheromones in phytosaurs were also analyzed and the candidates for this role were only the external nares and the choanae, because they lacked incisive foramina. Due to their long rostrum, Senter (2002) judged as few plausible that phytosaurs could have possessed a tongue long, flexible, and maneuverable enough to transfer vomodors to the choanae. The external nares were also dismissed as possible areas for collection of pheromone because of their unusual position near the eyes, in the top of the skull.

The last evidence of Senter (2002) for inferring the lack of vomerolfaction in phytosaurs came from the living outgroups, based on the Extant Phylogenetic Bracket (Witmer, 1995), although the author did not mention this method explicitly. Crocodylians and birds bracket phytosaurs in cladograms, so it is possible to infer that the lack of VNOs is apomorphic for archosaurs, including the phytosaurs and other fossil *taxa*, which is in agreement with the other features analyzed by the author that support the same inference.

We agree with Senter (2002) about the probable lack of vomerolfaction in phytosaurs due to their impossibility of collecting pheromones from the surroundings via the usual means of collection observed in living *taxa*, in this case, the external nares and choanae. We also support that the absence of VNOs must be at least an apomorphy of crown-group Archosauria, because they are absent in living and extinct *taxa*.

However, it is worth emphasizing that septomaxillae are only indirectly related to VNOs due to their association with nasolacrimal ducts when these extend forward. In the absence of nasolacrimal ducts or when they do not pass forward to the vicinity of VNOs, septomaxillae are

missing elements in the nasal cavity wall of tetrapods, while the inverse relationship is not always true (Hillenius, 2000). With respect to VNOs, they can be present even when the nasolacrimal ducts and septomaxillae are absent, which is the case of turtles (Parsons, 1970), or when the nasolacrimal ducts do not pass near these organs, as in many mammals (Hillenius, 2000). Thus, it is necessary to analyze with more scrutiny those taxa within the phylogenetic interval prior to Archosauria in which septomaxillae are missing in order to determine more precisely, if possible, the moment of the reduction and loss of vomerolfaction.

Inferring the presence or the absence of VNOs in rhynchosaurs has been shown difficult so far. The lack of a good osteological correlate and the equivocal assessment of the outgroup node make the EPB non-elucidative for this issue (Fig. 3). When the EPB does not contribute satisfactorily, Witmer (1995) suggests that inferences about soft-tissue structures must rely on anatomical evidences that strongly points to their presence, independently of the condition observed in the living outgroups. This sort of argument was referred as “an argument of compelling morphological evidence” by Witmer (1995:28).

This argument is also not easy to be made in the present case, because the condition of VNOs observed in extant taxa is so diverse that makes difficult to find a pattern to extrapolate or compare with fossil groups (Hillenius, 2000; Baxi et al., 2006). Furthermore, the anatomical structures and morphological features analyzed in rhynchosaurs are at most concordant with the presence of VNOs or did not exclude the chance of their presence. Their possible location in the nasal cavity (Fig. 2) is also similar to the propositions regarding the primitive condition for amniotes and extinct therapsids (Hillenius, 2000); therefore, this hypothesis contains an elevated degree of speculation with the sense employed by Witmer (1995) and finds support only in the early ontogenetic stages of crocodylians and birds. If present, the location of VNOs would make possible the receipt of vomodors via nostrils and/or choanae.

Therefore, the best conclusion is that the issue concerning the presence or absence of VNOs in rhynchosaurs remains inconclusive. However, it is still possible to gather some insights about the functionality of the VNOs (if they were present) in this taxon, and much of this discussion relies on the nasolacrimal ducts. Because these ducts are indirectly related to VNOs through the Harderian glands, it is most fair to functionally compare rhynchosaurs with living taxa that possess VNOs but lack nasolacrimal ducts in the vicinities of these organs, which are turtles and mammals.

Historically, the opinions about the VNOs of turtles have been extremely different. They have already been considered absent in these animals, because they are not encased by a cartilaginous capsule in the nasal cavity. Posteriorly, became evident the presence of a typical vomeronasal epithelium in the ventral half of their nasal cavities; therefore, the VNOs are now considered present (Parsons, 1970; but see Butler & Hodos, 2005 and Kardong, 2009). Then the matter of discussion changed to their functionality. The absence of nasolacrimal ducts must imply a series of consequences for the functions carried out by the VNOs, as the Harderian secretions are not transferred to them. Many authors consider the VNOs of turtles as totally or almost totally non-functional (Northcutt, 1970), but some experiments have shown that they do sense some chemicals dissolved in the water (Manton et al., 1972; Shoji and Kurihara, 1991; Taniguchi et al., 1996), so they may be functional at least underwater (Schwenk, 2008). It is possible that in living fishes some cells diffused among the olfactory epithelium are sensitive to vomodors, which is also speculated as the primitive condition, prior to the emergence of VNOs as a distinct sensory system (Liman, 1996). This configuration roughly resembles the one found in turtles because both fishes and turtles do not possess vomeronasal epithelium isolated by a physical barrier from the olfactory epithelium and this may be related to their sensory roles underwater.

In mammals, the disassociation between Harderian glands and VNOs is possibly related to the changes in function of the formers (Hillenius, 2000). Similar to what happened to turtles, these

changes must have caused some effects on the functionality of VNOs of mammals. Mammals usually gather vomodors via tongue in the urine and special gland secretions, including those associated with reproductive organs, and then transfer them to the VNOs through incisive foramina, which communicate with the VNO ducts (Døving and Trotier, 1998; Hillenius, 2000). Other anatomical feature that contributes to the gathering of vomodors is the rhinarium, which is the moist surface that covers the nostrils and communicates with the oral cavity via a groove called philtrum (Hillenius, 2000). The urine of mammals contains a class of proteins called major urinary proteins (MUPs), which play different roles in vomerolfaction of placental mammals (Døving and Trotier, 1998; Brennan and Keverne, 2004; Logan et al., 2008). Furthermore, many mammals display a facial grimacing known as flehmen behavior and/or investigate the substrate rubbing the snout, both of which are considered as mechanisms to enhance the collection of vomodors by the VNOs (Estes, 1972; Døving and Trotier, 1998; Hillenius, 2000).

Meredith (1998) mentions the preference of VNOs of turtles and mammals to sense vomodors that are more water soluble, which may be somehow related respectively to the lack of nasolacrimal ducts and the functional disassociation between these ducts and the organs. Thus, the points discussed above about turtles and mammals represent particular strategies adopted by each group to compensate the necessity of liquids to dissolve and disperse pheromones and other vomodors.

Rhynchosaurs, however, were fully terrestrial animals and hence it was very improbable that their VNOs would have had any role underwater. They would not also have had any sort of behavior similar to flehmen, because it requires an extremely developed facial musculature only found nowadays in mammals (Kardong, 2009). The only facial musculature that seems to have been relatively well-developed in rhynchosaurs was that of cheek regions (Benton, 1983; Langer and Schultz, 2000). Even if the nostrils could have had a cover similar to the rhinarium of mammals, they did not have had any communication with the oral cavity in a way comparable to the

mammalian philtrum. This reasoning is supported by the fact that the premaxillae of rhynchosaurs would have constituted a sort of physical barrier to any secretion from the nostrils passing to the mouth (Fig. 1). As terrestrial animals that inhabited arid to semi-arid environments and whose reproduction occurred via cleidoic eggs, rhynchosaurs would probably have excreted a solid to semi-solid urine rich in uric acid, but with considerably reduced contents of water when compared with ammonotelic and ureotelic animals (Schmidt-Nielsen, 2002; Kardong, 2009). Although there are some exceptions to this assumption, they are explained by a series of anatomical features and ecological adaptations that could unlikely be extended to rhynchosaurs. Ostriches, for example, are uricotelic animals with extremely liquid urine, which is possible due to their coprodeum that works as a urinary bladder separating the urine from the feces (Skaudhage et al., 1984; Lavery and Skaudhage, 2008). This is not observed in other birds, including other ratites (Skaudhage et al., 1984). Aquatic birds also have urine with high contents of both uric acid and water, but this is explained by the abundance of available water to them. Finally, the urine of rhynchosaurs did not have had MUPs because these proteins are found only in placental mammals (Logan et al., 2008).

