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

ESTIMATIVA DE MASSA CORPORAL EM VERTEBRADOS FÓSSEIS E SUAS IMPLICAÇÕES PARA A PALEOECOLOGIA DO RAUISSÚQUIO *PRESTOSUCHUS CHINIQUENSIS* (PARACROCODYLOMORPHA, LORICATA) DO MESOTRIÁSSICO DO RS.

SILVIO MARQUES DE JESUS VIEIRA

ORIENTADOR - Prof. Dr. Cesar Leandro Schultz

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Porto Alegre, 2023

Lista de Figuras

Lista de Tabelas

“I was so frightened
I almost ran away
I didn't know that I could do
Anything I needed to

And then a bolt of lightning
Hit me on my head
Then I began to see
I just needed to believe in me…”

KISS - “I”

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organizar e de seguir em frente. Certo que fui um paciente teimoso, mas de pouquinho em pouquinho, entendia os fios que precisava puxar para esta rede ser tecida.

RESUMO

O estudo da paleoecologia, especialmente de vertebrados fósseis, perpassa por uma série de fatores que influenciam em possíveis interpretações acerca das características dos animais analisados. Um destes fatores chave se encontra na estimativa de massa destes organismos fósseis, que oferece uma gama de propriedades provenientes da obtenção deste dado, como dieta, aspectos biomecânicos, fisiológicos e morfológicos. Este trabalho descreve algumas metodologias de obtenção de massa de organismos fósseis (especificamente regressão matemática, modelos matemáticos e modelos em escala, físicos e digitais), as quais foram aplicadas, como estudo de caso, no predador de topo de cadeia alimentar no Mesotriássico do RS, *Prestosuchus chiniquensis*, e como os diferentes valores obtidos pelas distintas metodologias influenciam as interpretações ecológicas possíveis para o animal estudado. Neste estudo, aplicamos as distintas metodologias sobre um espécime hipotético com 4,50 m de comprimento, usando como parâmetro as dimensões do esqueleto quase completo do espécime UFRGS-PV-0629-T, da Coleção de Paleovertebrados da UFRGS. Após a comparação e discussão dos resultados obtidos, concluímos que a estimativa mais consistente apontaria uma massa de 365 kg para um *Prestosuchus* de 4,5m, baseando-se não só no trabalho proposto, como também comparando com organismos semelhantes viventes e extintos, como por exemplo o dragão de Komodo e o rauissúquio *Postosuchus kirkpatricki* (Chatterjee, 1985) dos EUA, único táxon equivalente a *Prestosuchus* para o qual já foi feita uma análise semelhante. Tomando como base a massa obtida pudemos considerar os aspectos mecânicos e ecológicos de *Prestosuchus*, o qual provavelmente adotaria uma estratégia de caça por emboscada, incluindo uma possível mudança para a postura bípede e ortógrada durante as atividades de caça.

Palavras-chave: *Prestosuchus chiniquensis*, estimativa de massa, paleoecologia. Rauisuchia, Mesotriássico

ABSTRACT

The study of paleoecology, especially of fossil vertebrates, involves a series of factors that influence possible interpretations regarding the characteristics of the animals analyzed. One of these key factors is the estimated mass of these fossil organisms, which offers a range of properties resulting from obtaining this data, such as diet, biomechanics, physiology and morphological aspects. This work describes some methodologies for obtaining the mass of fossil organisms (specifically mathematical regression, mathematical models and scale models, physical and digital), which were applied, as a case study, to the top predator of the Mesotriassic food chain in RS, *Prestosuchus chiniquensis*, and how the different values obtained by different methodologies influence the possible ecological interpretations for the animal studied. In this study, we applied such different methodologies to a hypothetical specimen measuring 4.50 m in length, using as a parameter the dimensions of the almost complete skeleton of the specimen UFRGS-PV-0629-T, from the UFRGS Paleovertebrate Collection. After comparing and discussing the results obtained, we concluded that the most consistent estimate would indicate a mass of 365 kg for a 4.5m *Prestosuchus*, based not only on the proposed work, but also comparing with similar living and extinct organisms, such as, for example, the Komodo dragon and the rauisuchian *Postosuchus kirkpatricki* (Chatterjee, 1985) from the USA, the only taxon equivalent to *Prestosuchus* for which a similar analysis has already been carried out. Based on the mass obtained, we were able to consider the mechanical and ecological aspects of *Prestosuchus*, which would probably adopt an ambush hunting strategy, including a possible change to a bipedal and orthograde posture during hunting activities.

Keywords: *Prestosuchus chiniquensis*, body mass estimates, paleoecology, Rauisuchia, Mesotriassic.

SUMÁRIO

Estrutura desta dissertação

Esta dissertação está organizada conforme a norma *Norma 118 – Submissão de teses e dissertações na forma de artigos do PPGGeo-UFRGS*, e se encontra estruturada da seguinte maneira:

I) Texto introdutório sobre o problema de pesquisa, os objetivos almejados com este trabalho, os métodos que foram utilizados para sua realização, e a discussão dos resultados obtidos.

II) Artigo submetido em “***The Anatomical Record: Advances In Integrative Anatomy and Evolutionary Biology”***, Qualis Capes A4. desenvolvido durante o percurso do mestrado acadêmico, conforme o tópico 1.1 da norma 118, apresentado aqui de forma diferente ao que foi submetido, adequando-se à formatação necessária.

III) Anexos, entre elas figuras, tabelas e equações, necessários para a viabilidade do trabalho e seus resultados.

1. Introdução

A grande extinção do final do Permiano determinou uma mudança radical nas teias tróficas dos vertebrados terrestres. Pela primeira vez na História, os diápsidos (mais especificamente os arcossauros) passaram a ser os predadores de topo de cadeia, inicialmente com formas quadrúpedes pequenas, mas que atingiram tamanhos estimados de até 9m (e.g. *Saurosuchus*) no início do Neotriássico, e posteriormente com formas bípedes, especialmente os dinossauros.

Nesse contexto (surgimento de formas gigantes e passagem de quadrúpedes para bípedes), os arcossauros passaram por importantes mudanças posturais em seus esqueletos, sendo que são justamente as características morfológicas dos ossos que nos permitem inferir suas propriedades biomecânicas e, a partir delas, sua Paleoecologia. Entretanto, para embasar estas inferências é necessário, antes de tudo, determinar a massa do animal que se esteja analisando.

A obtenção dos dados de massa de um animal fóssil traz consigo uma gama de alternativas interpretativas, levantando novos questionamentos com possíveis respostas plausíveis acerca, especialmente, da sua paleoecologia. Estimar a massa de um animal nos confere informações da fisiologia, como taxa metabólica, respiração, tempo de digestão, tempos de gestação, estratégias reprodutivas, densidades populacionais, nichos ecológicos, modos de locomoção, construção do esqueleto, entre outros (Schmidt-Nielsen, 1984). A área da ecologia também é extremamente favorecida com a obtenção da possível massa do animal fóssil, podendo ser inferidas informações sobre dietas, modo de forrageamento e compartimentalização de nichos (Egi, 2001). Também deve ser levado em consideração que o objeto de estudo muda sua forma e tamanho em diferentes estágios ontogenéticos de sua vida, sendo necessário um olhar mais crítico ao observar os resultados obtidos pois dependendo do estágio de vida, comportamentos e processos fisiológicos tendem a ser diferentes (Hopkins, 2018).

De acordo com o material disponível para estudo, metodologias distintas podem ser utilizadas para estimar a massa de um animal fóssil. No presente estudo, foram utilizados diferentes modelos em escala, os quais foram escaneados, digitalizados e manipulados no software Blender, a partir dos quais foram calculados seu comprimento, volume e consequentemente, sua massa. Outras metodologias, tais como equações de regressão e modelos matemáticos também foram testadas, para comparar os resultados e testar a coerência destas metodologias entre si.

2. Objetivos

2.1 Geral:

O propósito do presente estudo é apresentar e discutir diferentes metodologias utilizadas para estimar a massa de vertebrados fósseis, incluindo métodos de regressão matemática, modelos matemáticos e modelos (físicos e digitais) em escala. Como estudo de caso, foram aplicadas estas técnicas no arcossauro triássico *Prestosuchus chiniquensis*, usando como parâmetro o esqueleto quase completo do espécime UFRGS-PV-0629-T, da coleção do Setor de Paleovertebrados da UFRGS. Partindo da premissa que este esqueleto corresponde a um animal que teria 4,5m de comprimento, a determinação de sua massa corporal, em vida, permitiria estabelecer inferências quanto à sua paleoecologia, incluindo a velocidade de deslocamento, possibilidade de bipedalismo, estratégia de caça e outras.

2.2 Específicos:

a) Levantar dados sobre as diversas metodologias utilizadas em estimativa de massas de vertebrados fósseis;

b) Contextualizar filogeneticamente *Prestosuchus chiniquensis* e Rauisuchia dentro de Archosauria;

c) Caracterizar a morfologia de um espécime de *Prestosuchus chiniquensis* com 4,5m de comprimento;

d) Estimar, com base em diversas metodologias (regressão matemática, modelos matemáticos e modelos em escala), a massa de *Prestosuchus chiniquensis*;

e) Analisar, de acordo com as medidas alcançadas, inferências paleoecológicas e biomecânicas, além de discutir quais dos métodos utilizados forneceram resultados mais plausíveis;

3. O Estado-da-arte do estudo da pesquisa

3.1 Metodologias para a obtenção de estimativas de massa

Existe uma série de metodologias disponíveis para a obtenção da possível massa de um animal extinto, desde cálculos de densidade, equações de regressão, "fatiamento" geométrico, diâmetro do côndilo occipital (para mamíferos térios), entre vários outros (Brassey, 2016). Para este trabalho, utilizamos as metodologias de equações de regressão matemática (com base nas medidas ósseas do fóssil UFRGS-PV-0629-T), modelos matemáticos (com base no esqueleto inteiro do espécime UFRGS-PV-0629-T, transformamos-o em uma semi-elipse) e modelos em escala (utilizamos quatro modelos diferentes, três de *Prestosuchus chiniquensis* – argila, plástico e 3D digital; e um de *Postosuchus kirkpatricki* em plástico, e calculamos seus volumes e densidades).

Tendo como foco os cálculos de densidade, utilizamos um modelo, em escala reduzida, confeccionado em plástico maciço, de uma reconstituição de *P. chiniquensis,* produzida pela Safari Ltd.®, a qual foi elaborada a partir das proporções dos esqueletos disponíveis para a espécie, descritos na literatura e com a consultoria de paleontólogos, incluindo um dos autores do presente estudo (CLS). Este modelo foi escaneado com um equipamento Artec Space Spider 3D Structured Light Scanner (Artec 3D a) no Laboratório de Paleovertebrados da UFRGS, para a obtenção de um modelo digital 3D, utilizando o software Artec Studio 17 Professional (Artec b). A seguir, as dimensões do modelo foram ajustadas para corresponder a um espécime de 4,50m de comprimento, sendo então calculada a sua massa, a partir do volume digital (Figura 1).

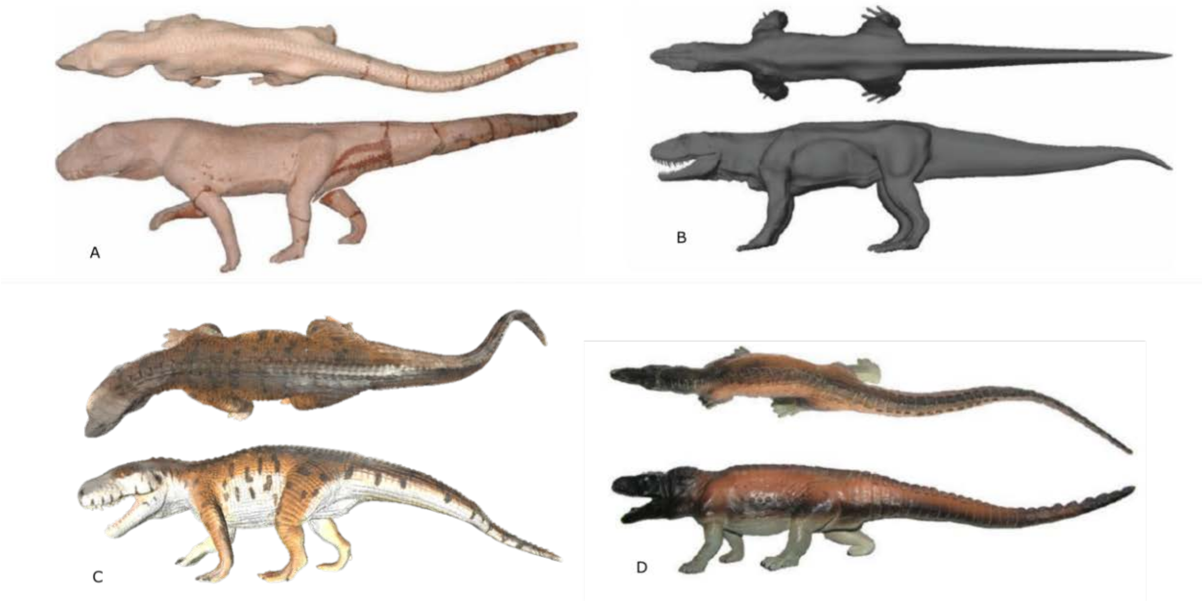

Figura 1 – Vistas lateral e dorsal dos modelos em escala utilizados para estimar a massa do espécime UFRGS-PV-0629-T. (A) Modelo em escala de *Prestosuchus* em argila, confeccionado por Leonardo Morato; (B) escultura 3D de *Prestosuchus*, produzida totalmente em meio digital por Adolfo Bittencourt; (C) modelo em escala de *Prestosuchus* em plástico, produzido pela Safari Ltd.® e (D) modelo comercial de plástico representativo de *Postosuchus.* As figuras não estão em escala.

3.2 Modelagem 3D

A utilização de modelos tridimensionais em escala para o uso científico, especialmente para a estimativa de massa de animais fósseis, pode ser desenvolvida a partir de um leque de opções, a depender da disponibilidade e da capacidade artística das partes envolvidas. Desde modelagem digital até modelos físicos de argila ou plástico podem ser utilizados tranquilamente como ferramentas para estimar a massa de um organismo, levando em consideração, por exemplo, metodologias de densidade, com base no deslocamento da água ou da areia, ou equações de regressão. Esta metodologia destacou-se a partir do trabalho de Gregory (1905), no qual a partir de uma escala de um para dezesseis (1:16), pode reconstruir detalhadamente *Brontosaurus excelsus*, 1879, e estimar seu volume com base no deslocamento ao mergulhá-lo em água, fazendo então uma "escala reversa" e podendo inferir, com certa semelhança, uma massa próxima ao que sabemos dos saurópodes atuais (Brassey, 2016). Colbert (1962) também utilizou desta metodologia, porém observando o deslocamento da areia, ao invés da água, ao manusear modelos em escalas de dinossauros. Já outros autores seguiram o modelo de Alexander (1983b), cuja metodologia se baseava ao pesar os modelos tanto no ar quanto na água (Brassey, 2016).

Ao utilizarmos modelagem 3D para obter estimativas de massas de animais extintos, devemos levar em consideração uma série de fatores que podem dificultar o uso desta metodologia. Um modelo 3D é uma representação aproximada, baseada em reconstrução muscular e óssea, que leva consigo certa liberdade artística em sua concepção, especialmente em elementos de tecidos moles, como músculos. Modelos 3D também demandam certa completude do animal fóssil para que haja precisão em sua reconstrução, assim como um correto manuseio dos scanners e softwares de modelagem. Entretanto, a utilização deste método, dada as adversidades que pode apresentar em sua utilização, como a posse prévia de modelos 3D de animais fósseis específicos, se mostra uma forma ágil e simples de aplicação para estimativas de massa, cuja facilidade de experimentação, especialmente acerca de volumes e escalas, pode ser testada à exaustão sem necessidade de danificar o material original.

3.3 ***Prestosuchus chiniquensis***:

Prestosuchus é um gênero fóssil de arcossauro predador de grande porte (Figura 2), cujos restos são encontrados em rochas do Mesotriássico (Ladiniano) do sul do Brasil e da Tanzânia e que, juntamente com *Luperosuchus fractus*, da Argentina, representou o topo da teia trófica da porção sul da Gondwana naquele momento. Na Laurasia, uma forma muito semelhante (*Batrachotomus kupferzellensis*) é encontrada em rochas de mesma idade na Alemanha.

A espécie brasileira *Prestosuchus chiniquensis* Huene 1938, faz parte da Zona de Associação de *Dinodontosaurus* (Schultz *et al*., 2021), estratigraficamente incluída na Sequência Pinheiros-Chiniquá (Triássico Médio) da Supersequência Santa Maria (Horn et al., 2014).

Figura 2 - Representação artística de *Prestosuchus chiniquensis* por Adolfo Bittencourt (Modificado de Liparini, 2011)

Do ponto de vista taxonômico, *Prestosuchus* é comumente incluído num grupo heterogêneo denominado “rauissúquios”, que inclui uma assembleia de táxons de diferentes morfologias, incluindo grandes predadores quadrúpedes (e.g., *Prestosuchus, Batrachotomus, Postosuchus, Saurosuchus*), animais com espinhos neurais alongados no tronco, formando “velas” (como *Arizonasaurus* e *Ctenosauriscus*), além de formas cursoriais semelhantes a dinossauros (tais como *Effigia*, *Poposaurus* e *Shuvosaurus*). Não existe consenso quanto a todos os “rauissúquios” pertencerem a um grupo monofilético ou quais deles poderiam compor sub-grupos monofiléticos. Por exemplo, utilizando a hipótese filogenética de Brusatte *et al*. (2010), a espécie brasileira Prestosuchus chiniquensis formaria um grupo natural com a espécie alemã *Batrachotomus kupferzelensis*, grupo este que, por sua vez estaria mais proximamente relacionado à espécie argentina *Saurosuchus galilei*. Por seu turno, a hipótese filogenética apresentada por Nesbitt (2011) mostra um grupo formado por *Rauisuchus*, *Polonosuchus* e *Postosuchus*, que estaria mais proximamente relacionado aos crocodilomorfos (o que inclui os crocodilos atuais) do que a outros rauissúquios, tais como *Prestosuchus*, *Batrachotomus*, *Fasolasuchus* e *Saurosuchus* (Figura 3).

Independentemente de seu posicionamento filogenético, *Prestosuchus chiniquensis* está entre os maiores predadores do Mesotriássico, sendo que alguns ossos atribuídos a este táxon, presentes nas coleções triássicas do sul do Brasil, indicam que estes animais poderiam ter atingido comprimentos próximos a 8m. Entretanto, a estimativa de sua massa corporal (e as consequentes possibilidades biomecânicas vinculadas à mesma) permanece ainda alvo de estudos mais detalhados.

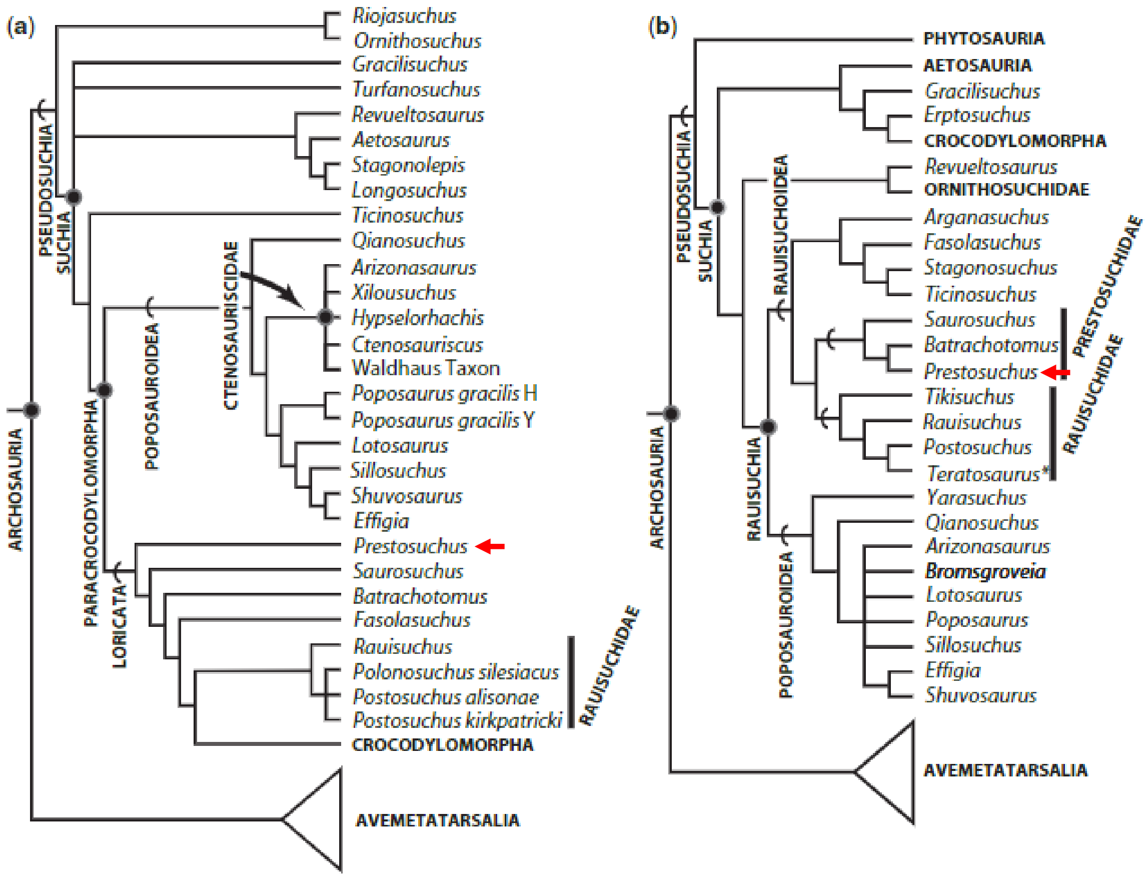

Figura 3 - Cladograma demonstrando duas hipóteses filogenéticas para *Rauisuchia* e *Prestosuchus chiniquensis* dentro de *Archosauria*. Lado A, proposta de Nesbitt (2011). Lado B, proposta de Brusatte *et al*. (2010) Modificado de Nesbitt (2013).

Em relação à paleoecologia de *P. chiniquensis*, é consenso entre os autores que suas características morfológicas (crânio relativamente alto e estreito, portando dentes zifodontes, largos e comprimidos labio-lingualmente, pontudos e recurvados) e seu tamanho (maior que qualquer outro componente da paleofauna em que ocorre) indicam que o mesmo se tratava do predador de topo da cadeia alimentar, mas existem diferentes propostas relativas ao modo como ele exerceria esta carnivoria (se por emboscada ou por perseguição, a que velocidade poderia correr, se em 2 ou 4 patas, etc.). Tendo em vista que, entre os “rauissúquios”, existem tanto formas quadrúpedes quanto bípedes, alguns autores discutiram a hipótese de *P. chiniquensis* poder ser um bípede ocasional. Liparini (2011), baseado em aspectos da morfologia do esqueleto e numa estimativa de massa corporal de 400 Kg (para um espécime de 4,5m de comprimento), concluiu que *P. chiniquensis* seria uma forma preferencialmente quadrúpede e cursorial, podendo atingir uma velocidade máxima de 40 km/h. Entretanto, com estes parâmetros, poderia também exercer uma estratégia de caça por emboscada, adotando repentinamente uma postura bípede, ortógrada, com algum arqueamento ventral da coluna, na tentativa de surpreender a presa e capturá-la logo na fase inicial da investida.

Liparini (2011) ressaltou, no entanto, que tanto a inferência de velocidade quanto a de adoção de uma postura bípede ocasional estavam diretamente relacionadas à estimativa de massa corporal por ele obtida, a qual, no entanto, mostrou-se bastante variável, dependendo da metodologia que fosse adotada, sendo que o valor escolhido (de 400Kg para um animal de 4,5m) foi adotado como “o mais provável” dentro de uma variação entre 230 kg e 1350 kg, levando também em consideração animais de porte e comportamento semelhante ao *Prestosuchus*, como crocodilos e grandes lagartos.

4. Materiais e Métodos

No presente estudo, utilizamos três metodologias distintas para estimar a massa de um *Prestosuchus chiniquensis* com 4,5m.