Although the issue concerning the presence of VNOs in rhynchosaurs remains open, inferring their functionality if they were present is more viable. Rhynchosaurs probably did not have nasolacrimal ducts inside their nasal cavities close to the probable location of VNOs. This fact should have been compensated by behavioral and physiological adaptations to keep the organs functional, as it happens in turtles and mammals, but they also seem to have been absent in rhynchosaurs. Therefore two scenarios are possible: (1) rhynchosaurs did not have VNOs, or (2) they have them in a vestigial, non-functional or few-functional form.

Both scenarios point to the reduction of vomerolfaction in rhynchosaurs. If the absence of septomaxillae is really correlated to the lack of nasolacrimal ducts in the nasal cavity of other rhynchosaurs, it is possible to hypothesize that the functional disassociation between Harderian

glands and VNOs was already present in the most basal taxa of the group, like *Mesosuchus* and *Howesia*, and was retained in the later and more derived genus (Dilkes, 1998). Therefore, in archosaur lineage, there were at least two independent reductions of vomerolfaction, one in Rhynchosauria and other in Archosauria, but the last one probably initiated in the phylogenetic interval proposed by Senter (2002).

The reduction of the relative importance of vomerolfaction for the sensory paleobiology of rhynchosaurs certainly had behavioral implications. As the VNOs play important roles during prey catching and feeding basically in Squamata (Kubie and Halpern, 1979; Halpern, 1987) the implications for rhynchosaurs might have been mainly for intraspecific interactions. As mentioned by Senter (2002), behaviors employed in territory defense and reproduction receives more contribution from vision, audition and tact when tetrapods do not possess a developed sense of vomerolfaction. In the case of phytosaurs, the most obvious modern analogues are the crocodylians (Chatterjee, 1978; Hunt, 1989), which were the basis for ethological inferences about the formers (Senter, 2002).

In the case of rhynchosaurs, the living animal more superficially comparable to them is maybe the *Sphenodon*, which was already regarded as the sister-group of the formers (Huxley, 1869; Romer, 1956; Benton, 1983). However, *Sphenodon* have functional VNOs, what means that their behavior during intraspecific interactions cannot be extrapolated to rhynchosaurs. Little is known about the inner ear of rhynchosaurs, especially concerning the cochlea; Benton (1983) reported a mould of the inner ear of *Hyperodapedon gordonii* figuring basically the semicircular canals, while *T. sulcognathus* (UFRGS-PV-0232-T) have only the anterior and posterior semicircular canals preserved (unpubl. data). Thus, it is difficult to make any assertion about the role played by audition in the social and reproductive behavior of rhynchosaurs. In the other hand, olfaction seems to have been well-developed in hyperodapedontine rhynchosaurs due to the large olfactory bulbs and nasal cavities of these animals (Benton, 1983). If olfaction could have inherited some

of the roles played by the VNOs is a hypothesis difficult to test, but this possibility was discarded by Senter (2002), a reasoning that may be a mistake after Schwenk (2008).

Rhynchosaurus also had great orbits and well developed sclerotic rings. These features are regarded as real evidences of large eyeballs in these animals and a good sense of vision (Benton, 1983). If it was true as it seems to have been, vision was the sense that probably best compensated the reduction of the importance of vomerolfaction for the social and reproductive behavior. In many modern mammals without the VNOs or with them reduced, including catarrhine primates like us, vision is extremely developed and important for behavioral biology (Senter, 2002; Liman and Innan, 2003), which is consistent with the inferences made for rhynchosaurus. Therefore, during the territory defense and courtship, for example, rhynchosaurus might have had employed typical movements along with some kind of sound or vocalization. As both living outgroups of rhynchosaurus have color vision (Kardong, 2009; Vitt and Caldwell, 2009), these extinct reptiles must also have possessed it, which would have made also plausible the employment of colors in sexual display or in other aspects of their social behavior.

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FIGURE CAPTIONS

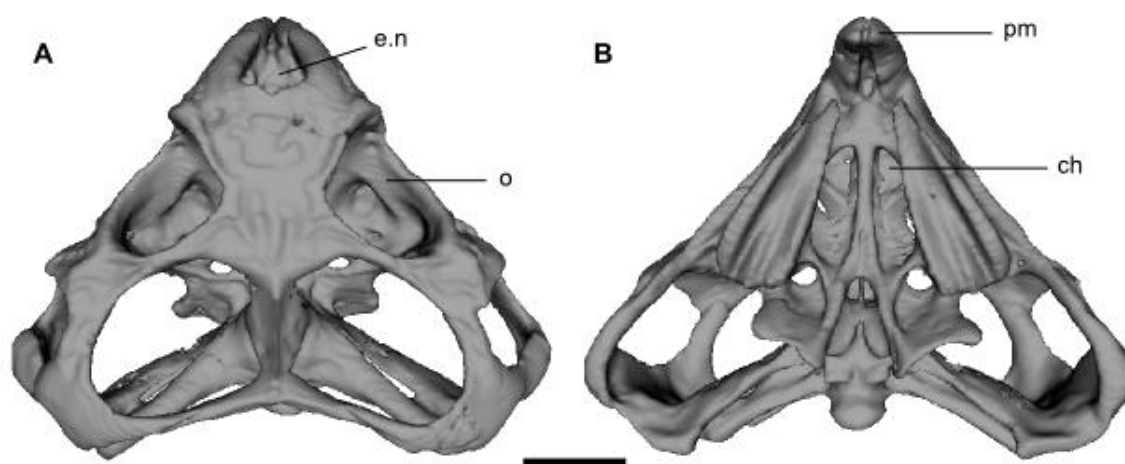


FIGURE 1. Digital rendering of the holotypic skull of *Teyumbaita sulcognathus* (UFRGS-PV-0232-T). **A**, dorsal view. **B**, palatal view. **Abbreviations:** **ch**, choana; **e.n**, external nares; **o**, orbit; **pm**, premaxilla. Scale bar equals 5 cm. [planned for page width]

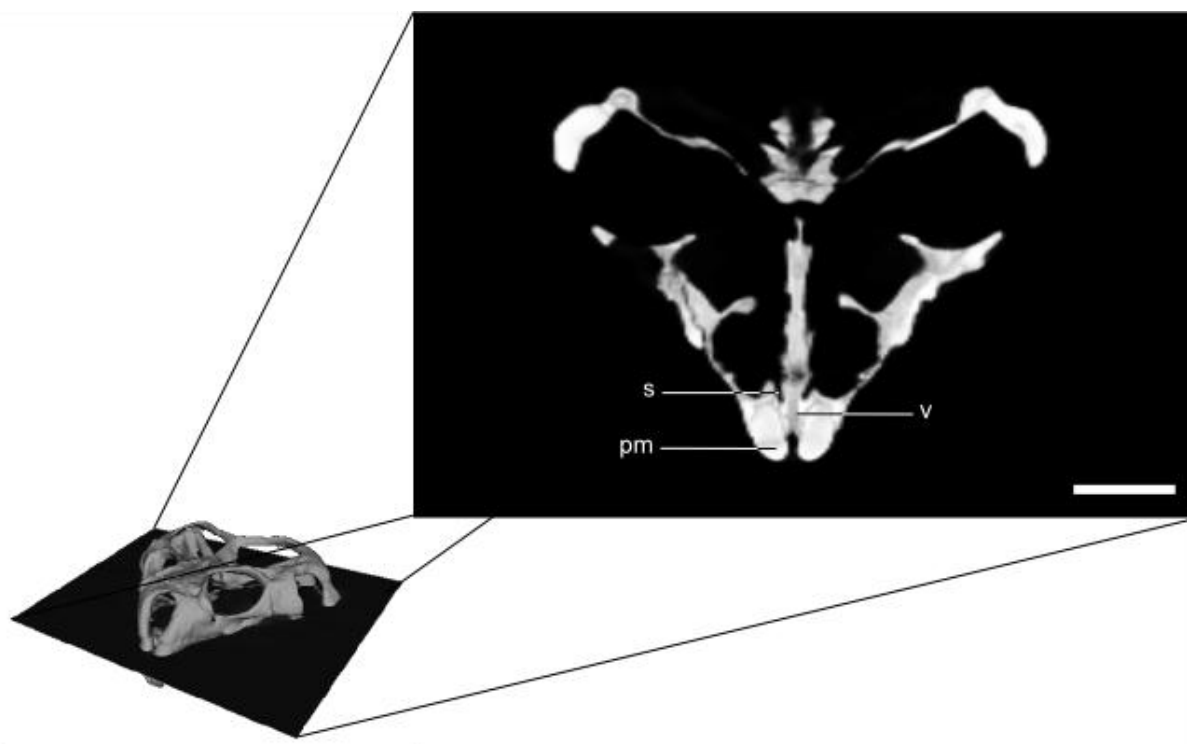


FIGURE 2. Axial slice of the skull of *Teyumbaita sulcognathus* (UFRGS-PV-0232-T). In the left lower corner, the digital reconstruction of the specimen showing the position of the slice.