Aplicamos as equações de regressão, as quais se validam de acordo com a utilização de proxies, como dimensões dentárias ou os diâmetros dos ossos dos membros (Ruff 1988, 2003; Ruff *et al.* 1991) (Tabela 1). Os proxies dentários tem a vantagem de estarem intimamente relacionados com o processo alimentar e o metabolismo, apesar de serem mais comumente utilizados em mamíferos, e possuem relação direta à massa corporal. As dimensões ósseas dos membros nos dão informações associadas à massa corporal de acordo com a carga suportada pelos membros ao sustentar o corpo em terra firme (Anderson, 2004). As vantagens desta metodologia se dão devido à simplicidade de aplicação, uma vez obtidos os materiais necessários, como por exemplo, medidas ósseas diretas feitas com paquímetros (Tabela 2), assim como são técnicas muito objetivas, sem necessidade de interpretações artísticas do organismo fóssil, do mesmo modo que podemos utilizadas em restos fósseis incompletos. Porém, devido a esta simplicidade, a aplicação incorreta pode dificultar as interpretações técnicas (Smith, 1993; Kaufman & Smith, 2002; Smith, 2009).

Também aplicamos os modelos matemáticos, metodologia que pode ser executada quando uma quantidade significativa do esqueleto do animal tenha sido recuperada em um estado não distorcido, arranjando uma montagem do esqueleto e calculando seu volume por meio de cálculos de sólidos (Graphic Double Integration - GDI) (Hulburt, 1999) ou fatiamento geométrico (3D Mathematical slicing) (Henderson, 1999; Montani, 2001; Mazzetta *et al*., 2004). Especificamente, utilizando a metodologia de Seebacher et al (1999), aproximações do volume corporal a formas geométricas para estimar o volume de crocodilos também são válidos, aproximando a forma do animal a uma meia elipse (Tabela 1). Ao multiplicar este volume pela densidade geral pré-selecionada do tecido do animal estudado, é possível então obter sua massa.

Referência	**Equação**
Anderson et al. 1985	$BM = 7.9 \times 10^{-5} \times (C_h + C_f)^{2.75}$ [1]
Christiansen and Fariña 2004	$BM = 6.3 \times 10^{-7} \times L_f^{3.21}$ [1]
Farlow et al. 2005 $[L]_f$	$BM = 1.6 \times 10^{-6} \times L_f^{3.35}$ [1]
Farlow et al. 2005 [TL]	$BM = 1.6 \times 10^{-10} \times TL^{3.39}$ [1]
Klein et al. 2005 and Jossep et al. 2006	$BM = 1.4 \times 10^{-5} \times SVL^{3.13}$ [1]
Seebacher et al. 1999	$BM = 0.5\pi d \times (h^2 + 5.19 \times 10^{-4} \times h + 8 \times 10^{-8})$

Tabela 1 - Equações de regressão e modelo matemático aplicados para estimar a massa do espécime UFRGS-PV-0629-T de *Prestosuchus*. [1] Parâmetros recalculados a partir dos dados dos trabalhos citados. Abreviações: BM, massa corporal estimada (em kg); C_f, circunferência do fêmur na porção média da diáfise (em mm); C_h, circunferência do úmero na porção média da diáfise (em mm); d, densidade corpórea (em kg/m^3); h, altura da cintura pélvica (em m); L_f, comprimento total do fêmur (em mm); SVL, comprimento rostro-cloacal (em cm); TL, comprimento total (em mm).

Parâmetro	Medida (mm)
Altura da cintura pélvica [h]	500 mm
Circunferência do fêmur na porção média da diáfise [C_f]	221 mm
Circunferência do úmero na porção média da diáfise [C_h]	136 mm
Comprimento rostro-cloacal [SVL]	2300 mm
Comprimento total [TL]	4500 mm [1]
Comprimento total do fêmur [L_f]	462 mm
Densidade corpórea	0,965 kg/L

Tabela 2 - Medidas do fóssil UFRGS-PV-0629-T, usadas para estimar a massa de *Prestosuchus*. [1] valor estimado.

Por fim, empregamos a metodologia de modelagem física, que consiste em uma reconstrução completa do esqueleto com tecidos moles, e a partir deste modelo, calculamos a massa baseando-se no volume e na densidade média. Porém, este método requer a existência de esqueletos muito bem preservados e uma capacidade artística de modelagem significativa, além de envolver um certo grau de subjetividade.

A estimativa de massa a partir dos modelos paleoartísticos foi realizada calculando-se o volume do modelo, multiplicando este volume pelo fator de escala volumétrica do modelo (quantas vezes o modelo é menor do que o organismo era na realidade) e por fim multiplicando este valor pela densidade corpórea assumida para a espécie. A escala volumétrica do modelo corresponde ao cubo da escala de medidas lineares do modelo. Por exemplo, o fêmur do modelo de argila foi mensurado em 35 mm, enquanto a medida do fêmur fóssil de UFRGS-PV-0629-T é de 462 mm, logo, o animal era aproximadamente 13 vezes maior do que o modelo que o representa (462 mm / 35 mm = 13). Sendo assim, a escala volumétrica considerada seria de 13^3 = 2197 vezes, na qual o volume calculado para o modelo corresponderia seria 2197 vezes menor do que o volume real esperado para o espécime em estudo.

Para determinar o fator de escala dos modelos físicos, foram tomadas as medidas lineares do comprimento do ramo mandibular, fêmur, úmero, largura da porção posterior do teto craniano e comprimento desde a porção mais anterior do crânio até o início da cauda do material fóssil (assumindo como sendo aproximadamente o comprimento rostro-cloacal). A seguir, estas medidas foram divididas pelos comprimentos equivalentes a estas mesmas porções nos modelos em escala. As medidas nos modelos foram obtidas através de um paquímetro Mitutoyo 200 (+-0,05) mm e as medidas no material fóssil foram obtidas através de um paquímetro Mitutoyo 60 (+- 0,02) cm. Cada elemento foi medido cinco vezes e o valor médio foi utilizado como referência para o cálculo dos fatores. No caso dos elementos pares (por exemplo fêmur, úmero e ramo mandibular), quando se encontravam preservados, foram tomadas as cinco medidas de cada um dos lados e a média total foi utilizada como referência para o elemento. Cada fator de escala obtido separadamente foi então somado e dividido pelo número total de fatores individuais utilizados (n) - no caso 5 - obtendo-se então um fator de escala médio.

Dois dos modelos físicos em escala (Figura 3A e 3B) tiveram seus volumes calculados através de uma adaptação da metodologia proposta por Colbert (1962) na qual um recipiente foi completamente preenchido com a areia fina - agitando e batendo levemente o recipiente sobre a bancada, para que a areia se acomodasse e ocupasse todo o espaço vazio - e nivelado com o uso de uma régua. Esse volume determinado de areia foi então retirado do recipiente, o modelo inserido, e a areia novamente assentada e nivelada. O volume de areia excedente foi medido com a proveta e então registrado, sendo este equivalente ao volume do modelo mensurado.

A seguir, foi obtido um modelo digital 3d a partir do modelo em escala reduzida (com cerca de 12 cm de comprimento) confeccionado em plástico maciço pela Safari Ltd.®. Este modelo foi escolhido como sendo representativo para *Prestosuchus* por ter sido elaborado a partir das proporções dos esqueletos disponíveis para a espécie descritos na literatura, contando com a consultoria de paleontólogos, incluindo um dos autores do presente estudo (CLS) (Figura 4C). O modelo em plástico foi escaneado no Laboratório de Paleovertebrados da UFRGS pelo Dr. Roland Sookias com um equipamento Artec Space Spider 3D Structured Light Scanner (Artec 3D a), para a obtenção de um modelo digital 3D, utilizando o software Artec Studio 17 Professional (Artec b). O volume do modelo 3D gerado foi calculado a partir de uma ferramenta de análise volumétrica do software Blender® v 2.92.0.

Por sua vez, o modelo 3D em escala de *Prestosuchus* reconstruído digitalmente pelo Dr. Adolfo Bittencourt, do Instituto de Artes da UFRGS (Figura 4B) foi criado em programa específico (Autodesk Maya®, versão 2008) para manipulação de malhas digitais em três dimensões. O fator de escala linear médio foi calculado da mesma maneira como mostrado acima, utilizando as medidas equivalentes no espécime fóssil UFRGS-PV-0629-T. Neste caso, o volume do modelo foi obtido no próprio programa Autodesk Maya®, que efetua este cálculo através do comando computePolysetVolume.

Por fim, para se obter a massa corporal do material em estudo (BM) o volume real do animal deve ser multiplicado pela densidade corpórea assumida para este animal. Colbert (1962) usou para os dinossauros um valor de d = 0,9kg/L. Outros autores assumem uma densidade igual à da água, i.e 1,0 kg/L (Alexander, 1989; Hurlburt, 1999), no entanto, foi observado na literatura que os limites das densidades de animais terrestres viventes podem estar entre 1,08 e 0,85 kg/L para crocodilos adultos e jovens, respectivamente (Cott, 1961 apud Allen; Paxton; Hutchinson, 2009; Seebacher; Grigg; Beard, 1999; Allen; Paxton; Hutchinson, 2009), e 0,85 kg/L para aves como o emu (Seebacher 2001). No presente trabalho, utilizamos o valor de 0,965 kg/L, considerando o valor médio, entre os valores máximos de 1,08 kg/L e mínimos de 0,85 kg/L descritos para os arcossauros viventes, apresentados acima.

5. Contexto Geológico e Paleoclimático

Segundo Mancuso *et al.* (2021) o estudo do Triássico é essencial para compreender a evolução dos ecossistemas mesozóicos não marinhos, particularmente em relação aos vertebrados e o contexto climático em que viveram. Na história paleobiogeográfica da Terra, a Pangea foi o único supercontinente global que se distribuiu por uma área praticamente simétrica em relação à linha do equador. Esta configuração paleogeográfica, combinada com um elevado nível global do mar e a ausência de calotas polares, teria tido um efeito extraordinário no clima global. Condições climáticas flutuantes dominaram a porção ocidental da Gondwana no Triássico, com um clima árido a semiárido durante o Triássico Inferior, passando a semiárido sazonal no Triássico Médio (com uma sazonalidade mais úmida do que o Triássico Inferior) e o Triássico Superior sendo dominado por condições subúmidas sazonais com um ou mais intervalos semiáridos, particularmente no interior continental.

O táxon aqui estudado (*Prestosuchus chiniquensis*) provém dos níveis mais basais do pacote Meso-Neotriássico do Rio Grande do Sul, o qual constitui uma Sequência Aloestratigráfica de Segunda ordem [Supersequência Santa Maria, Horn et al. (2014)], dividida em 3 sequências de Terceira Ordem (Figura 4). A Zona-de-Associação de *Dinodontosaurus,* em cuja fauna *Prestosuchus* representa o predador de topo, é incluída estratigraficamente na Sequência Pinheiros-Chiniquá (Triássico Médio). Todas as sequências da Supersequência Santa Maria começam com rios entrelaçados efêmeros de baixa sinuosidade, caracterizados por arenitos conglomeráticos acinzentados com estratificação cruzada e planar (Zerfass et al, 2003; Horn et al., 2018). Tais rochas são sobrepostas por camadas métricas de argilitos avermelhados massivos contendo níveis com alterações pedogenéticas (calcretes) (Da Rosa et al., 2005; Horn et al., 2013). Estas rochas foram interpretadas como grandes planícies loessicas com retrabalhamento fluvial esporádico (Horn e al., 2018).