Abbreviations: pm, premaxilla; s, sulcus in the dorsal surface of the vomer; v, vomer. Scale bar equals 5 cm. [planned for page width]

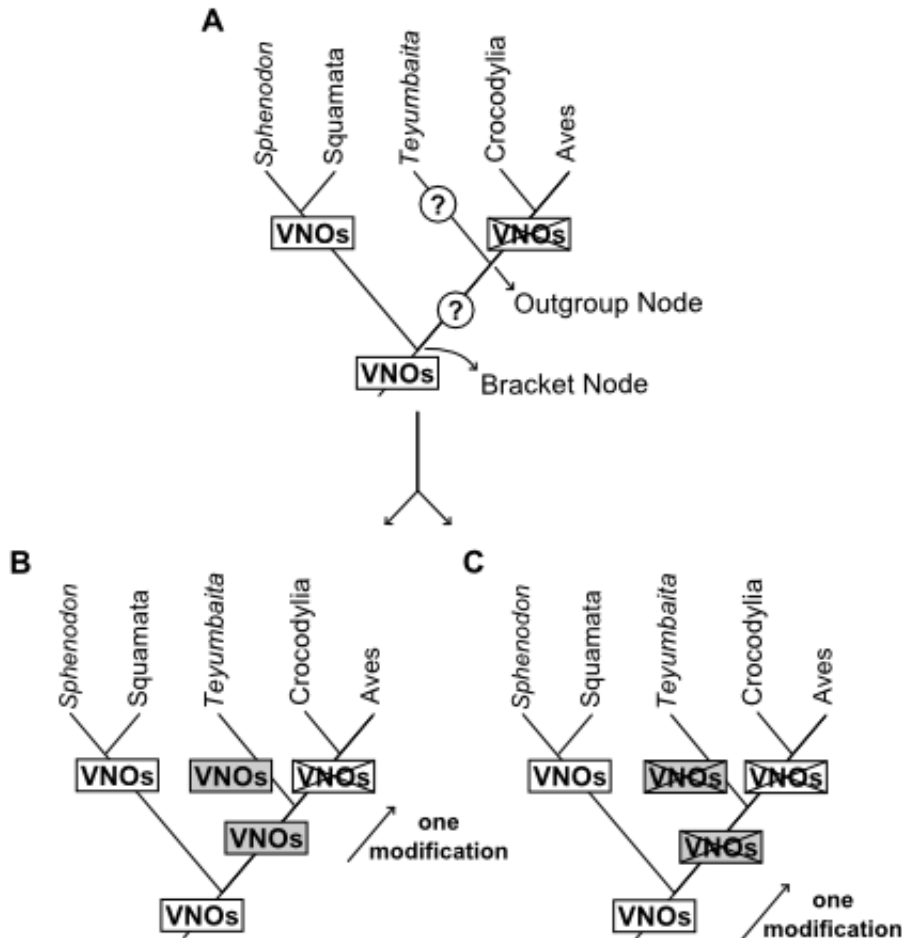


FIGURE 3. Cladogram with the extant brackets of rhynchosaur and rhynchosaur, here represented by *Teyumbaita sulcognathus*, and a parsimony analysis of the presence/absence of VNOs in the outgroup node. **A**, Cladogram with the distribution of the VNOs within Diapsida, emphasizing the unknown condition of rhynchosaur and the outgroup node. **B**, First hypothesis, in which having VNOs is the condition proposed for the outgroup node and, then, inherited only by rhynchosaur. **C**, Second hypothesis, in which the condition for the outgroup node is the lack

of VNOs. Both hypotheses require only one evolutionary modification: the loss of VNOs solely in living archosaurs or, even before, in the outgroup node. The white squares and the white squares with a cross represent, respectively, the presence and absence of VNOs. The hypothesized presence or absence of these organs is indicated by grey squares and grey squares with a cross, respectively. [planned for 2/3 of a whole page width]

2.2 ARTIGO SUBMETIDO À REVISTA *PALAEONTOLOGIA ELECTRONICA*

Paleoneurology of *Teyumbaita sulcognathus* (Diapsida: Archosauromorpha) and the sense of smell in rhynchosaurs

Keywords: paleoneurology; rhynchosaurs; cranial endocast; computed tomography; behavior; olfaction

Marcos A. F. Sales and Cesar L. Schultz

Marcos A. F. Sales. Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 9500, Agronomia, CEP 91501-970, Porto Alegre, Rio Grande do Sul, Brazil. marcos.paleo@yahoo.com.br

Cesar L. Schultz. Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 9500, Agronomia, CEP 91501-970, Porto Alegre, Rio Grande do Sul, Brazil. cesar.schultz@ufrgs.br

ABSTRACT

Rhynchosaurs were a group of archosauromorphs that dominated the guild of herbivores during the early Late Triassic. Despite the large number of specimens available, some paleobiological studies are rare in the literature, especially concerning the South American species. Here we analyze the paleoneurology of *Teyumbaita sulcognathus*, a Brazilian hyperodapedontine rhynchosaur, along with its nasal cavity, based on tomographic images of the specimen UFRGS-PV-0232-T. Although the endocast just reveals the morphology of the posterior half of the encephalon due to the incompletely ossified braincase, it is possible to infer the presence of great olfactory bulbs because of their impressions left on the ventral surface of the frontals. Although the snout is relatively short, the areas of the nasal cavity probably devoted to olfaction were also large and, along with the size of the olfactory bulbs, it is possible to infer that olfaction was important for the behavior and ecology of *T. sulcognathus*, as previously proposed for *Hyperodapedon*.

PLAIN LANGUAGE SUMMARY

Computed tomographic images of the skull of *Teyumbaita sulcognathus*, a reptile from the early Late Triassic of Southern Brazil, was obtained in order to gather more information about the endocranial anatomy and the ecology of this taxon. Data revealed that a rocky mould was preserved within the braincase cavity of this reptile, but it corresponded only to the posterior half of the brain. In the other hand, the olfactory portion of the brain left its impressions on the ventral surface of the skull roof and, based on their size along with the size of the nasal cavity, it was possible to infer that *T. sulcognathus* had a good sense of smell.

INTRODUCTION

Paleoneurology is the branch of paleobiology devoted to the study of brains of extinct vertebrates (Butler and Hodos, 2005), although it usually includes other structures housed in the braincase.

Therefore, it represents the interface between two broader areas, paleontology and neurology.

Among the variables considered by it is the geological time and, therefore, paleoneurology can be also defined as the study of brain evolution (Buchholtz and Seyfarth, 2001; Witmer et al., 2008; Witmer and Ridgely, 2008).

The study of brains of extinct taxa is based in most cases on analyzes of cranial endocasts, which will be referred throughout this text solely as endocasts. They are naturally formed by the infilling of the cavity of braincase by sediments and their consolidation during fossil diagenesis.