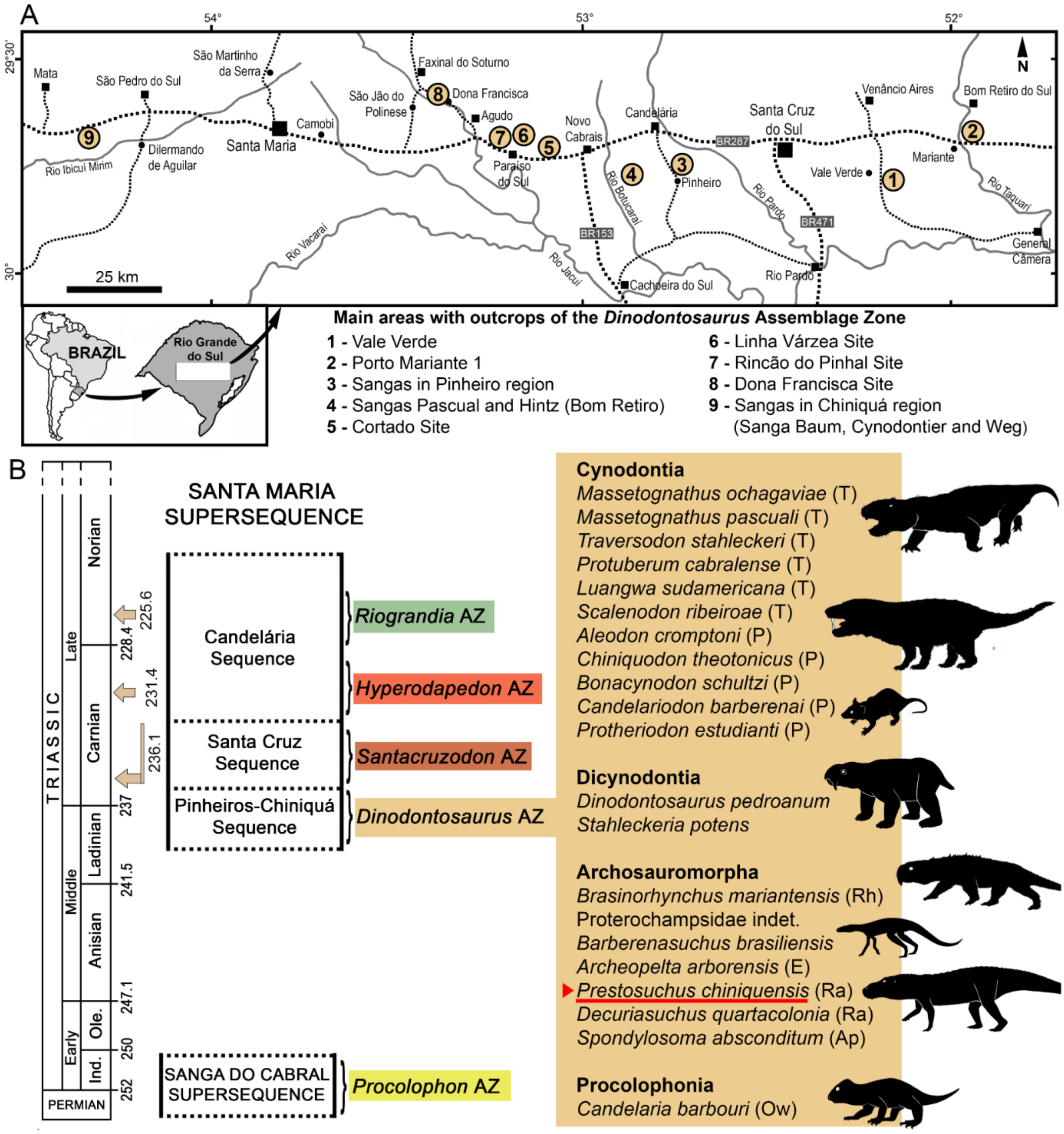

Figura 4 - Área geográfica de ocorrência (A) e arcabouço crono e bioestratigráfico (B) das unidades triássicas do sul do Brasil, listando os conteúdos fossilíferos das diversas cenozonas de vertebrados, com destaque para *P. chiniquensis*. Modificado de Schultz *et al*. (2021)

6. Discussão Integradora

Neste trabalho, estimamos a massa de *Prestosuchus chiniquensis* e a partir dos resultados obtidos, utilizando diferentes metodologias, interpretamos os dados sob a luz da paleoecologia do animal, fazendo um comparativo com organismos extantes e extintos com hábitos e morfologias semelhantes ao *P. chiniquensis*. Os resultados mais detalhados foram publicados no artigo anexo **"Estimating body mass and its implications for the paleoecology of *Prestosuchus chiniquensis* (Paracrocodylomorpha, Loricata)"**, no qual aprofundamos a discussão sobre a biomecânica, ecologia e morfologia do animal estudado.

De todo modo, podemos destacar entre os resultados obtidos:

- As massas obtidas de três metodologias específicas foram muito discrepantes em relação com as outras metodologias utilizadas, as quais demonstraram certa constância nos valores médios (entre 300 kg e 400 kg) para um animal com prováveis 4.5 m de comprimento total. Excluindo-se estas três metodologias que apresentaram valores significantemente fora da média, pudemos obter um valor médio de 365 kg para o *P. chiniquensis*.
- Com base na morfologia do esqueleto e nas estimativas de massa obtidas, entendemos que o espécime de *Prestosuchus chiniquensis* aqui estudado poderia apresentar uma postura bípede ocasional. Entretanto, é possível que seus membros torácicos contribuíssem para o suporte de sua massa corporal. E é plausível interpretar que o animal adotaria uma estratégia de emboscada ao caçar, incluindo a possível mudança de postura bípede e ortógrada ao praticar tais atividades.

7. Conclusões

Este trabalho deixa claro que a aplicação de apenas uma metodologia para a estimativa de massa de um animal extinto pode não se mostrar suficiente ou totalmente coerente. Fazendo um comparativo claro com a literatura citada no presente trabalho, a utilização de diversas metodologias de estimativas de massa proporciona um panorama muito mais completo acerca das possibilidades ecológicas, biomecânicas e morfológicas do animal estudado. Deve-se notar também que modelos digitais diferentes, utilizando diferentes softwares, apresentaram resultados ligeiramente diferentes, mas que foram em sua maioria concordantes entre si. Considerar que um espécime de *Prestosuchus chiniquensis* de 4,50 m de comprimento teria por volta de 365 kg não só se alinha com hábitos e morfologias externas de táxons extantes semelhantes como também parece plausível em comparação com outros rauissúquios já analisados com o mesmo fim, como *Postosuchus kirkpatricki* (Chatterjee, 1985) que possuía ecologia similar.

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Estimating body mass and its implications for the paleoecology of Prestosuchus chiniquensis (Paracrocodylomorpha, Loricata)

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Estimating body mass and its implications for the paleoecology of *Prestosuchus chiniquensis* (Paracrocodylomorpha, Loricata)

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Abstract

The use of mass estimates in paleontology is an extremely important tool for analyzing palaeoecological, biomechanical, physiological, behavior and morphological aspects of fossil animals. Taking this premise into consideration, the current work aims to present a series of different methodologies for estimating the body mass of the rauisuchid *Prestosuchus chiniquensis*, using mathematical regression equations (using specimen UFRGS-PV-0629-T), mathematical models (using a simplified mathematical model of a half-elipse) and volume calculations based on scale models (both *Prestosuchus chiniquensis* and *Postosuchus kirkpatricki*) of the animal studied. We sought to observe the plausibility of comparing the results obtained, taking into account the purpose and the material used, and their inference in the palaeoecology of the animal studied, with the aim of suggesting a possible hunting strategy, posture and cursorial speed of this animal, observing a parallel with published works on other rauisuchians and extant animals.

Keywords: *Prestosuchus chiniquensis*; body mass estimates; paleoecology.

1. Introduction

Prestosuchus is a fossil genus of large predatory archosaur whose remains are found in Mesotriassic (Ladinian) rocks from southern Brazil and Tanzania and which, together with *Luperosuchus fractus* from Argentina, represented the top of the trophic web in the southern portion of Gondwana at that time. In Laurasia, a very similar form (*Batrachotomus kupferzellensis*) is found in rocks of the same age in Germany.

The Brazilian species *Prestosuchus chiniquensis* Huene 1938, the subject of this study, is part of the *Dinodontosaurus* Association Zone (Schultz et al., 2021 - Fig.1), stratigraphically included in the Pinheiros-Chiniquá Sequence (Middle Triassic) of the Santa Maria Supersequence (Horn et al., 2014).

There are proposals for a second species, in Brazil, for the genus *Prestosuchus* (e.g. *P. loricatus* Huene 1938), but, in addition to being a controversial issue, the possible differences between the two do not include aspects related to body size, so this taxonomic issue becomes irrelevant to the study carried out here, which deals with the mass estimate for a specimen with an estimated size of 4.5m, based on an almost complete skeleton (UFRGS-PV-0629-T) attributed to *P. chiniquensis*. Thus, the target taxon of this study will henceforth be referred to simply as *Prestosuchus*.

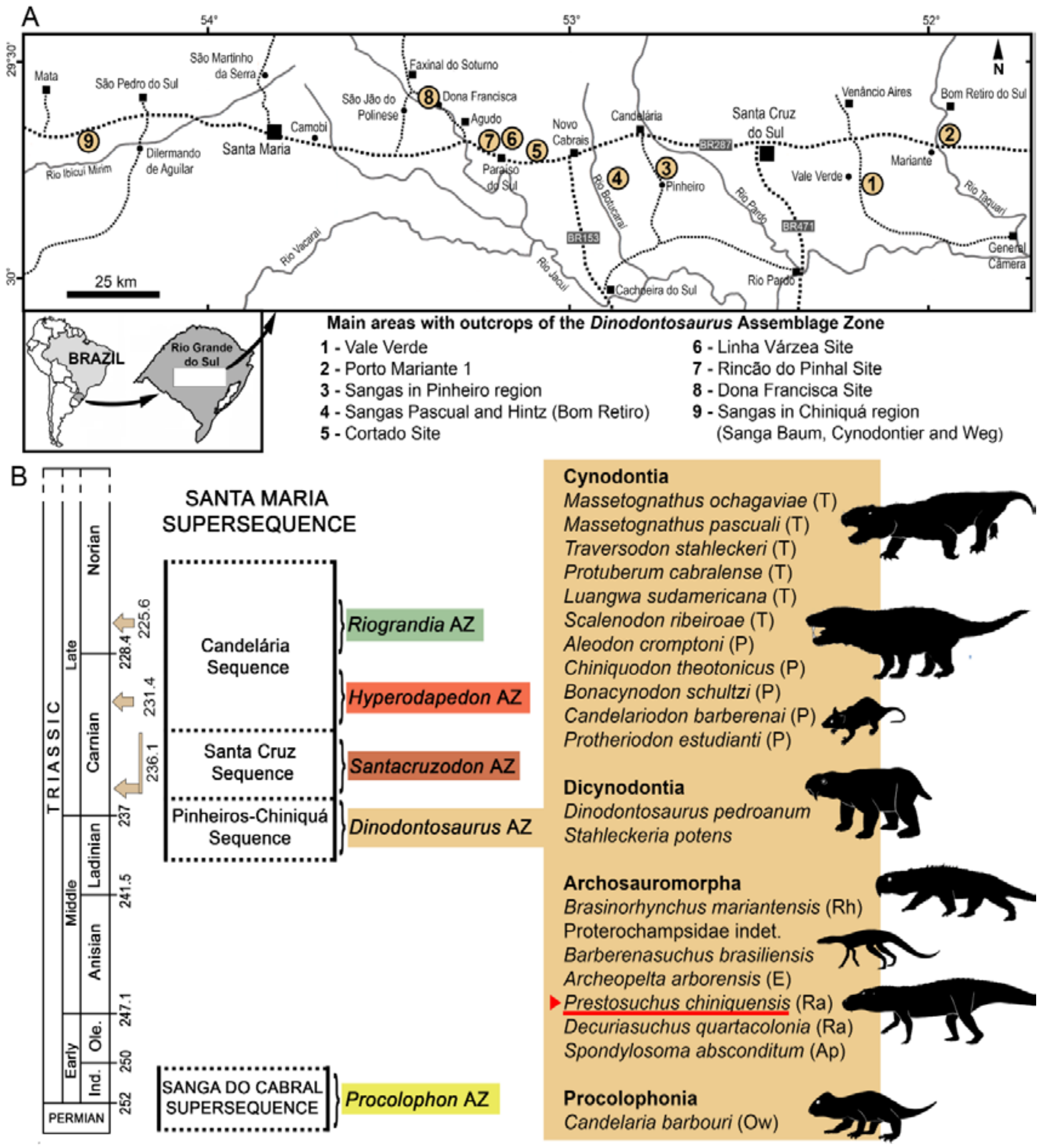

Figure 1 - Geographical area of occurrence (A) and chronostratigraphic and biostratigraphic framework (B) of the Triassic units of southern Brazil, listing the fossiliferous contents of the various vertebrate cenozones, with emphasis on *P. chiniquensis*. Modified from Schultz *et al.* (2021)

From a taxonomic point of view, *Prestosuchus* is commonly included in a heterogeneous group called "rauisuchians", which includes an assembly of taxa with different morphologies, including large quadruped predators (e.g.*, Prestosuchus, Batrachotomus, Postosuchus, Saurosuchus*), animals with elongated neural spines on the trunk, forming "sails" (such as *Arizonasaurus* and *Ctenosauriscus*), as well as dinosaur-like cursorial forms (such as *Effigia, Poposaurus* and *Shuvosaurus*). There is no consensus as to whether all "rauisuchians" belong to a monophyletic group or which of them could make up monophyletic subgroups. For example, using the phylogenetic hypothesis of Brusatte *et al.* (2010), the Brazilian species *Prestosuchus chiniquensis* would form a natural group with the German species *Batrachotomus kupferzelensis,* which in turn would be more closely related to the Argentinian species *Saurosuchus galilei* (Figure 2B). Following this, the phylogenetic hypothesis presented by Nesbitt (2011) shows a group formed by *Rauisuchus, Polonosuchus* and *Postosuchus,* which would be more closely related to crocodilomorphs (which includes present-day crocodiles) than to other rauisuchians, such as *Prestosuchus, Batrachotomus, Fasolasuchus and Saurosuchus* (Figure 2A).