As these casts replicate the internal morphology of the braincases, they also provide data concerning the morphology of encephalon that was housed within the last ones, but the amount of details that can be recovered from these casts varies among taxa. This is explained by the fact that the brains of many animals do not fill entirely the cranial cavity and, therefore, the meninges and venous sinuses located between the brain and the braincase walls are thicker and prevent that the brain surface leaves detailed impressions on the internal surface of the braincase (Hopson, 1979; Buchholtz and Seyfarth, 2001; Rogers, 1999). In this context, mammals and birds have brains whose morphologies and some other features of their surfaces can be recovered with a greater precision from endocasts (Radinsky, 1969; 1971; Buchholtz and Seyfarth, 2001; Dominguez-Alonso et al., 2004; Macrini et al., 2007a, 2007b; Dong, 2008). Among fossil diapsids, pterosaurs, oviraptorosaurs, and probably other small theropods are clearly examples of exceptions among non-avian archosaurs because they also have brains nearly filling the cranial cavity completely (Dominguez-Alonso et al., 2004; Osmólska, 2004; Kundrát, 2007).

Ancient brains can also be accessed indirectly by impressions left on the ventral surfaces of skull roofs and artificial endocasts (Hopson, 1979; Buchholtz and Seyfarth, 2001; Osmólska, 2004;

Zelenitsky et al., 2009). Although these techniques have been already applied since many decades ago, the employment of computed tomography gave a new impulse for paleoneurology allowing it a non-invasive analyzes of rare specimens (Buchholtz and Seyfarth, 2001; Witmer et al., 2008; Witmer and Ridgely, 2008). From CT images it is possible to digitally reconstruct with specialized softwares the endocast of many taxa, and dinosaurs are classic examples whose paleoneurology has been revised and greatly expanded last years (Rogers, 1999; Brochu, 2000; Larsson et al., 2000; Fransoza and Rowe, 2005; Knoll and Schwarz-Wings, 2009; Rogers, 2005; Sanders and Smith, 2005; Kunderát, 2007; Sampson and Witmer, 2007; Sereno et al., 2007; Witmer et al., 2008; Witmer and Ridgely, 2008; Witmer and Ridgely, 2009).

Among non-avian archosaurs, along with non-avian dinosaurs, crocodyliforms, aetosaurs and pterosaurs are examples of groups with endocasts figured in the literature (Hopson 1979; Witmer et al., 2003; Kley et al., 2010). Benton (1983) showed a natural internal mould of the braincase of a basal archosauromorph, more precisely, the rhynchosaur *Hyperodapedon gordonii*, also reporting the occurrence of impressions of olfactory bulbs on the ventral surface of the frontals of this species. Considering the size of these impressions and the nasal cavity of *Hyperodapedon*, this author proposes that rhynchosaur had a keen sense of olfaction.

While the interspecific variation and evolution of neurological features is somehow well-known in taxa like dinosaurs and extinct carnivores (Radinsky, 1969, 1971; Dong, 2008; Sereno et al., 2007; Witmer and Ridgely, 2009), the same cannot be said about rhynchosaur. Thus, testing any generalization for this group requires the study of other species. Thus, we present here some paleoneurological data gathered by computed tomography (CT) from *Teyumbaita sulcognathus*, a rhynchosaur from the Late Triassic of Brazil. We also discuss briefly its nasal cavity to provide more clues for inferences concerning the olfaction of this taxon.

MATERIAL AND METHODS

The analyzed material is the holotypic skull of *Teyumbaita sulcognathus* (UFRGS-PV-0232-T), housed at Universidade Federal do Rio Grande do Sul. It was found at Linha Facão locality (29°40'12"S; 52°43'30"W), near the boundary between Candelária and Vera Cruz towns, in Rio Grande do Sul State, Brazil, in the stratigraphic levels known as the lower parts of Caturrita Formation, which encase fossils of the *Hyperodapedon* Assemblage Zone (Azevedo, 1982; Schultz, 1986, Azevedo and Schultz, 1987; Langer et al., 2007; Montefeltro et al., 2010). These levels are now considered to be the upper portions of a highstand system tract named Santa Maria Sequence 2 and are probably late Carnian in age (Azevedo and Schultz, 1987; Zerfass et al, 2003; Langer et al., 2007). *T. sulcognathus* was first described as belonging to the genus *Scaphonyx* (Azevedo, 1982; Schultz, 1986, Azevedo and Schultz, 1987), but its reallocation in the present genus was made in 2010 (Montefeltro et al., 2010). It is a derived form of rhynchosaur and is included in the subfamily Hyperodapedontinae, being probably the sister-taxon of *Hyperodapedon* (Montefeltro et al., 2010).

The skull is fairly complete, being well preserved and articulated, ideal for CT scanning. Actually, the only disarticulated elements are both epipterygoids, but only the right one is missing. The scanning procedure took place at Hospital das Clínicas de Porto Alegre, Porto Alegre, Brazil, using a Phillips Brilliance 16-Slice CT Scanner and yielded 249 slices in coronal slice plan with dimensions of 512x512 pixels, each pixel measuring 0,666 mm. The other CT scan parameters are: slice thickness of 1 mm, slice increment (interslice spacing) of 1 mm, field of view of 341 mm, 140 kV, and 275 mA. Data were output from the scanner in DICOM format, and then imported into InVesalius 3.0 - Beta 2 (Centro de Tecnologia da Informação Renato Archer - CTI, Brazil). This software was used to visualize the impressions of olfactory bulb and to digitally extract a natural endocast preserved inside the braincase of *Teyumbaita sulcognathus*.

The discussion about nasal cavity is based on the morphology of the osseous nasal cavity and employs the anglicized version of the terms adopted by Parsons (1970).

PALEONEUROLOGY OF *TEYUMBAITA SULCOGNATHUS*

The braincase can be totally or partially ossified. In the first case, the endocast reflects the whole shape of the encephalon, and, in the second case, the preserved endocast corresponds to a varying degree of the entirety of the encephalon depending on the taxa. Rhynchosaurs fall within the second scenario and, hence, their endocasts are the internal moulds of the cavity delimited by the parietals, prootics, opisthotics, supraoccipital, exoccipitals, basioccipital and basisphenoid (Benton, 1983; Azevedo, 1982; Montefeltro et al., 2010).

An endocast was naturally formed and is partially preserved inside the braincase of *Teyumbaita* and is similar to the one of *Hyperodapedon gordonii* (Benton, 1983) in its overall shape (Figures 1.3 and 3). It corresponds to the posterior half of the endocranial cavity and so brings information concerning only about the posterior end of the encephalon, which limits the range of discussion. The contour of its anterior surface, if present, was probably destroyed during the preparation of the skull much before this study. The foramen magnum was almost empty, so its cavity was digitally filled and this procedure extended until the point where the supraoccipital stopped covering the medullar channel. This procedure prevented the endocast to contain also the cast of hypoglossal foramen.

A dorsal protrusion or peak in the point of inflexion of the dorsal surface of the endocast is easily recognized and its extension is considerable. Some endocasts of dinosaurs also show peaks or expansions in the same location and they were identified by Witmer et al. (2008) and Witmer and Ridgely (2009) as a dorsal venous sinus or dural expansions, which are soft structures located between the brain and the inner surface of the braincase walls. However, these structures are extremely less developed and pointed than in *Teyumbaita sulcognathus*; therefore, a dorsal

venous sinus can explain only partially this peak of this rhynchosaur. As this structure projects parallel to the roof of the skull and seems to be absent in the endocast of *Hyperodapedon gordonii* (Benton, 1983), it is probably the result of a taphonomic distortion, despite of the good preservation of the skull. In fact, Montefeltro et al. (2010) considered this skull to be more flat than it was when the animal was alive, so some degree of dorsoventral distortion is admissible to PV-0232-T. If we accept that a force compressed the skull in a dorsoventral plane, it is possible to assume that the vertical walls changed their orientation slightly and this movement could have enlarged the space that was later filled, forming or, at least, enlarging the dorsal protrusion in the endocast.