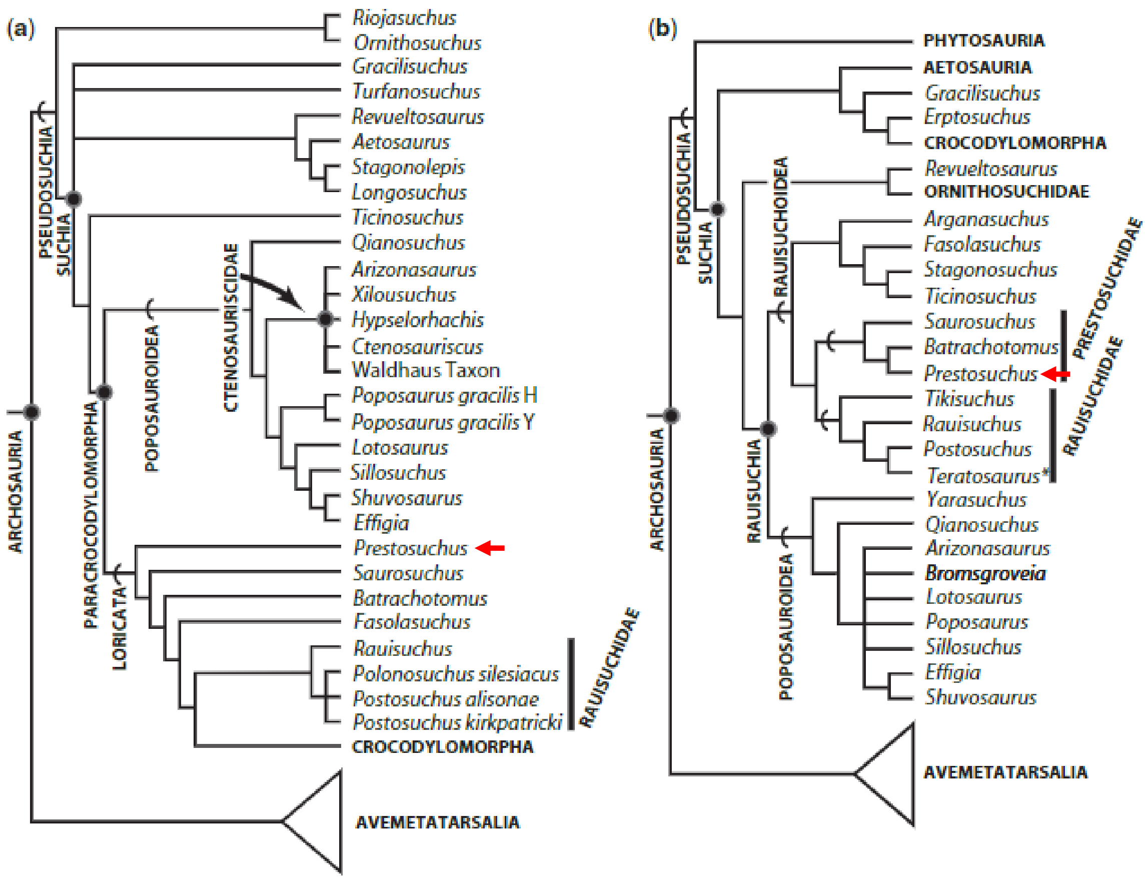

Figure 2 - Two phylogenetic hypotheses for the positioning of the "rauisuchians" (with emphasis on *Prestosuchus*) within Archosauria. A) Nesbitt (2011); B) Brusatte et al. (2010) with the addition of cnetosauriscids in Butler et al. (2011). Modified from Nesbitt (2013).

Regardless of its phylogenetic position, *Prestosuchus* are among the largest predators of the Mesotriassic, and some of the bones attributed to this taxon in Triassic collections in southern Brazil indicate that these animals could have reached lengths of about 8m. However, the estimation of their body mass (and the consequent biomechanical possibilities linked to it) is still the subject of more detailed studies, which is the main goal of this article.

Body mass is one of the most fundamental properties of an organism. Important aspects of physiology (metabolic rates, growth rates), biomechanical aspects (running speed, posture), ecology (population densities, ecological niches), and behavior (predation interactions, mating systems) are strongly influenced by body size (Schmidt-Nielsen, 1984 and references). Body mass is therefore a prerequisite for many studies within the field of comparative biology and is particularly well documented for living mammals and birds (Silva and Downing, 1995; Dunning, 2007), but the same cannot be said for reptiles and amphibians. An additional complicating factor for calculating this property in fossil organisms, which should always be considered, is that body mass varies significantly during an organism's life, in response to age, health, lactation (in mammals), gestation, food availability and other factors.

To infer these aspects in fossil specimens, therefore, an accurate mass estimate for the taxon in question is critical, but there is often no current analog that can be used as a parameter. In the case of the "rauisuchians" - and particularly *Prestosuchus* - the closest current group phylogenetically is the crocodiles, but these have a completely different body plan and biomechanics, as well as occupying a different ecological niche, hindering comparison. It is therefore necessary to use other types of approach, preferably more than one, to estimate their body mass.

As far as the paleoecology of *Prestosuchus* is concerned*, there is a* consensus among authors that its morphological characteristics (relatively tall and narrow skull, bearing wide, labio-lingually compressed zyphodont teeth, pointed and recurved) and its size (larger than any other component of the paleofauna in which it occurs) indicate that it was the top predator in the food chain, but there are different proposals regarding how it exercised this carnivory (whether by ambush or chase, how fast it could run, whether on 2 or 4 legs, etc.). Bearing in mind that among the "rauisuchia" there are both quadrupedal and bipedal forms, some authors have discussed the hypothesis that *Prestosuchus* could be an occasional biped. Liparini (2011), based on aspects of the morphology of the skeleton and an estimated body mass of 400 kg (for a 4.5 m long specimen), concluded that *Prestosuchus* would be a preferentially quadrupedal and cursorial form, and could reach a maximum speed of 40 km/h. However, with these parameters, it could also exercise an ambush hunting strategy, suddenly adopting a bipedal, orthograde posture, with some ventral arching of the spine, in an attempt to surprise the prey and capture it in the initial phase of the attack. Chatterjee (1985) postulated that *Postosuchus kirkpatricki* would have been the largest animal in the terrestrial communities of the Late Triassic of Dockum, Texas, USA, and that, due to its morphological and bony characteristics, such as a facultatively bipedal and erect posture, rapid movement and predatory dentition, it would have been the alpha predator of the ecosystem in which it lived, being able to feed on any organisms it could capture. According to Chatterjee (1985, p. 440), *Postosuchus kirkpatricki* had a predominantly ambush-type hunting strategy, also suggesting that this species could hunt in packs.

Liparini (2011) pointed out, however, that both the inference of speed and that of adopting an occasional bipedal posture would be directly related to the body mass estimate he obtained. Liparini (2011), however, points out that attention should be paid to the methodology used to make these estimates, as they can vary greatlyTaking into account different methodologies that cover animals of a similar size and behavior to *Prestosuchus*, such as crocodiles and large lizards like the Komodo dragon, Liparini (2011) concludes that the most realistic estimate for the *Prestosuchus* specimen mentioned above would be around 400 kg. Among the forms morphologically most similar to *Prestosuchus*, Chatterjee (1985, p. 432) estimated a mass of approximately 250 to 300 kg for *Postosuchus kirkpatricki, based* on a skeleton approximately 4 m long, inferring that the animal could occasionally assume a bipedal posture, in which it would reach a height of around 2 m. The author, however, did not specify the methodology he used to estimate the mass of the specimen studied.

2. Material and Methods

This paper will present and compare different methods for estimating the body mass of a 4.5 m long *Prestosuchus* specimen, discussing the different results obtained from each of the methods, in an attempt to evaluate which one represents the most appropriate for the case in question and, based on the estimated mass value, also discuss the postural and locomotor habits, as well as the most likely hunting strategy for this taxon. The choice of a standard size of 4.5 m for the application of the different methodologies is based on the existence of a partial skeleton of this species (UFRGS-PV-0629-T), which would have this estimated size, stored in the UFRGS Paleovertebrate collection (Figure 3).

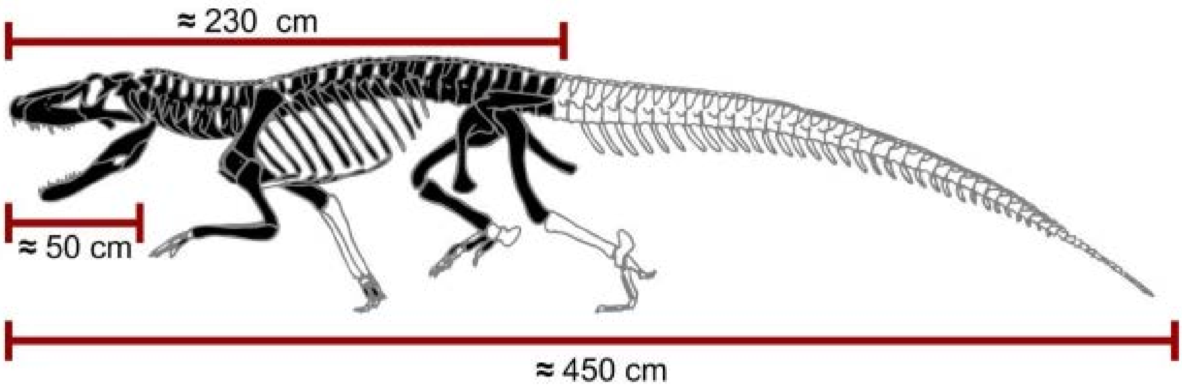

Figure 3 - Schematic representation of the *Prestosuchus* skeleton (based on specimen UFRGS-PV-0629-T) highlighting the preserved bones of the specimen (in black). Modified from Liparini (2011)

2.1 Most commonly used methods for obtaining mass estimates of extinct species

2.1.1 Regression equations

Before the advent of digital methods, which allow 3D reconstruction of fossil organisms, the most widely used method for estimating body mass in extinct vertebrates was "predictive" mathematical models based on mathematical regressions (Damuth & MacFadden. 1990 and references). In this method, the most commonly applied proxies for obtaining mass estimates use dental dimensions or the diameters of limb bones (Ruff 1988, 2003; Ruff et al. 1991). Dental proxies are most commonly used for mammals and are based on the direct relationship between food processing capacity and metabolism (which is mainly related to body mass), having the advantage of using the most identifiable and most "preservable" elements of a mammalian skeleton, the teeth. Limb proxies, on the other hand, have the advantage of depending more directly on the relationship between body mass and the load borne by the limbs as they support the animal's weight on dry land (Anderson, 2004). Multiple proxies are usually required for a robust estimate of mass in a fossil organism (Barbosa et al., 2023). Here, we applied a variety of ways in order to determine which of the various mass estimates would be the most reliable.

The dimensions used to estimate body mass are generally derived from elements subjected to weight support during locomotion, such as the circumferences of the femur and humerus (Anderson et al., 1985; Campione and Evans, 2012), the width of the femoral head (Ruff et al., 1991) and the diameter of the glenoid in flying birds (Field et al., 2013). Cranial measurements have also been used to estimate mass

(Aiello and Wood, 1994; Wroe et al., 2003; Spocter and Manger, 2007). Assuming that there is a proportionality between the size of some bones (for example, the femur and the humerus) and their mass, after establishing the equation that describes this relationship of proportionality, it is possible to estimate the mass of an individual with only the measurement of the bone needed to solve the established equation. Anderson et al. (1985), for example, after surveying the body masses of 33 species of quadruped mammals and recording the circumferences of their humeri and femurs, arrived at the following equation:

$$W = 0.078 \times (C)_{h+f}^{2,73} \text{ (Equation 1)}$$

where W is the mass in grams and C_{h+f} is the sum of the circumferences of the humerus and femur, in the middle portion of the diaphysis, in millimeters. Therefore, using the same principle, from the measurements of the circumferences of these two bones of a preserved fossil individual, it would be possible to estimate its mass. It should be considered, however, that such estimates may have limitations, depending on the fossil group studied, its phylogenetic relationship, ontogenetic stage and also its paleobiology.

Mass estimates based on regressions have some advantages over other alternatives. Because of their simplicity, allometric equations can be generated using direct measurements on the bones, with the use of calipers, thus requiring little training. Regression-based techniques are also highly objective, involving no assumptions regarding the "presumed" appearance of the fossil taxon. Perhaps most importantly, such estimation equations can be applied to incomplete fossil remains. However, there are also disadvantages to using such regression equations for mass estimates. The apparent simplicity and lack of training required for this method can increase the risk of misapplications or misinterpretations of statistical techniques (Smith, 1993; Kaufman & Smith, 2002; Smith, 2009). Furthermore, when more than one fossilized element is available for study, some degree of subjectivity is still required to determine which bone measurement will be used as a basis for mass estimation, and with which modern group their data will be calibrated and compared (Brassey, 2016).

2.1.2 Scale model

In *taxa* without good living analogues, several authors argue that the best method of estimating mass is to make a complete reconstruction of the skeleton, superimpose soft tissues on this reconstruction and estimate body mass based on the volume and estimated average density of the reconstructed model. This method, however, requires the existence of well-preserved skeletons and substantial modeling capacity, which involves some degree of subjectivity.

Several of the earliest published dinosaur mass estimates were derived from scale models. Gregory (1905) built a complete reconstruction of *Brontosaurus excelsus at* a scale of 1:16, after inferring the animal's external contours from its internal structure. The final model was immersed in water and its volume estimated by distension, then scaled back to its original size. To convert this volume to mass, the next stage necessarily requires an estimate of the animal's body density, which, for fossil taxa, can only be speculated. Colbert (1962) determined the volume of dinosaur scale models by displacing sand instead of water. Alexander (1985), for the first time, carried out a volumetric analysis attempting to quantify both the body mass and the center of mass of some dinosaur species, incorporating the hypothetical volumes of the lung cavities into the calculations. These different approaches demonstrate that mass predictions based on scale models undeniably involve a certain degree of artistic license in relation to the models and the positioning of soft tissues around the skeleton, so that are therefore subject to controversy.

2.1.3 Mathematical models

In cases where the majority of the skeleton has been recovered and in an undistorted state, a skeletal assemblage can be arranged, on which mathematical methods for calculating its volume can be applied, such as calculating the volume of a solid by Graphic Double Integration (GDI) (Hurlburt, 1999) or by 3D mathematical slicing (Henderson, 1999; Montani, 2001, Mazzetta et al., 2004). There are also proposals for approximating body volume to geometric shapes, such as the proposal by Seebacher et al. (1999) to estimate the volume of crocodiles by approximating their shape to that of a half ellipse. By multiplying this volume by the pre-selected general density of the animal's tissue, it is then possible to obtain its mass. Among the methods that do not involve a complete 3D digital reconstruction of the animal, these mathematical models may be one of the most accurate methods currently available, as they deal with complete or almost complete specimens.

Montani (2001) applied a method of estimating masses for vertebrates using silhouettes (obtained from the presumed outline of the animals, based on their skeletons), which were then transformed into three-dimensional computer models using specific visualization software, such as Paleomass (Montani, 2023). This method divides the animal's silhouettes into specific "slices" (e.g., head, trunk, tail, hind limbs, forelimbs), transforming each of these parts into ellipses, and then, from these, some equations for measuring areas and volumes are applied. The work uses current animals such as cetaceans and horses as parameters, noting that there is no possibility of testing the results for extinct animals. The author warns, however, that this methodology presents errors intrinsic to its purpose, as it assumes that ellipses can accurately simulate the natural shapes of vertebrate bodies and that not all these bodies have adequate cross-sections for the full application of this methodology.

2.2 Methodologies used to estimate the mass of Prestosuchus

In this study, we set out to estimate the mass of the UFRGS-PV-0629-T specimen, corresponding to a partially complete skeleton with an estimated total length of 4.5m. Based on the proportions of the bones, we applied 4 linear regression equations and a simplified mathematical model of a half ellipse, proposed by Seebacher et. al. 1999 (Table 1). In addition, estimates were made based on the calculation of the volumes of 3 paleoartistic scale models reconstructions of *Prestosuchus* and one of *Postosuchus kirkpatricki* (Figure 4).

Table 1: Regression equations and mathematical model used to estimate the mass of *Prestosuchus* specimen UFRGS-PV-0629-T. [1] Parameters recalculated from the data in the works cited. Abbreviations: **BM**, estimated body mass (in kg); **C_f**, circumference of the femur at the mid-diaphysis (in mm); **C_h**, circumference of the humerus at the mid-diaphysis (in mm); **d**, body density (in kg/m^3); **h**, pelvic girdle height (in m); **L_f** , total femur length (in mm); **SVL**, rostro-cloacal length (in cm); **TL**, total length (in mm).

Reference	Equation
Anderson et al. 1985	$BM = 7.9 \times 10^{-5} \times (C_h + C_f)^{2.75}$ [1]
Christiansen and Fariña 2004	$BM = 6.3 \times 10^{-7} \times {L_f}^{3.21}$ [1]
Farlow et al. 2005 [L]f	$BM = 1.6 \times 10^{-6} \times {L_f}^{3.35}$ [1]
Farlow et al. 2005 [TL]	$BM = 1.6 \times 10^{-10} \times TL^{3.39}$ [1]
Klein et al. 2005 and Jossep et al. 2006	$BM = 1.4 \times 10^{-5} \times SVL^{3.13}$ [1]

Seebacher et al. 1999	$BM = 0.5\pi d \times (h^2 + 5.19 \times 10^{-4} \times h + 8 \times 10^{-8})$

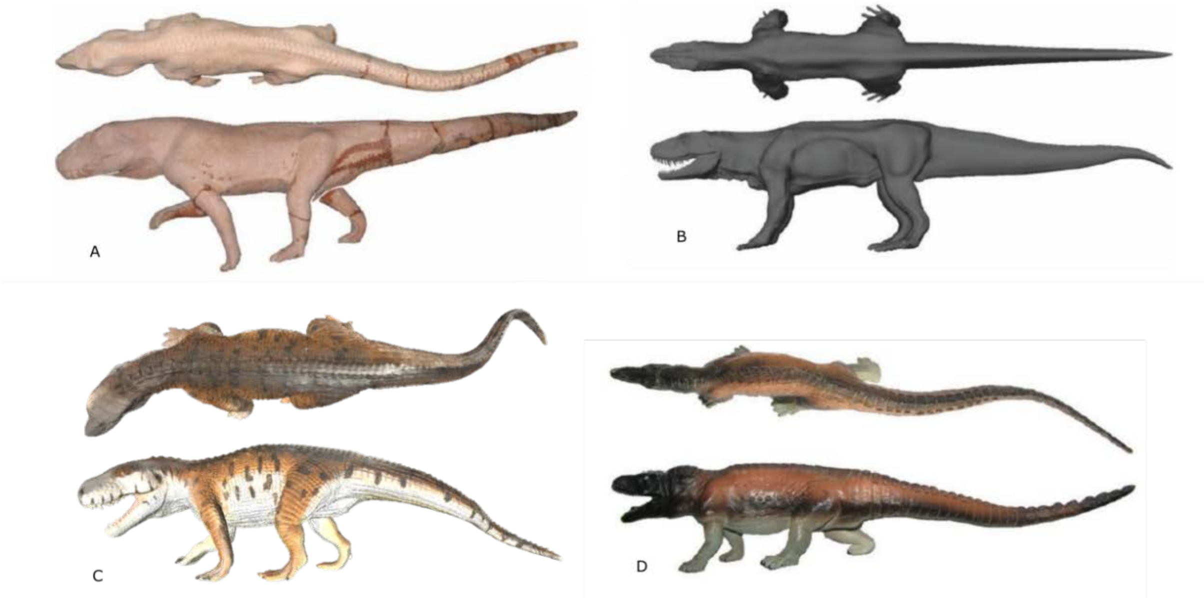

Figure 4 - Lateral and dorsal views of the scale models used to estimate the mass of specimen UFRGS-PV-0629-T. (A) Scale model of *Prestosuchus in* clay, made by Leonardo Morato; (B) 3D sculpture of *Prestosuchus*, produced entirely digitally by Adolfo Bittencourt; (C) scale model of *Prestosuchus in* plastic, produced by Safari Ltd.® and (D) commercial plastic model representing *Postosuchus*. The figures are not to scale.

The variables needed to solve the formulas were measured with a caliper, when smaller than 600 mm, or a tape measure directly on the UFRGS-PV-0629-T fossil, when larger than 600 mm (Table 2).

Table 2 - Measurements of fossil UFRGS-PV-0629-T, used to estimate the mass of *Prestosuchus*[1] estimated.

Parameter	**Size (mm)**
Pelvic girdle height [h]	500 mm
Circumference of the femur at the mid-diaphysis $[C]_f$	221 mm
Circumference of the humerus at the mid-diaphysis $[C]_h$	136 mm
Rostro-cloacal length [SVL]	2300 mm
Total length [TL]	4500 mm [1]

Total femur length $[L]_f$	462 mm
Body density	0.965 kg/L

Mass was estimated from the paleoartistic models by calculating the volume of the model, multiplying this volume by the model's volumetric scale factor (how many times smaller the model is than the organism was in reality) and finally multiplying this value by the body density assumed for the species. The volumetric scale of the model corresponds to the cube of the scale of the model's linear measurements. For example, the femur of the clay model was measured at 35 mm, while the measurement of the fossil femur of UFRGS-PV-0629-T is 462 mm, so the animal was approximately 13 times larger than the model that represents it (462 mm / 35 mm = 13). Therefore, the volumetric scale considered would be 13^3 = 2197 times, in which the volume calculated for the model would be 2197 times smaller than the real volume expected for the specimen under study.

To determine the scale factor of the physical models, linear measurements were taken of the length of the mandibular ramus, femur, humerus, width of the posterior portion of the cranial roof and the length from the most anterior portion of the skull to the start of the tail of the fossil material (assumed to be approximately the rostro-cloacal length). These measurements were then divided by the equivalent lengths of these same portions in the scale models. The measurements on the models were taken using a Mitutoyo 200 (+-0.05) mm caliper and the measurements on the fossil material were taken using a Mitutoyo 60 (+- 0.02) cm caliper. Each element was measured five times and the average value was used as a reference for calculating the factors. In the case of even elements (e.g., femur, humerus and mandibular ramus), when they were preserved, five measurements were taken on each side and the total average was used as a reference for the element. Each scale factor obtained separately was then added together and divided by the total number of individual factors used (n) - in this case 5 - to obtain an average scale factor.

Two of the physical scale models (Figure 4A and 4B) had their volumes calculated using an adaptation of the methodology proposed by Colbert (1962) in which a container was completely filled with fine sand - by shaking and lightly tapping the container on the bench so that the sand settled and occupied all the empty space - and leveled using a ruler. This determined volume of sand was then removed from the container, the model inserted, and the sand re-settled and leveled. The volume of excess sand was measured with a beaker and then recorded, which was equivalent to the volume of the model measured.

Next, a 3D digital model was obtained from the reduced scale model (about 12 cm long) made in solid plastic by Safari Ltd.®. This model was chosen as being representative of *Prestosuchus* because it was based on the proportions of the skeletons available for the species described in the literature, with the advice of paleontologists, including one of the authors of this study (CLS) (Figure 4C). The plastic model was scanned at the UFRGS Paleovertebrate Laboratory by Dr. Roland Sookias with an Artec Space Spider 3D Structured Light Scanner (Artec 3D a), to obtain a 3D digital model using the Artec Studio 17 Professional software (Artec b). The volume of the 3D model generated was calculated using a volumetric analysis tool in the Blender software® v 2.92.0.

In turn, the 3D scale model of *Prestosuchus* digitally reconstructed by Dr. Adolfo Bittencourt, from the UFRGS Arts Institute (Figure 4B) was created in a specific program (Autodesk Maya®, version 2008) for manipulating digital meshes in three dimensions. The average linear scale factor was calculated in the same way as shown above, using the equivalent measurements on the UFRGS-PV-0629-T fossil specimen. In this case, the volume of the model was obtained from the Autodesk Maya® program itself, which performs this calculation using the *computePolysetVolume* command.