However, Benton (1983) identified in *Hyperodapedon gordonii* a pit in the ventral surface of the parietals and considered it to be the site of the pineal organ. Such a pit is also found in *Teyumbaita sulcognathus*, although it seems to be more posteriorly placed than in Benton's (1983) illustration (Figure 2). In *T. sulcognathus*, this pit covers the dorsal surface of the tip of the dorsal protrusion of the endocast, which may suggest that this structure is actually a cast of an anomalously enlarged pineal organ. Witmer and Ridgely (2009) found two dorsal peaks in digital endocasts of the theropod dinosaurs *Majungasaurus*, *Allosaurus* and *Struthiomimus*, of which the anteriormost one was identified as a cast of a pineal organ. Nevertheless, the location of the inferred pineal cast is much more anterior than the one suggested for rhynchosaurs.

Moreover, the dorsal protrusion found in *T. sulcognathus* is located in a position more similar to the dorsal peaks found in those theropods. Thus, we suggest that the pit under the parietals is not the site of a pineal organ and the dorsal peak in the endocast is actually a taphonomically enlarged cast of a venous sinus or a dural expansion. More specimens will certainly clarify this question.

The anterior portion of the encephalon of *Teyumbaita sulcognathus* cannot be accessed analyzing the endocast. When the frontals are the only ossified elements that surrounded the anterior half of

the encephalon, it is necessary to look for impressions of the central nervous system in the ventral surface of frontals that usually have an hourglass shape (Ali et al., 2008; Zelenitsky et al., 2009). The frontals of *T. sulcognathus* do have a groove clearly referable to the impressions of the olfactory peduncle and the olfactory bulbs (Figure 1.2). These impressions are constrained by the cristae cranii and were already observed in *Hyperodapedon gordonii* by Benton (1983). As it can be seen, the olfactory bulbs are connected to the brain by a developed olfactory peduncle or olfactory tract as in most tetrapods. In the other hand, pterosaurs, birds, and some dinosaurs have reduced olfactory tracts or seem to lack them in a recognizable fashion (Witmer et al., 2003; Dominguez-Alonso et al., 2004; Evans, 2006; Kundrát, 2007; Witmer et al., 2008). Near the midpoint of the length of frontals, the groove bifurcates and the arising branches acquires an oval shape before reaching a large and ellipsoid depression, the last one almost entirely placed under the nasals. Benton (1983) inferred that the olfactory bulbs were located in large circular pits under the frontals of *H. gordonii*, so these pits must be topological equivalent to the oval grooves found in *T. sulcognathus*. In *Tyrannosaurus*, the bifurcated portion of the groove was once interpreted as representing large olfactory bulbs (Brochu, 2000). However it is now interpreted as part of the olfactory region of the nasal cavity because the structure that divides the course of the groove is considered to be the mesethmoid, marking the anterior end of the olfactory bulbs (Ali et al., 2008; Witmer and Ridgely, 2009). A similar inference would be applicable to *Teyumbaita* due to the general topological correspondence. So, the shallow osseous structure that divides the impressions under the frontals could be the ossified portion of the nasal septum that corresponds to the avian mesethmoid. Thus, the olfactory bulbs would have occupied the space in the groove between the mesethmoid and the anterior end of the constricted portion of the hourglass, i.e., the olfactory peduncle. However, it would imply that the anterior end of the encephalon would be much more caudally positioned under the frontals in rhynchosaurs than in other diapsids. In addition, as these pits do not cross the boundaries between frontals and nasals

(Figure 3.1), we prefer following Benton (1983) and supporting that the olfactory bulbs of rhynchosaurs occupied most part of the pits under the frontals, implying that the small ossified ventral keel of the frontals may not be ossification of the nasal septum.

Finally, two of the three semicircular channels of each inner ear—the anterior and posterior ones—are recognizable within the braincase walls, but they await a full description and appreciation. However they enable us to infer the approximate location of the cerebellum (Figure 3.2).

THE NASAL CAVITY OF *TEYUMBAITA SULCOGNATHUS*

The nasal cavity can be seen as a tripartite structure in which the first and the last portion act as ducts that communicate the middle portion to the environment and the oral cavity, respectively (Figure 4). The first part is called (nasal) vestibule which is usually a duct-like chamber that opens anteriorly to the environment through the external nares and posteriorly to the middle part called nasal cavity proper. The middle portion is indeed a chamber in most cases and house outpocketings known as conchae in reptiles and birds and turbinates in mammals. The third part is the nasopharyngeal duct and connects the nasal cavity proper to the oral cavity through the choanae. Only the nasal cavity proper presents olfactory epithelium and the other regions are covered by respiratory epithelium (Parsons, 1970; Evans, 2006; Schwenk, 2008).

The description of the nasal cavity of *Teyumbaita sulcognathus* begins with the external nares. As in *Hyperodapedon gordonii* (Benton, 1983) and all rhynchosaurs, they are united in a single opening in the end of the snout, limited dorsally by the nasals and ventrolaterally by the premaxillae (Figures 3.1 and 4.2). With few exceptions among amniotes, the fleshy nostrils are located anteriorly and ventrally within the boundaries of the external nares and the same should have been true for rhynchosaurs (Witmer, 2001). Exceptions to this rule are always related to particular behavioral and physiological aspects that apparently were not present in rhynchosaurs,

but even if they were, the terminal position of the external nares would make the fleshy nostrils functionally comparable to the most common condition among amniotes.

The air entered into the nasal cavity through the fleshy nostrils and then ran along the vestibule to reach the nasal cavity proper. Although there is no nasal septum preserved, there is no reason to suppose that it was not present (Montefeltro et al., 2010) and this inference is even more plausible because the vomers support a dorsal expansion above which should have laid the septum (Figure 1.4; Benton, 1983). Because of the cartilaginous nature of other structures in the nasal capsule, it is not possible to determine exactly the specific internal details, specially the boundary between the vestibule and the nasal cavity proper. However some attempts are possible. The vestibule is usually short and simple in most tetrapods, but there is a great diversity of forms among squamates. This diversity may be explained by the different lifestyles adopted by lizards and snakes and the vestibules have the most complex courses and shapes in fossorial and aquatic species (Parsons, 1970). However, the position of the external nares and the abbreviated snout make improbable the fact that rhynchosaurs could have had nasal vestibules morphologically comparable to the extreme ones of some squamates. Rhynchosaurs seem to have lacked Jacobson's organs or have had them in a vestigial form (Sales and Schultz, in preparation). The cartilaginous capsule in the anterior portion of the nasal cavity that housed them should also have been absent or at least reduced, which implies that possibly there were no major obstacles to the airstream within the vestibule. Thus it is quite possible that the vestibules in *Teyumbaita* and other rhynchosaurs resembled those of terrestrial chelonians in general structure and had a relatively straight and horizontal course from the external nares to the nasal cavity proper (Figure 4.2; Parsons, 1970).

In many reptiles a ridge in the lateral wall of the cartilaginous capsule coincides with the boundary between the vestibule and the nasal cavity proper (Parsons, 1970). Such a ridge in the osseous wall of the nasal cavity was reported by Benton (1983) for *Hyperodapedon gordonii* and

he suggested that it marked the limits between the anterior portion of the cartilaginous nasal capsule and the posterior, olfactory region. A similar ridge was found in each side of the internal surface of the nasal cavity of *Teyumbaita sulcognathus*, but they seem to be more posteroventrally inclined and more curved than in *H. gordonii*. If these ridges also coincided with the end of the vestibules, the last ones probably extended until near the anterior end of the choanae of *T. sulcognathus*, as in *H. gordonii* (Benton, 1983). These inferences would also imply that the nasal cavity proper was restricted to the posterior half of the cavity delimited by the bones of the snout (Figure 4.2).

The nasal cavity proper of *Teyumbaita sulcognathus* is as difficult to consider as the vestibule. The snout of *T. sulcognathus* is very deep and wide in cross-section, which suggests that the nasal cavity proper was also large (Figures 1.4 and 4.2). The size of the nasal cavity proper must have been explained at least partially by the possession of large conchae. With the exception of turtles, amniotes in general have at least one concha in each nasal capsule (Parsons, 1970) and there is no reason to suppose it was absent in rhynchosaurs. The top of the nasal cavity proper must have been the large ellipsoid concavity in the ventral surface of the nasals, being posterior to the ridges in the internal surface of the snout (Figure 1.2). Dorsally its posterior end would have been just anterior to the olfactory bulbs. The olfactory epithelium is usually located posterodorsally within the nasal cavity proper and also covers the concha (Parsons, 1970). Due to the deepness and width of the snout, it seems that there was much space available for the sensory epithelium.

After the nasal cavity proper, the airstream passes through the nasopharyngeal duct to reach the oral cavity and then the upper respiratory tract. The nasopharyngeal ducts are longer in animals with secondary palate or with posteriorly displaced choanae (Parsons, 1970; Schwenk, 2008).

There was no secondary palate in rhynchosaurs and the nasal cavity proper lied dorsal to the

choanae, which indicates that the ducts were extremely reduced, or absent, as in tuataras and some lizards (Figure 4.2).

Finally, the nasal capsule was probably separated from the rest of the skull by internal ridges anterior to the orbits. They coincide with the inflexion point of the dorsal ridge of the palate considered by Benton (1983) to mark the boundary between the nasal septum and the interorbital septum. Thus, we also support the same inference.

DISCUSSION

Paleobiological inferences must be based whenever possible on phylogenetic framework following the basis of Extant Phylogenetic Bracket (Witmer, 1995). However the recognition of true osteological correlates of some structures of the nasal capsule is usually not possible because much of them rely on cartilaginous supports and does not leave clear impressions on the inner surface of the snout (Parsons, 1970). Other fact that complicates the employment of the EPB is that it is difficult to reconstruct the plesiomorphic condition of Lepidosauria, one of the clades that brackets rhynchosaur in cladograms, due to the great variety of types of nasal capsules among squamates (Parsons, 1970). Further considerations about paleoneurology of *Teyumbaita sulcognathus* are restricted to the preserved traits of the brain and its associated structures. In fact, as the brain of most reptiles does not fill entirely the endocranial cavity and the same should be expected for rhynchosaur, we must be cautious about the proposed inferences.

Analyzing the functionality and physiology of any structure of the nervous system requires the knowledge about the number of neurons and their arrangements along with the number and nature of interactions among them, i.e., the synapses. This sort of information is not possible to be gathered from fossils or endocasts (Hopson, 1979; Rogers, 2005) and so the discussion about paleoneurology relies on the principle of proper mass. In few words, this principle announces that the proportion (volume or mass) of a particular neural structure is proportional to the amount of

information processed or function carried out by it (Witmer et al., 2003; Butler and Hodos, 2005; Witmer et al., 2008). The unpreserved portion of the encephalon precludes inferences about the brain hemispheres and visual lobes and comparisons between them and olfactory bulbs (Figure 3). In such a framework, Benton (1983) suggested that the vision was good in *Hyperodapedon gordonii* because of the large orbits and well-developed sclerotic rings. He also proposed for that taxon a developed sense of smell due to the large size of the olfactory bulbs and nasal cavity as a whole. Rhynchosaurs in general have large orbits (Figure 2; Langer and Schultz, 2000) and the impressions of the olfactory bulbs of *Teyumbaita sulcognathus* are quite similar to the ones of *H. gordonii*.

Kundrát (2007) noticed reduced olfactory bulbs and the absence of olfactory peduncles in *Conchoraptor gracilis*, a condition also observed in birds. This could suggest a reduced olfaction in this theropod, but the author hypothesized that the sensory epithelium could have been developed in a way to compensate the small size of the nasal cavity and olfactory bulbs.

However, this sort of inference has no support and relies just on speculation (Witmer, 1995; Benton, 2010). In the other hand we must consider that the general proportions of sensory and neural structures may vary among animals without clear implications for their sensory biology. For example, crocodiles and theropods have different olfactory ratios and the formers possess the highest ratios (Zelenitsky et al., 2009). However, tyrannosaurids are thought to have a keen sense of olfaction, maybe better developed or with a greater relative importance for behavior than in crocodiles (Rogers, 2005; Brochu, 2000; Witmer et al., 2008; Witmer and Ridgely, 2009).

Although rhynchosaurs had abbreviated snouts (Langer and Schultz, 2000), the regions devoted to olfaction within the nasal cavities seem to have been very deep and there was no considerable reduction of the olfactory system during the evolution of the snout, with the retention of the olfactory tract and the bulbs being wider than the tract (Figure 1.2 and 3), different from what is observed in some herbivorous and omnivorous dinosaur taxa (Evans, 2006; Kundrát, 2007;

Witmer et al., 2008). It may be difficult to ideally appreciate these features without mathematically and statistically comparing proportions and ratios, once that it is not possible to determine precisely the size of olfactory bulbs and cerebral hemispheres for rhynchosaurus as was performed by Zelenitsky et al. (2009). However, along with the terminal position of the external nares (Witmer, 2001), these features do suggest a great importance of olfaction in the ecology and behavior of rhynchosaurus because these are the sort of evidences of the possession of a good sense of smell expected to be found in fossils. Moreover, the reduced size of the snout of rhynchosaurus seems to be more apparent than real once that Chatterjee (1974) noticed a greater development of the temporal region of the skull during the evolution of this taxon, instead of a true reduction of the snout. These assertions are in agreement with the observations here made about the olfactory system not being reduced or possibly even more developed than in other reptiles.

The inferences made for *Teyumbaita sulcognathus* are similar to those previously proposed for *Hyperodapedon gordonii*, and both taxa are included in the subfamily Hyperodapedontinae; therefore, good olfaction is possibly a feature of other hyperodapedontine rhynchosaurus. If it is also applicable to other rhynchosaurus is a hypothesis that still lack more evidences, requiring the analysis of other species. Hyperodapedontine rhynchosaurus probably had their perception of the environment based on good vision and olfaction (Benton, 1983). Moreover, olfaction might have been the only or the main chemical sense because of the reduction or absence of vomerolfaction (Sales and Schultz, in preparation) and the degree of development of the olfactory system. So, olfaction may have conveyed some social roles once played by vomerolfaction (Schwenk, 2008) and others like the recognition of offspring or location of predators in the surroundings. It may have been also useful for locating some kind of food resource and the nostrils far rostrally placed would favour the collection of any sort of odor. However reconstructing the behavior and its physiological aspects are more difficult than making anatomical inferences, because the last ones

rely on osteological correlates and preserved soft tissues, whereas the formers require other pieces of evidence (Benton, 2010). New clues are, thus, necessary to test the hypotheses proposed for the ecological role of the olfactory system of rhynchosaurs.

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CAPTIONS

FIGURE 1. CT slices and digital reconstruction of the skull of *Teyumbaita sulcognathus*. (1) Digital reconstruction of the skull with the slicing planes showed in B, C and D. (2) Coronal slice of the top of the skull with the impressions of the olfactory portion of the brain. (3) Sagittal slice with the preserved portion of the endocast. (4) Axial slice of the snout. Scale bars= 5cm, in (2), (3) and (4). Abbreviations: A, anterior; B, bottom; d.e.v, dorsal expansion of the vomer; d.p, dorsal peak of the endocast; e, endocast; L, left; n.c, nasal cavity; o.b, olfactory bulb; o.t, olfactory tract; P, posterior; R, right; T, top.

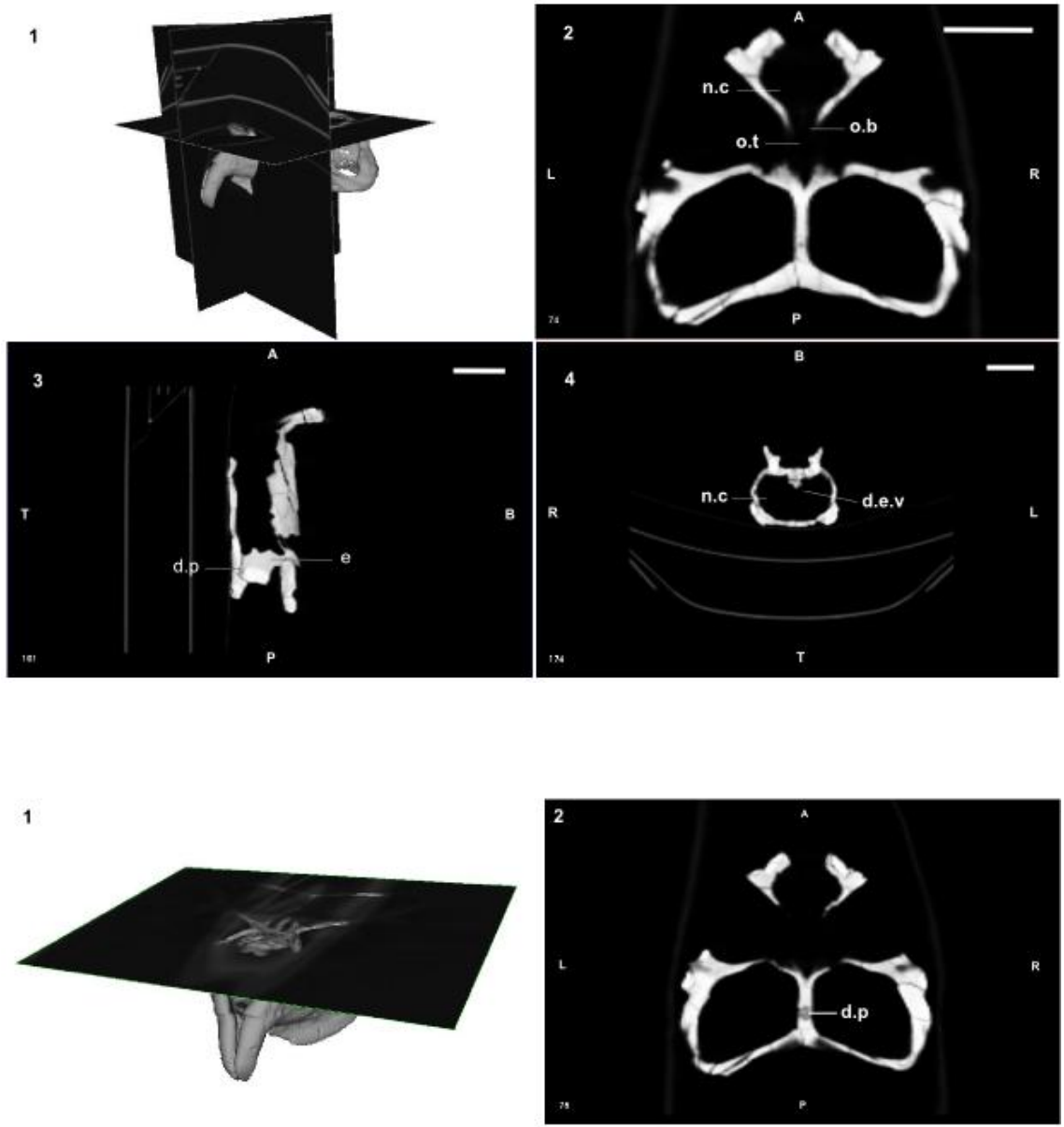
FIGURE 2. In (1) skull of *Teyumbaita sulcognathus* digitally rendered showing the position of a coronal slice (2), in which is possible to note a cast of what once was interpreted by Benton (1983) as the cast of a pineal organ in *Hyperodapedon gordonii*. However, the present data suggest that this structure is actually part of the dorsal peak of the endocast of *T. sulcognathus* and it represents probably a venous sinus or a dural expansion. Scale bar equals 5 cm, in (2). Abbreviation: d.p, dorsal peak.

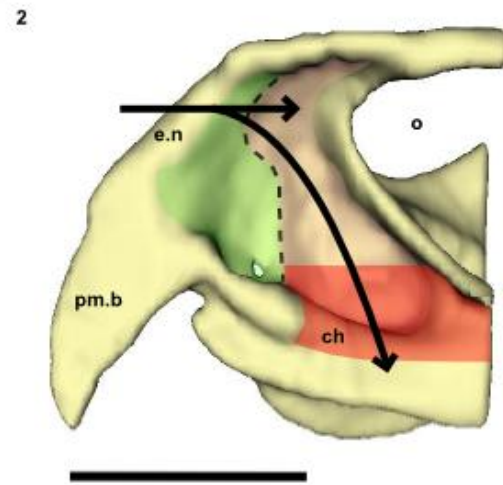
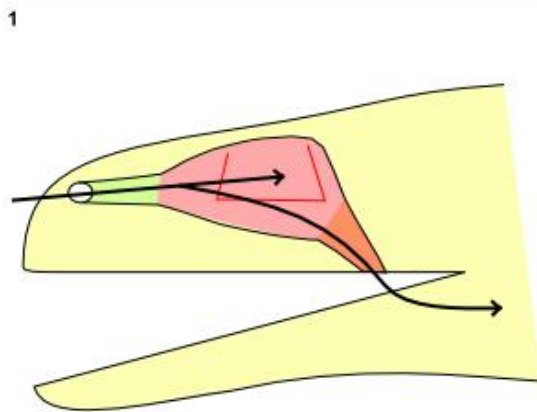
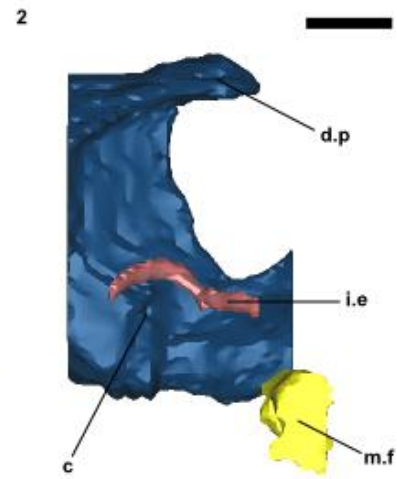
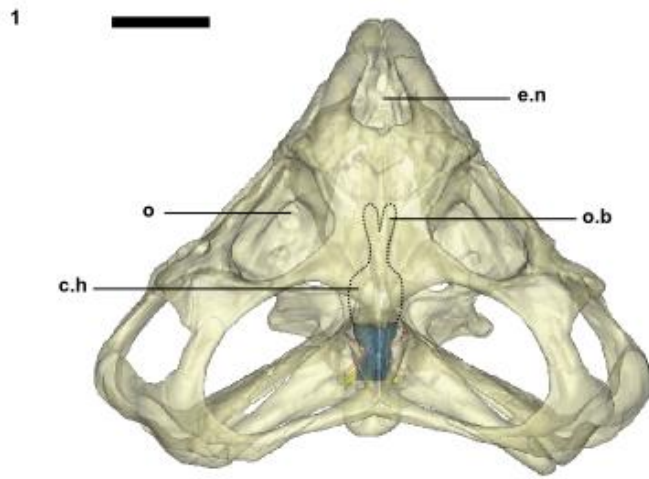
FIGURE 3. Cranial endocast of *Teyumbaita sulcognathus*. (1) Semi-transparent skull for allowing the visualization of the endocast. The dotted line represents the inferred anterior contours of the brain based on the impressions of the olfactory bulbs. (2) Cranial endocast in left lateral view. Scale bars equal 5 cm and 1 cm in (1) and (2), respectively. Abbreviations: c, cerebellum; c.h, cerebral hemispheres; d.p, dorsal peak of the endocast; e.n, external nares; i.e, left inner ear; m.f, metotic foramen; o, orbit; o.b, olfactory bulb; o.t, olfactory tract.

FIGURE 4. Nasal cavity of a generalized tetrapod (1) and the digital reconstruction of the right half of the snout of *Teyumbaita sulcognathus* in medial view (2). The horizontal and vertical

arrows represent the airstream passing, respectively, to the olfactory part of the nasal cavity and the oral cavity and then the upper respiratory tract. In green, the nasal vestibule, which is followed by the nasal cavity artificially colored in pink. A concha is located within the nasal cavity proper of the generalized tetrapod and has its contours in red. The last portion of the nasal capsule is the nasopharyngeal duct here indicated in red, but its presence in *T. sulcognathus* is speculative. The dashed line indicates the course of the internal ridge that possibly marks the boundary between the vestibule anteriorly and the nasal cavity proper posteriorly. Scale bar = 5 cm, in (2). Abbreviations: ch, choana; e.n, external nare;; o, eye orbit; pm.b, pre-maxillary beak.

FIGURES





3. ANEXO A – RESUMO APRESENTADO NO VIII SBPV

Paleoneurological traps: the risks of mistakes in behavioral inferences

¹ Marcos A. F. Sales*, Cesar L. Schultz

Paleoneurology, defined as the study of brain evolution, can also shed some light on how extinct vertebrates behaved. Here we discuss some of the main mistakes present in behavioral inferences based on cranial endocasts. Understanding neuroanatomy of extinct taxa and how it was related to behavior requires comparisons with living outgroups, but it must be taken into account which behaviors are derived or how different they are from the primitive condition present in the last common ancestor of living and extinct taxa. For example, theropods and crocodylians have similar endocasts, but crocodylians receive and process sensory stimuli related to their semi-aquatic habits and hence they are behaviorally very different from dinosaurs and their last common ancestor, which had terrestrial habits. The principle of proper mass states that the amount of neural tissues is proportional to the functions or the relative importance carried out by them. It may lead to an underestimation of how an extinct animal could behave, as it becomes limited to the behavior suggested by the endocast general morphology, or it may be insufficiently elucidative when a feature can be related to more than one possible behaviors. The expanded olfactory bulbs of *Tyrannosaurus rex* may have been useful for both active predation and scavenging. Actually, tooth marks and the relative importance of vision suggest it could perform active predation. Paleoneurological inferences can be even biased by teleological reasonings, where a set of neuroanatomical features evolved in a given taxon to play a specific function instead of being a heritage from ancestors that evolved under different selective pressures. Large olfactory bulbs, for example, fits well with the sensory requirements of carnivorous animals, so a selective pressure to explain it in herbivorous dinosaurs (e.g. sauropods) is thought to be unknown. However, large olfactory bulbs are present in theropods and crocodylians, so this condition seems to be primitive for Saurischia

and maybe also for Dinosauria + Crocodylia. The encephalization quotient is a good index concerning the allometric relationship between brain and body sizes, but is not exactly related to cognition, because an increase in brain size may include neural tissues with no cognitive function. In dinosaurs, the proportion of such tissues cannot be determined because their neuroanatomy is not precisely recorded in many endocasts. Moreover, other neuroanatomical features may be a more reliable prediction of cognitive capabilities, as the degree of brain folding in mammals, but it is a sort of data not always recovered safely from endocasts. In conclusion, behavioral inferences require caution when based on endocast morphology. Other pieces of evidences, including comparisons with modern analogues, should be taken into account in order to have a glimpse of what a fossil vertebrate could do or not. [* Bolsista CNPq].

¹ Universidade Federal do Rio Grande do Sul (UFRGS), Instituto de Geociências, Departamento de Paleontologia e Estratigrafia, Laboratório de Paleovertebrados, Av. Bento Gonçalves, 9500, Bloco 4327, Agronomia, 91501-970, Porto Alegre, Brasil. E-mail: marcos.paleo@yahoo.com.br, cesar.schultz@ufrgs.br

4. ANEXO B – CARTA DE SUBMISSÃO DO ARTIGO À REVISTA JOURNAL OF VERTEBRATE PALEONTOLOGY

RE: Manuscript No. JVP-2013-0027

Dear Mr. Sales:

We have received your manuscript entitled "Rhynchosaurs and the evolution of Jacobson's organs" in our Editorial Office, and it is presently being given full consideration for publication in Journal of Vertebrate Paleontology. A copy of this email has also been sent to all co-authors, who according to system records are: Sales, Marcos.

Please refer to the above manuscript number in all future correspondence. If there are any corrections to your postal address or e-mail address, please let us know or log into ManuscriptCentral to update your profile.

Please note that the author is responsible for obtaining written permission from all persons cited as 'pers. comm.' in JVP manuscripts.

If any of the co-authors does not receive a copy of this email, it might be because incorrect contact information is entered in the database. Please let us know if you learn of such a situation.

Thank you for submitting your interesting work. We will be in touch with you in due course concerning the acceptability of your manuscript for publication in JVP.

Sincerely,

Sent automatically by ScholarOne on behalf of:
Receiving Editor,
Journal of Vertebrate Paleontology

5. ANEXO C – CARTA DE SUBMISSÃO DO ARTIGO À REVISTA PALAEONTOLOGIA ELECTRONICA

Your manuscript 'Paleoneurology of Teyumbaita sulcognathus (Diapsida: Archosauromorpha) and the sense of smell in rhynchosaurs' has been submitted to Palaeontologia Electronica. Thank you for your submission - we hope to be in touch soon with reviews and an initial decision

Best Regards

David Polly, Executive Editor, Palaeontologia Electronica

This email automatically generated on 11th February 2013 03:21:53 (UTC)
by PEMSATS (Palaeontologia Electronica Manuscript Submission And Tracking System)
PEMSATS is available at: http://palaeo-electronica.org/PEMSATS/pemsats_login.php

6. ANEXO D – HISTÓRICO ESCOLAR



Informações Acadêmicas do Aluno

Histórico Escolar

Emissão: 10/02/2013 às 12:32

Aluno



Marcos Andre Fontenele Sales

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Atividades Desenvolvidas UFRGS

Atividades de Ensino

Período Letivo	Atividade de Ensino	Turma	Créditos	Conceito	Nome Professor	Situação	Órgão
2012/2	Elementos fundamentais de Tafonomia	A	5	-	<ul style="list-style-type: none"> ● CESAR LEANDRO SCHULTZ 	Matriculado	Programa de Pós-Graduação em Geociências
2012/2	T.E. em Paleontologia: Reconstruções musculares aplicados à paleontologi	A	2	A	<ul style="list-style-type: none"> ● CESAR LEANDRO SCHULTZ 	Aprovado	Programa de Pós-Graduação em Geociências
2012/1	T. E. em Paleontologia: sistemática cladística aplicada à paleontologia	A	2	B	<ul style="list-style-type: none"> ● CESAR LEANDRO SCHULTZ 	Aprovado	Programa de Pós-Graduação em Geociências
2011/2	Bioestratigrafia do Triássico do RS com base em tetrápodes	A	3	-	<ul style="list-style-type: none"> ● CESAR LEANDRO SCHULTZ 	Matriculado	Programa de Pós-Graduação em Geociências
2011/2	EVOLUÇÃO DOS MAMÍFEROS SUL-AMERICANOS	A	3	A	<ul style="list-style-type: none"> ● - 	Aprovado	Programa de Pós-Graduação em Geociências
2011/2	Paleontologia de Vertebrados III	A	5	A	<ul style="list-style-type: none"> ● MARINA BENTO SOARES 	Aprovado	Programa de Pós-Graduação em Geociências
2011/1	Paleoecologia e Bioestratigrafia: conceitos e aplicações	A	6	A	<ul style="list-style-type: none"> ● JOAO CARLOS COIMBRA ● CESAR LEANDRO SCHULTZ ● ROBERTO IANNUZZI ● PAULO ALVES DE SOUZA 	Aprovado	Programa de Pós-Graduação em Geociências
2011/1	Paleontologia de Vertebrados I: Estudo do Esqueleto Cranial	A	4	A	<ul style="list-style-type: none"> ● CESAR LEANDRO SCHULTZ 	Aprovado	Programa de Pós-Graduação em Geociências
2011/1	Paleontologia de Vertebrados II - Est. Esqueleto Pós-Cranial	A	5	A	<ul style="list-style-type: none"> ● CESAR LEANDRO SCHULTZ 	Aprovado	Programa de Pós-Graduação em Geociências