Finally, to obtain the body mass of the material under study (BM), the actual volume of the animal must be multiplied by the body density assumed for this animal. Colbert (1962) used a value of d = 0.9kg/L for dinosaurs. Other authors assume a density equal to that of water, i.e. 1.0 kg/L (Alexander, 1989; Hurlburt, 1999), however, it has been observed in the literature that the limits of the densities of living terrestrial animals can be between 1.08 and 0.85 kg/L for adult and young crocodiles, respectively (Cott, 1961 apud Allen; Paxton; Hutchinson, 2009; Seebacher; Grigg; Beard, 1999; Allen; Paxton; Hutchinson, 2009), and 0.85 kg/L for birds such as the emu (Seebacher 2001). In the present work, we used the value of 0.965 kg/L, considering the average value, between the maximum values of 1.08 kg/L and minimum values of 0.85 kg/L described for living archosaurs, presented above.

The volumes calculated for each of the models and their volumetric scale factors are shown in Table 3 below.

Table 3 - Volumes and volumetric factors.

Model	Volume	Volumetric scale factor
In clay	0.273 L	1331
3D sculpture	0.119 L	3375
3D of *Prestosuchus* in plastic	0.087 L	3638
Physical plastic *Postosuchus*	0.079 L	5178

3. Results

Table 4 below summarizes the results for the estimated masses of individual UFRGS-PV-0629-T, using the different methods here presented.

Table 4: Masses estimated from different methods applied to the specimen of *Prestosuchus* UFRGS-PV-0629-T.

Method	Estimated mass (kg)
Anderson et al. 1985 *(Mathematical Regression)*	827
Christiansen and Fariña 2004 *(Mathematical Regression)*	225
Farlow et al. 2005 $[L]_f$ *(Mathematical Regression)*	1351
Farlow et al. 2005 [TL] *(Mathematical Regression)*	388
Klein et al. 2005 and Jossep et al. 2006 *(Mathematical Regression)*	345
Seebacher et al. 1999 *(Mathematical Model)*	379
Clay model of *Prestosuchus* *(Scale Model)*	351
Digital sculpture of *Prestosuchus* *(Scale Model)*	388

3D plastic model of *Prestosuchus* *(Scale Model)*	305
Plastic *Postosuchus* model *(Scale Model)*	395

The results show that the mass estimated for the UFRGS-PV-0629-T specimen of *Prestosuchus chiniquensis* showed a large discrepancy in three of the methodologies used (Table 4), the possible meanings of which will be discussed below. However, among the alternatives used to estimate the mass of a fossil animal, constancy between results is a good indication of a more coherent estimate. The methods applied here, despite having occasionally varied drastically in maximums and minimums, showed a remarkable constancy in the average values (between 300kg and 400kg) for an animal of probably 4.5m in total length. Except for the three methodologies that showed values significantly different from the mean, the average estimated mass for the specimen under study was 365 kg, with a standard deviation of just 32 kg, considering the application of 7 distinct and methodologically independent inferences. It is worth noting that all the estimates made using volumetric scale models, from a wide variety of contexts (see material and methods), showed an average of 360 kg for *Prestosuchus*. By understanding what each methodology represents and the objectives and restrictions of its application, it was possible to discuss each of the three discrepant results obtained.

4. Discussion

For comparison purposes, some reference values were selected for the weight of animals from different groups, with sizes or weights close to that estimated for the UFRGS-PV-0629-T specimen. Among living groups, the largest terrestrial lizard ever measured and published was a captive Komodo Dragon (*Varanus komodoensis*), with a total length of 2.75 m and a weight of 80 kg (Cioffi, 1999). Among crocodiles, Seebacher, Grigg and Beard (1999) recorded two specimens of saltwater crocodiles (*Crocodylus porosus*) with dimensions similar to the specimen studied here, one of which was 4.2 m long and weighed 383 kg and the other 4.6 m long and weighed 520 kg (Seebacher; Grigg; Beard, 1999). Webb and Manolis (1989) discussed that these animals rarely exceed 5.2 m and 500 kg, but that, nevertheless, a 6.7 m *C. porosus* has already been recorded, whose weight was estimated at 1,500 kg.

In the data presented by Farlow et al. (2005), there are two specimens of American crocodiles (*Alligator mississippiensis*) with lengths close to that of the *Prestosuchus* specimen in question. Both specimens are from captivity, with one having a total length of 4 m and 304 kg and the other, with a rostro-cloacal length of 2 m, weighing 277 kg (Farlow et al., 2005).

Among mammals, lions (*Panthera leo*), one of the largest terrestrial predators, have average masses of between 150 and 170 kg (Valkenburgh, 1990). The zebra (*Equus burchelli*) and the polar bear (*Ursus maritimus*) are among those whose recorded weights are around four hundred kilos. Anderson J., Hall-Martin and Russel (1985) recorded an average mass of 378 kg for zebras and 448 kg for polar bears.

An interesting comparison that can also be made is with the extinct lizard *Megalania prisca*, from the Pleistocene of Australia. This animal, described in 1859 by Richard Owen, has had its weight and total length estimated by different authors, with very different results. Hetch (1975) estimated a total length of 7 m and a body mass of between 600 and 620 kg for *M. prisca.* Auffenberg (1981) estimated a mass of 2,200 kg for a *M. prisca of* 4.5 m in total length. Using the specific regression equation for varanids calculated by Blob (2000), a *M. prisca* with a rostro-cloacal length of 2.3 m would have a mass of 97 kg (Wroe, 2002). Considerations on each of the methodologies employed, including some erroneous assumptions, were discussed by Wroe (2002) and will not be addressed here. However, the most recent estimates calculated for *M. prisca* are in the works by Burness, Diamond and Flannery (2001) and Wroe (2002), where the former estimated a mass of 380 kg for *M. prisca* - the size of which was not made explicit - while the latter estimated a mass of 331 kg for a *M. prisca* with an estimated total length of 4.5 m.

Comparing the data presented above, it seems reasonable to assume a weight of 365 kg for the *Prestosuchus* specimen analyzed here, considering that it is a terrestrial animal of approximately 4.5 m, with a general external morphology similar to that of large lizards or crocodiles.

Next, we will discuss why the application of regression equations based on mammals (Anderson J.; Hall-Martin; Russel, 1985), theropod dinosaurs (Christiansen; Fariña, 2004) and the length of crocodile femurs (Farlow et al., 2005) showed such divergent results for specimen UFRGS-PV-0629-T.

Using the regression equation, original or recalculated from the data of Anderson J., Hall-Martin and Russel (1985), the estimates for the mass of UFRGS-PV-0629-T were around 700 to 800 kg, practically double the value obtained by most other methodologies. It is important to note, however, that the data used by these authors to calculate the regression equation came entirely from quadruped mammals. Comparing the sum of the circumferences of the humerus and femur of the study material (i.e., 357 mm) with these same values in the mammal group, it was observed that it has values close to those of the giraffe (*Giraffa camelopardalis)* and the bison (*Bison* bison), with 365 mm and 359 mm respectively for the sum of the circumferences. These animals have an average body mass of 710 kg for giraffes and 1,179 kg for bison (Anderson J.; Hall-Martin; Russel, 1985).

This comparison makes it possible to reflect on some questions relating to the posture and resistance of the bones, as well as questions about the preservation of the fossil specimen itself. Biewener (1989), Blob (1999) and Blob and Biewener (1999, 2001) studied the distribution of efforts exerted on limb bones when animals such as mammals, lizards and crocodiles assume different postures (i.e., plantigrade, mesograde or orthograde, the latter of which can be somewhat "columnar", depending on the arrangement of the femoral head and the flexion of the joints). Larger mammals (> 200 kg), in order to maintain a safety factor against bone breakage, assume more columnar postures (i.e., flexing the knee and ankle joints less). By assuming this posture, these animals are able to keep their limbs more aligned with the ground reaction force, thus reducing the muscular efforts - which are proportional to the animal's weight - and, consequently, the force that the bones have to resist in order to counterbalance the force of the joint moments (Biewener, 1989).

Experimental data on the locomotor biomechanics of lizards and crocodiles has shown that the plantigrade or mesograde posture assumed by these animals results in greater torsion forces and lower flexion forces on their femurs, when compared to the orthograde posture of birds and mammals (Blob, 1999). In addition, the safety factor observed for this bone in lizards and crocodiles was higher than that normally found in birds and mammals. Finally, when these animals assume postures closer to orthograde, there are greater efforts on the pelvic limb bones, as the knee and ankle extensor muscles exert greater forces to maintain this posture, which is reflected on the bones (Blob; Biewener, 2001).

Considering that the posture of the animals most closely related to *Prestosuchus* would be orthograde, as suggested by several authors (Benton, 1984; Bonaparte, 1984; Kischlat, 2000, 2003; Parrish, 1986), but that they may not have had adaptations, such as those observed in larger mammals, to reduce the efforts exerted by the muscles on the limb bones, the same value for the sum of the circumferences of the humerus and femur in a terrestrial crurotarsian would be able to support, in a non-columnar orthograde posture, a smaller body mass than that of a mammal with a similar value for the sum of the circumferences of the stylopods (referring to the arm and thigh).

Thus, the femur of a rauisuchid, for example, with proportions equivalent to those observed in mammals, could only support a smaller body mass than that achieved by this other group. Therefore, what the equations obtained from the Anderson J., Hall-Martin and Russel (1985) data actually estimated was the body mass of a mammal with a humerus and femur similar in size to that of the UFRGS-PV-0629-T specimen, overestimating the mass that the latter would have.

Another aspect mentioned above, which could also be related to the value obtained for the estimated mass based on the data from Anderson J., Hall-Martin and Russel (1985), refers to the fossilization process to which the material was subjected. Considering the cracks observed in the fossil, it is possible that it may have undergone, to some degree, deformation as a result of the expansive diagenetic process (see Holz & Schultz, 1998) that commonly affects bones from the Brazilian Triassic, which may have altered (by more) its original volume. In this context, despite not appearing to have a high degree of deformation externally, only microscopic observation could determine whether or not this process has significantly affected the circumference of these bones.

As no other methodology took into account the circumference of the stylopods, it is not possible to compare whether the possibly overestimated mass was due to a different locomotor biomechanics between mammals and crurotarians, or whether it merely reflected a deformation (in diameter) of the thickness of the fossil, without a significant deformation of its long axis, since the estimates using the length of the femur - except for Farlow and collaborators (2005), which will be discussed below - apparently do not show such discrepant values.

If, on the one hand, the values estimated for the mass of UFRGS-PV-0629-T, based on data from Anderson J., Hall-Martin and Russel (1985), were considered to be overestimated, those obtained from data on femur length and the mass of alligators (Farlow et al., 2005), can be considered to be even more exacerbated. However, considering a variable other than femur length (i.e., total length), the same data seems to estimate a mass that would be close to the average value prevailing among the methodologies applied to the material under study (Table 4).

The explanation for this discrepancy may lie in the semi-aquatic habit of the animals used as parameters (crocodiles). Although no work has been found that deals directly with the relationship between the dimensions of the femur and the semi-aquatic habit of crocodiles, it has been observed that the relationship between the length of the femur and the total length in crocodiles is different from that shown by terrestrial species of lizards, for example.

The ratio between the length of the femur and the total length of a set of 85 crocodile specimens results in an average of 0.069 ±0.002, for a range of sizes between 70 cm and 4 m [value obtained from data by Farlow and collaborators (2005)]. Of these, 33 presented rostro-cloacal length values, with the average ratio of femur length to rostro-cloacal length being 0.136 ±0.008. Irschick and Jayne (1999) have provided some data that allows us to make some simple comparisons. From a set of 19 specimens, among 5 species of small lizards (total length between 12 and 17 cm), the average ratio of femur length to total length is 0.10 ±0.03 and that of rostro-cloacal length is 0.21 ±0.03.

This data may not be representative, as the sample obtained for comparison is small, but it does draw attention to a possible pattern. The femur of crocodiles is relatively smaller, in relation to the size of the animal, when compared to quadruped land animals with similar general external morphology. This distinction could be explained by the fact that these animals have a semi-aquatic habit and do not have to support their entire weight whenever they move, unlike terrestrial animals. This would allow femurs of the same size to support larger body masses in animals with aquatic habits, when compared to their terrestrial analogues.

This hypothesis becomes more plausible when we compare the linear measurements of specimen UFRGS-PV-0629-T with those of current crocodiles. The largest crocodile with a rostro-cloacal length recorded in Farlow et al. (2005) data has this measurement equal to 2 m, while the specimen studied here has a rostro-cloacal length of 2.3 m. The difference in femur size between the two species is much more significant, with the RWR 22 crocodile measuring 262 mm and the prestosuchid 462 mm. Using the linear regression equations that relate total length and rostro-cloacal length to femur length (Farlow et al., 2005), a crocodile with a femur of 462 mm would have an estimated total length of approximately 7 m and a rostro-cloacal length close to 3.5 m. This would not be the case for the RWR 22 crocodile. This would be quite different with the specimen under study, because, although the total length was estimated, the approximate rostro-cloacal length was measured directly from the material, which shows this region completely preserved and would not exceed 2.5 m. A complementary fact is that the ratio between the length of its femur and the rostro-cloacal length is equal to 0.20 - a value within the average calculated for terrestrial lizards, mentioned above, and outside that calculated for crocodiles.

Therefore, it is possible that the mass estimated for specimen UFRGS-PV-0629-T based on the length of its femur is actually representing the mass of a crocodile approximately 7 meters long. It would be more coherent to consider the specimen under study as having a body mass closer to that of a crocodile approximately 4.5 meters long. This value would be represented by the estimate made from the ratio between the total length of crocodiles and their mass (Table 4).

The last methodology discussed individually in this section is the one obtained using data from Christiansen and Fariña (2004). The values estimated by both the original equation and the recalculated one seem to have resulted in underestimated values when compared to the results obtained using the other methodologies. The divergence between the results observed may be due to the fact that the equations drawn up by Christiansen and Fariña (2004) aimed to estimate the mass of a specific group of dinosaurs (i.e., theropods) which, despite having a wide range of sizes - somewhere between 2 and 13 m - are relatively restricted in terms of posture, all being exclusively bipedal.

Quadruped animals tend to have functional specializations between the thoracic and pelvic limbs. While the former specializes in weight-bearing, with a non-longitudinal arrangement of muscle fibers capable of absorbing energy better, generating more force at higher speeds with less muscle volume, the latter specialize in propulsion (power), with greater muscle volume and greater contraction capacities, allowing the animal's body to accelerate more (Jayes; Alexander, 1978; Smith et al. 2006). Bipedal animals, on the other hand, do not have such specializations, as the pelvic limb performs both the function of accelerating the body and supporting the animal's weight (Smith et al., 2006). This possibly alters the relationship that the body mass of a biped or quadruped would have on each of the limb bones.

Therefore, considering equations that demonstrate the relationship between the mass and morphology of the femur of a bipedal animal, such as those published by Christiansen and Fariña (2004), could disregard the relationship that the humerus represents in supporting the animal's weight. In this sense, a bipedal animal with a femur of the same length as that of a quadruped could have a lower body mass, since all its weight would have to be supported by this bone, and this weight would not be shared with the humerus, as occurs in quadrupeds.

There is no consensus on the posture of the rauisuchids, with some species considered strictly quadrupedal, such as *Ticinosuchus ferox,* and others strictly bipedal, such as *Effigia okeeffeae*. In turn, *Postosuchus* spp. has already been interpreted and reconstructed as having a bipedal (Parrish, 1986; Weinbaum, 2008) or quadrupedal posture (Peyer et al., 2008).

Based on the morphology of its skeleton and the mass estimates obtained, we understand that the *Prestosuchus* specimen studied here could occasionally have a bipedal posture (Liparini 2011); however, it is possible that its thoracic limbs contributed to supporting its body mass. Therefore, it would be acceptable to consider that a regression equation relating mass to femur length, based only on bipedal species, is actually underestimating the mass of the study material considered.

Some studies, which in addition to estimating the mass of extinct forms calculate their center of mass, consider the effect that the volume occupied by the lungs would have on these estimates (Alexander, 1985; Henderson, 1999). In this study, it was decided not to consider this variable for two reasons: (i) to calculate the mass from the volume of the animal, the influence of the lungs is already considered in the density value, or else a density close to 1.11 kg/L should be considered for a total volume that disregards the space occupied by the lungs (Alexander, 1985); (ii) reducing the volumes obtained for the scale models by 10% - to disregard the space occupied by the lungs, which would already be an overestimated volume compared to the values observed in actual species (Gans; Clark, 1976; Gehr et al., 1981) - the mass values remain between the 300 and 400 kg estimated using the other methodologies, in which the volume of the lungs does not interfere.

Other estimated values for the mass of the specimen studied could be obtained by applying some other existing methodologies for estimating the mass of extinct forms (e.g., Gunga et al., 2007; Henderson, 1999; Hutchinson; Ng-Thow-Hing; Anderson, F., 2007).

Based on 3D "slices" obtained from the lateral and dorsal contours of reconstructions of extinct species, Henderson (1999) proposed a mathematical/computational model to calculate the volumes and centers of mass of these species. The results obtained by Henderson (1999), when estimating the mass and center of mass of current forms whose values for these variables were already known, indicated that this is an efficient methodology for estimating these variables in fossil forms.

Hutchinson, Ng-Thow-Hing and Anderson, F. (2007) used an adaptation of Henderson's (1999) proposal, in which they developed an algorithm to calculate various variables - such as center of mass, volume and moments of inertia - of a body segment fitted to a 3D solid whose properties (e.g., density) can be adjusted. This algorithm proved efficient in modeling and estimating the variables of the trunk segment of an ostrich and was then applied to describe some biomechanical properties of *Tyrannosaurus rex*.

Finally, Gunga and colleagues (2007) estimated the mass - among other variables - of a prosauropod dinosaur (*Plateosaurus engelhardti*) based on a 3D reconstruction of the complete skeleton digitized using a laser scanner. This methodology avoids the discrepancies observed in the scaling factors calculated for each element, more faithfully maintaining the proportions of the extinct taxon.

These methodologies would undoubtedly help to increase the comparisons made here; however, it was not possible to apply them in this work due to the deadline set for its end, and this will have to be done in a future publication.

5. Conclusion

Looking at the results obtained in this study, it is clear that applying just one methodology to estimate the mass of an extinct animal may not be sufficient or entirely coherent. Making a clear comparison with the literature cited in this paper, the use of different mass estimation methodologies provides a much more complete overview of the ecological, biomechanical and morphological possibilities of the animal studied. It should also be noted that different digital models, using different software, presented slightly different results, but were mostly in agreement with each other. Considering that a 4.50 m long specimen of *Prestosuchus chiniquensis* would be around 365 kg not only aligns with the habits and external morphologies of similar extant taxa, but also seems plausible in comparison with other rauisuchids already analyzed for the same purpose, such as *Postosuchus kirkpatricki* (Chatterjee, 1985), which had a similar ecology

As a concluding thought, it's safe to infer that, based on all that's been discussed on this paper about the probable body mass of the animal, it's reasonable to assume that *Prestosuchus chiniquensis* would adopt the ambush hunting strategy that was previously suggested by Liparini (2011), including the occasional bipedal and orthograde posture during forage activities.

6. Acknowledgements

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Parte III

Anexos

Tabela 1 - Equações de regressão e modelo matemático aplicados para estimar a massa do espécime UFRGS-PV-0629-T de *Prestosuchus*. [1] Parâmetros recalculados a partir dos dados dos trabalhos citados. Abreviações: BM, massa corporal estimada (em kg); C_f, circunferência do fêmur na porção média da diáfise (em mm); C_h, circunferência do úmero na porção média da diáfise (em mm); d, densidade corpórea (em kg/m^3); h, altura da cintura pélvica (em m); L_f, comprimento total do fêmur (em mm); SVL, comprimento rostro-cloacal (em cm); TL, comprimento total (em mm).

Referência	**Equação**
Anderson et al. 1985	$BM = 7.9 \times 10^{-5} \times (C_h + C_f)^{2.75}$ [1]
Christiansen and Fariña 2004	$BM = 6.3 \times 10^{-7} \times {L_f}^{3.21}$ [1]
Farlow et al. 2005 [L]f	$BM = 1.6 \times 10^{-6} \times {L_f}^{3.35}$ [1]
Farlow et al. 2005 [TL]	$BM = 1.6 \times 10^{-10} \times TL^{3.39}$ [1]
Klein et al. 2005 and Jossep et al. 2006	$BM = 1.4 \times 10^{-5} \times SVL^{3.13}$ [1]
Seebacher et al. 1999	$BM = 0.5\pi d \times (h^2 + 5.19 \times 10^{-4} \times h + 8 \times 10^{-8})$

Tabela 2 – Medidas do fóssil UFRGS-PV-0629-T, usados para estimar a massa do *Prestosuchus chiniquensis,* [1] estimado.

Parâmetro	**Medida (mm)**
Altura da cintura pélvica [h]	500 mm
Circunferência do fêmur na porção média da diáfise [C_f]	221 mm
Circunferência do úmero na porção média da diáfise [C_h]	136 mm
Comprimento rostro-cloacal [SVL]	2300 mm
Comprimento total [TL]	4500 mm [1]
Comprimento total do fêmur [L_f]	462 mm
Densidade corpórea	0.965 kg/L

Tabela 3 - Volumes e fatores volumétricos.

Modelo	**Volume**	**Fator de escala volumétrico**
Em Argila	0.273 L	1331
Escultura 3D	0.119 L	3375
Prestosuchus em plástico	87.673 L	3.638
Postosuchus em plástico	0.079 L	5178

Tabela 4 - Massas estimadas a partir de diferentes métodos aplicado ao espécime de *Prestosuchus* UFRGS-PV-0629-T.

Método	**Massa estimada (kg)**
Anderson et al. 1985 *(Regressão matemática)*	827
Christiansen and Fariña 2004 *(Regressão matemática)*	225
Farlow et al. 2005 [L]$_f$ *(Regressão matemática)*	1351
Farlow et al. 2005 [TL] *(Regressão matemática)*	388
Klein et al. 2005 and Jossep et al. 2006 *(Regressão matemática)*	345
Seebacher et al. 1999 *(Modelo matemático)*	379
Modelo em argila de *Prestosuchus* *(Modelo em escala)*	351
Escultura digital de *Prestosuchus* *(Modelo em escala)*	388

Modelo 3D plástico de *Prestosuchus (Modelo em escala)*	305
Modelo plástico de *Postosuchus (Modelo em escala)*	395

ANEXO I

Título da Dissertação:

"ESTIMATIVAS DE MASSA CORPORAL E SUAS IMPLICAÇÕES PARA A PALEOECOLOGIA DE PRESTOSUCHUS CHINIQUENSIS (PARACROCODYLOMORPHA, LORICATA) DO TRIÁSSICO DO RS."

Área de Concentração: Paleontologia

Autor: **Silvio Marques de Jesus Vieira**

Orientador: Prof. Dr. Cesar Leandro Schultz

Examinador: Prof. Dr. Mario Trindade Dantas

Data: 20 de novembro de 2023

Conceito: A

PARECER:

A dissertação está bem escrita, apresenta um forte arcabouço teórico, e explora bem as metodologias existentes para sugerir a massa corporal de uma espécie extinta. Acredito que poderiam propor uma regressão para massa corporal usando dados de lagartos atuais, e testar se ela é eficiente também. Seria uma novidade interessante ao trabalho. Como correções, sugiro que o discente se policie para construir parágrafos menores e revise o inglês que em muitos pontos esta confuso no artigo.

Assinatura: Data: 21/11/2023

Ciente do Orientador:

Ciente do Aluno:

ANEXO I
Título da Dissertação:
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Área de Concentração: Paleontologia
Autor: **Silvio Marques de Jesus Vieira**
Orientador: Prof. Dr. Cesar Leandro Schultz
Examinador: Dr. Marcel Baeta Lacerda Santos
Data: 04/11/2023
Conceito: D (insuficiente)
PARECER: Ver Arquivo em Anexo
Assinatura: Data: 04/11/2023
Ciente do Orientador: Ciente do Aluno:

ANEXO I

Título da Dissertação:

"ESTIMATIVAS DE MASSA CORPORAL E SUAS IMPLICAÇÕES PARA A PALEOECOLOGIA DE PRESTOSUCHUS CHINIQUENSIS (PARACROCODYLOMORPHA, LORICATA) DO TRIÁSSICO DO RS."

Área de Concentração: Paleontologia

Autor: **Silvio Marques de Jesus Vieira**

Orientador: Prof. Dr. Cesar Leandro Schultz

Examinadora: Profa. Dra. Bianca Martins Mastrantonio

Data: 14/11/2023

Conceito: C

PARECER:

A presente dissertação de mestrado apresenta um tema de grande relevância para o estudo dos arcossauros triássicos, em especial para o táxon *Prestosuchus chiniquensis*. No entanto, o texto apresenta diversos problemas, desde a estrutura do texto até a falta de referências importantes para o assunto. Considero fundamental realizar alguns ajustes para a publicação definitiva do artigo. As sugestões estão detalhadas no arquivo da dissertação que irei encaminhar.
Atenciosamente,

Assinatura: Data:14/11/2023

Ciente do Orientador:

Ciente do Aluno: