UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
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NEOICNOLOGIA DOS FLAMINGOS (AVES, PHOENICOPTERIDAE): ESTRUTURAS BIOGÊNICAS, COMPORTAMENTO PRODUTOR, TAFONOMIA E IMPLICAÇÕES PALEOAMBIENTAIS

ANDRÉ BARCELOS SILVEIRA

ORIENTADOR – Prof. Dr. Cesar Leandro Schultz
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Assim, as questões mais fundamentais são: Qual é a função específica representada pelo traço? Como isso mudará à medida que o organismo traçador for influenciado por outros estímulos genéticos, fisiológicos ou ecológicos? Em quais fácies isso provavelmente ocorrerá? E quais viéses de preservação são capazes de modificar o registro fóssil desse comportamento e sua distribuição ambiental? Abordado deste ponto de vista, o presente é de fato uma chave para o passado icnológico e vice-versa.

Frey & Seilacher (1980)

DEDICATÓRIA

Cris, Neusa, Sofi, Mia e aos oprimidos do mundo (humanos e não humanos).

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Enfim, aqui chegamos! Nestes SEIS anos de doutorado, o mundo era de um jeito no começo e, hoje, está irremediavelmente mudado. Assim como meus colegas e professores, a vida acadêmica e pessoal foi sacudida (para dizer o mínimo) por pandemia, radicalização política, crise econômica interminável e, agora, no finalzinho, a mão voraz do poder econômico imperialista abre as portas da Terceira Grande Guerra. Concluir uma tese nestas condições é algo para ser lembrado, comemorado e agradecido ao esforço extra-humano daqueles que me apoiaram e não deixaram cair a peteca.

A lista é longa, com certeza esquecerei alguém.

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RESUMO

Os flamingos são aves filtradoras que empregam diferentes métodos de forrageio, produzindo grande diversidade de estruturas biogênicas. O pisoteio rotatório é um comportamento de forrageio que produz uma estrutura complexa, consistindo de um montículo central circundado por uma depressão. Embora conspícuas e abundantes, estas estruturas são desconhecidas para o registro fóssil relacionado aos flamingos, predominando as pegadas fósseis. Descrições precisas dessas estruturas são escassas, assim como suas implicações para o registro fóssil. Desta forma, a presente tese visa preencher esta lacuna no conhecimento da icnologia dos flamingos, descrevendo as estruturas sedimentares biogênicas resultantes do pisoteio, a sequência de movimentos responsável por sua produção, sua possibilidade de preservação e sua distribuição conforme variáveis taxonômicas e ambientais. Realizou-se observações de campo tanto do comportamento dos flamingos quanto das estruturas registradas, juntamente com uma extensa revisão bibliográfica e análise de vídeos em plataformas eletrônicas de ciência cidadã. Em um sistema deposicional lagunar-barreira, as estruturas de pisoteio produzidas por flamingos-chilenos (*Phoenicopterus chilensis*) apresentaram uma variedade de morfologias relacionadas ao tipo de agente tafonômico e ao grau de alteração decorrentes, evidenciando que estruturas formadas em ambientes de baixa energia próximas a uma fonte de sedimento eólico são rapidamente soterrados, aumentando suas chances de preservação com boa fidelidade morfológica. O banco de dados de registros de literatura e vídeos indica que os flamingos tendem a utilizar o pisoteio com mais frequência em ambientes costeiros, especificamente lagoas salobras de profundidades de água muito rasas (~22 cm) e ligeiramente alcalinas (~7,8 pH), contrastando com o padrão de rastros fósseis de flamingos encontrados principalmente em depósitos continentais e lacustres. Este estudo demonstra que estruturas conspícuas e com razoáveis probabilidades de preservação podem caracterizar a atividade de flamingos ancestrais não apenas em sistemas lacustres de alta salinidade, mas também em diversos outros tipos de habitat de águas rasas e com variáveis níveis de salinidade e alcalinidade, expandindo o rol de fácies possíveis de preservar icnocenoses relacionadas ao icnogênero *Phoenicopterichnum*. Com a presente tese, espera-se contribuir para a inserção dos flamingos como organismos-modelo no estudo e teste de hipóteses icnológicas.

Palavras-chave: Icnologia, flamingos, tafonomia, comportamento, paleoambiente.

ABSTRACT

Flamingos are filter-feeder birds that employ different foraging methods, producing a great diversity of biogenic structures. Rotating stamping is a foraging behavior that produces a complex structure consisting of a central mound surrounded by a peripheral trench. Although conspicuous and abundant, these structures are unknown in the flamingo fossil record, where fossil footprints predominate. Precise descriptions of these structures are scarce, as are their implications for the fossil record. This thesis therefore aims to fill this gap in the knowledge of flamingo ichnology by describing the biogenic sedimentary structures resulting from trampling, the sequence of movements responsible for their production, their possibility of preservation and their distribution according to taxonomic and environmental variables. Field observations were made of both the flamingos' behavior and the structures recorded, along with an extensive literature review and analysis of videos on electronic citizen science platforms. In a lagoon/barrier depositional system, the stamping structures produced by Chilean Flamingos (*Phoenicopterus chilensis*) showed a variety of morphologies related to the type of taphonomic agent and the resulting degree of alteration, showing that structures formed in low-energy environments close to an aeolian sediment source are quickly buried, increasing their chances of preservation with good morphological fidelity. The database of literature and video records indicates that flamingos tend to use trampling more frequently in coastal environments, specifically brackish lagoons with very shallow (~22 cm) and slightly alkaline (~7.8 pH) water depths, in contrast to with the pattern of fossil flamingo tracks found mainly in continental and lacustrine deposits. This study demonstrates that conspicuous structures with reasonable preservation probabilities can characterize ancestral flamingo activity not only in high salinity lake systems, but also in many other types of shallow water habitats with varying levels of salinity and alkalinity, expanding the list of possible facies for preserving ichnocenoses related to the ichnogenus *Phoenicopterichnum*. With this thesis, we hope to contribute to the inclusion of flamingos as model organisms in the study and testing of ichnological hypotheses.

Keywords: Ichnology, flamingos, taphonomy, behavior, paleoenvironment.

LISTA DE FIGURAS

SUMÁRIO

ESTRUTURA DA TESE

Esta tese de doutorado está estruturada em um artigo publicado no periódico Journal of South American Earth Sciences classificado no Estrato PPGGeo N3 e um artigo submetido ao periódico Palaeogeography, Palaeoclimatology, Palaeoecology classificado no Estrato PPGGeo N1. A organização da tese compreende os seguintes capítulos:

Parte 1 - Texto Integrador composto pelos seguintes capítulos: a) introdução com a formulação do problema de investigação e a hipótese; b) objetivos da pesquisa; c) o estado da arte do tema da pesquisa; d) os materiais e métodos utilizados; e) o contexto geológico da área e do objeto de estudo; f) resumo dos principais resultados obtidos, interpretações desenvolvidas nos artigos e discussão integradora dos resultados; g) conclusões; h) referências bibliográficas.

Parte 2 - Corpo Principal da Tese, constituído dos artigos conforme o item 1.2 da Norma 118 do Programa de Pós-Graduação em Geociências da Universidade Federal do Rio Grande do Sul.

PARTE I

1. INTRODUÇÃO

Os traços fósseis (icnofósseis) são frequentemente a única fonte de informação em paleobiologia e paleoecologia, uma vez que ocorrem em estratos sedimentares onde os fósseis corporais (somatofósseis) estão ausentes, são raros ou de baixa qualidade de preservação (Bromley, 1996; Hasiotis, 2004; Lockley *et al*., 2006). A interpretação dos sinais biológicos e ecológicos contidos nos icnofósseis atinge maior acurácia quando apoiada em análogos modernos, que estabelecem uma base empírica para a relação entre morfologia, comportamento e interações substrato-organismo (Lyman, 1994; Drumheller & Brochu, 2016). Para incrementar a acurácia de tais inferências, o conjunto de dados atualísticos deve ser o mais representativo possível das interações substrato-organismo entre a biota moderna e suas estruturas biogênicas. No entanto, muitos estudos baseiam-se em amostras taxonômicas limitadas, diminuindo o potencial preditivo das observações atualísticas em reconstruções paleoambientais, paleoecológicas e paleobiológicas (Drumheller & Brochu, 2016; Zonneveld, 2016). Como tal, é do maior interesse amostrar clados pouco conhecidos a fim de completar o levantamento atualístico, bem como descrever estruturas de morfologia incomum, relacionadas com comportamentos algo negligenciados (Catena & Hembree, 2014; Melnyk et al., 2022a). Estes traços modernos díspares podem contribuir para a compreensão de vestígios fósseis de difícil interpretação, incrementando a reconstituição dos paleoambientes e a história evolutiva das adaptações dos organismos antigos que neles viveram.

Os flamingos (Phoenicopteriformes, Phoenicopteridae) são uma linhagem de aves aquáticas adaptada a uma dieta filtradora, de longa história evolutiva e rico registro fóssil (~55 Ma) (Mayr, 2022). Porém, ainda há lacunas na compreensão de questões como a evolução do aparelho filtrador e a notória adaptação dos flamingos a ambientes de alto estresse. Neste sentido, os traços fósseis podem fornecer informação adicional, já que representam indícios da presença e do comportamento de flamingos ancestrais em depósitos onde os restos corporais são escassos ou ausentes. Desta forma, o conhecimento da variedade de estruturas produzidas por estas aves na atualidade auxilia na interpretação dos traços fósseis relacionados à sua linhagem.

Para além dos ninhos, as estruturas biogênicas produzidas pelas aves modernas têm recebido comparativamente pouca atenção, e poucas foram colocadas numa perspectiva filogenética e paleobiológica (Genise et al., 2009; Brewer & Falk, 2020). Sendo aves especializadas em alimentação por filtração, os flamingos passam a vida em constante utilização de substratos brandos, quer como fontes de alimento, quer como material de nidificação, o que lhes permite produzir uma variedade de traços (Rooth, 1965; Scott *et al*., 2012; Brown *et al*., 2021). Em ambientes de águas pouco profundas, os flamingos empregam habitualmente um comportamento conhecido como “stamping” (tentativamente traduzido nesta tese como “pisoteio”), em que a ave assume a típica postura de cabeça baixa e perturba o substrato com movimentos vigorosos e contínuos dos pés (Hainard, 1932; Rooth, 1965; Delfino & Carlos, 2021; Barcelos-Silveira *et al*., 2023). Durante estes movimentos, a ave tanto pode permanecer em um único ponto, mantendo-se na posição (“standing stamping” ou pisoteio estacionário), quanto deslocar-se para a frente ou para trás (“dislocating-stamping” ou pisoteio em deslocamento), ou ainda girar no sentido horário ou anti-horário no mesmo ponto (“rotating-stamping” ou pisoteio rotatório) (Rooth, 1965; Cifuentes, 2007; Johnson & Cézilly, 2007; Delfino & Carlos, 2021, 2022; Barcelos-Silveira *et al*., 2023). Todas estas variantes parecem ser fases diferentes da mesma técnica de forrageio; alguns autores referem que tanto o pisoteio estacionário quanto o pisoteio em deslocamento podem passar para o pisoteio rotatório, aparentando ser fases exploratórias deste último (Ingraham, 1896; Cifuentes, 2007).

O comportamento de pisoteio tem como função a exposição de organismos enterrados no substrato (Allen, 1956; Macnae,1960; Bildstein *et al*., 1991; Jonhson & Cézilly, 2007; Béchet *et al*., 2017). Apesar da alta energia gasta nesse método, a ave pode maximizar seu ganho de energia pela ingestão de presas de difícil acesso e caloricamente recompensadoras (Deville *et al*., 2013). Como muitos comportamentos estereotipados nessas aves gregárias (Figura 1), o pisoteio é realizado por bandos em uníssono, o primeiro indivíduo provocando o comportamento nos demais (Bildstein *et al*., 1991), criando assim uma superfície sedimentar altamente bioturbada por grandes extensões de terreno (Figura 2). A elevada atividade de bioturbação implica que os flamingos são engenheiros do ecossistema que desempenham papéis importantes na estrutura das comunidades bentônicas, bem como nas propriedades físicas dos seus ambientes (Glassom & Branch, 1997; Esté & Casler, 2000; Cifuentes, 2007; Lee & Mayorga-Dussarrat, 2016; Gihwala *et al*., 2017; El-Hacen *et al*., 2019; du Plessis & Pillay, 2022).

Figura 1. Flamingos-chilenos (*Phoenicopterus chilensis*) em comportamento de pisoteio rotatório. Parque Nacional da Lagoa do Peixe, Rio Grande do Sul, Brasil (cortesia de Henrique Delfino). Para imagens de vídeo, ver os links https://ars.els-cdn.com/content/image/1-s2.0-S0895981123002079-mmc7.mp4 (indivíduo), e https://ars.els-cdn.com/content/image/1-s2.0-S0895981123002079-mmc8.mp4 (grupo).

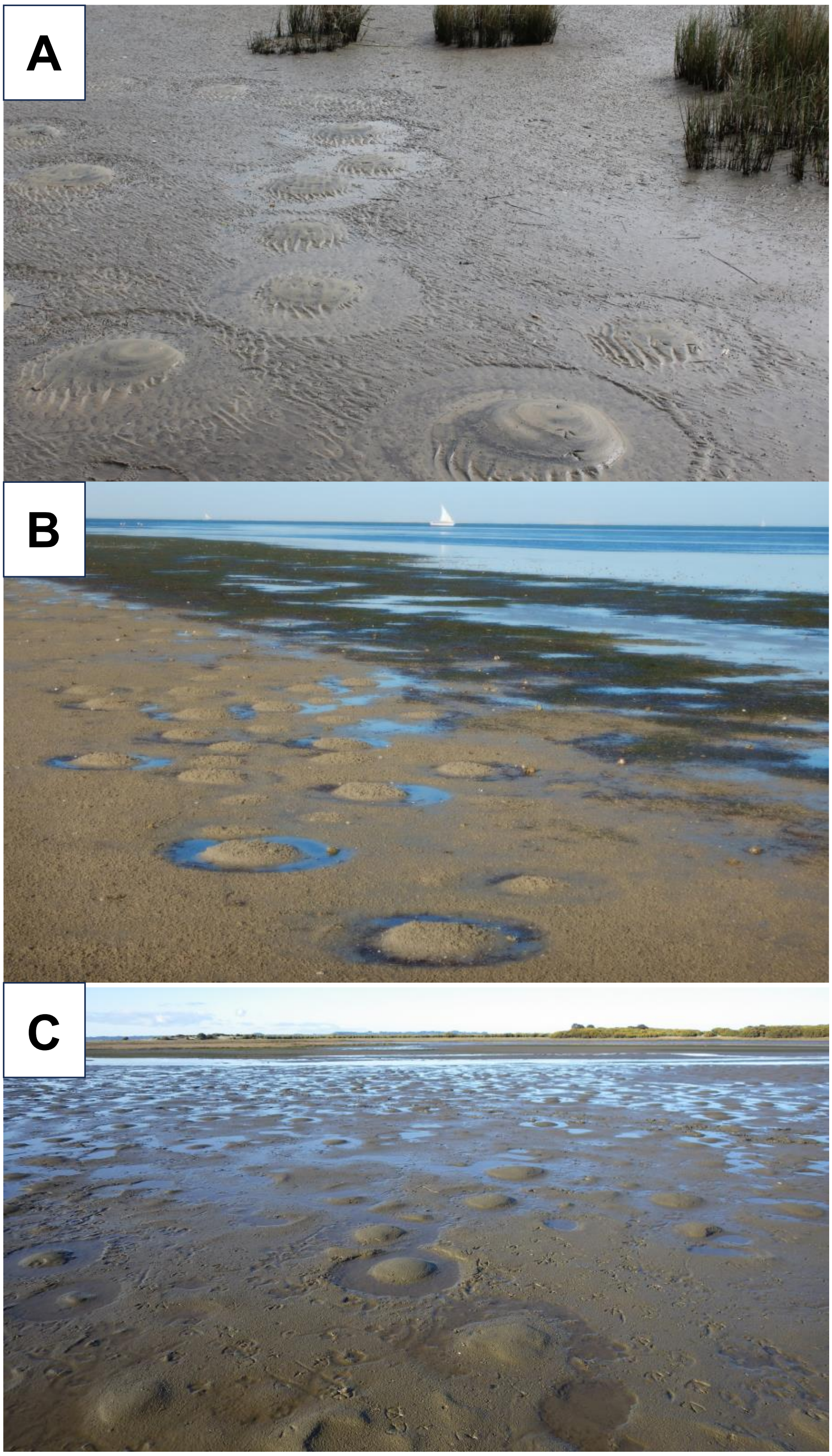

Figura 2. Exemplos de superfícies bioturbadas por flamingos em comportamento de pisoteio rotatório. (A) flamingo-chileno (*Phoenicopterus chilensis*), Parque Nacional da Lagoa do Peixe, Rio Grande do Sul, Brasil (cortesia de Heitor Francischini); (B) flamingo-comum (*Phoenicopterus roseus*), Banc d'Arguin, Mauritânia (cortesia de El-Hacen M. El-Hacen); (C) flamingo-chileno, Baía Caulyn, Chiloé, Chile (cortesia de Matthew Lee).

A técnica de pisoteio rotatório resulta em estruturas biogênicas arredondadas e dicotômicas, compostas por uma trincheira periférica, formada pelos autopódios da ave, e por um montículo central, erguido com as partículas sedimentares que são perturbadas, suspensas e depois decantadas (Figuras 2, 3). Aqui, emprega-se o termo "rotating-stamping structure (ROT)" para a estrutura biogênica feita por pisoteio, por considerar-se que tal termo abrange tanto a sua morfologia quanto o seu comportamento de origem. Uma vez registradas, as ROTs podem durar por semanas a meses, se a consistência do sedimento e a energia da água forem suficientes para impedir a sua desagregação (Macnae, 1960; El-Hacen *et al*., 2019, El-Hacen M. El-Hacen, comunicação pessoal). Descrições detalhadas destas estruturas são representativas apenas para as espécies de *Phoenicopterus* (Rooth, 1965; Johnson & Cézilly, 2007; Salvador *et al*., 2022), mas quase ausentes para as espécies dos gêneros *Phoenicoparrus* e *Phoeniconaias*, que compõem o restante da diversidade atual dos flamingos.

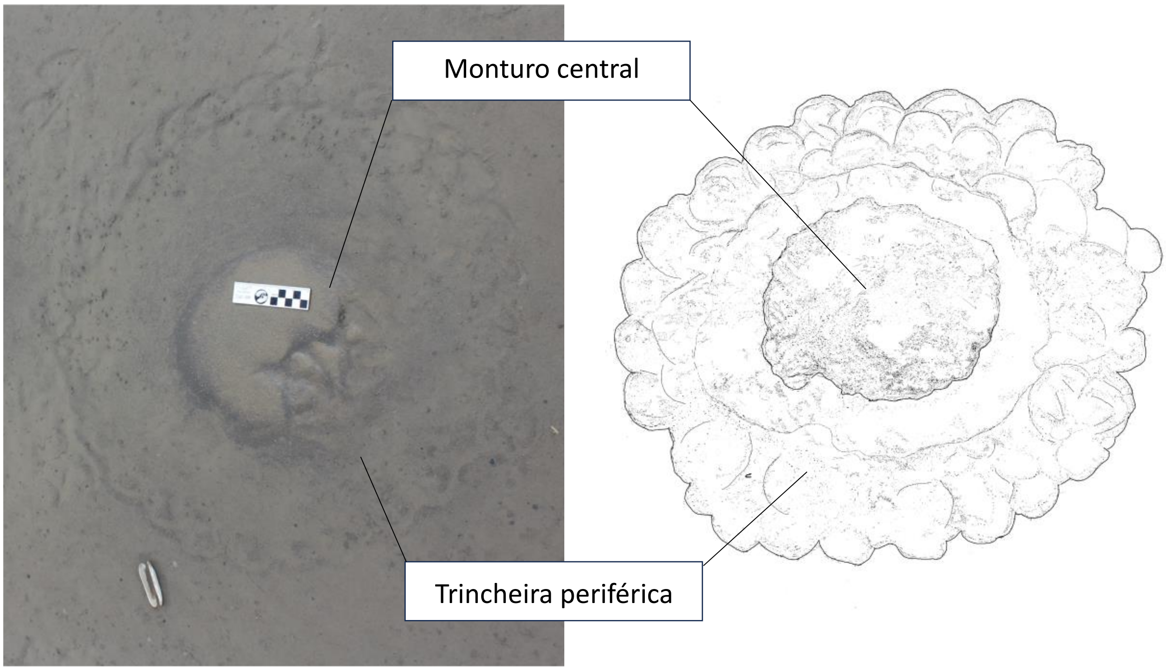

Figura 3. Fotografia e representação esquemática de uma estrutura de pisoteio rotatório (ROT) registrada por flamingo-chileno (*Phoenicopterus chilensis*) no Parque Nacional da Lagoa do Peixe, Rio Grande do Sul, Brasil. Adaptado de Barcelos-Silveira *et al*. (2023).

Apesar de sua conspicuidade, durabilidade e abundância, a ausência destas estruturas no registro fóssil expõe um paradoxo considerando a abundância de sua produção pelos flamingos modernos, em termos da abrangente gama de fatores sedimentares, físico-químicos e ecológicos onde os flamingos empregam o comportamento de pisoteio rotatório. Melchor *et al*. (2012) estipularam o comportamento de pisoteio para a origem de pares sobrepostos de pegadas fósseis encontrados na Formação Vinchina (Mioceno Tardio, La Rioja, Argentina) (Figura 4A); entretanto, os autores também colocam como explicação alternativa a alternância de apoio durante o repouso sobre um membro – comportamento típico dos flamingos e de outras aves aquáticas pernaltas (Anderson & Williams, 2010; Chang & Ting, 2017). O único registro provável de comportamento de pisoteio fossilizado provém de eolianitos do Pleistoceno da África do Sul, onde uma pequena sequência de estruturas organizadas linearmente foi atribuída a flamingos em pisoteio, possivelmente na fase de pisoteio em deslocamento (Helm *et al*., 2020) (Figura 4B). Porém, ainda se desconhece traços fósseis exibindo a típica estrutura dicotômica de monturo/trincheira dos ROTs.

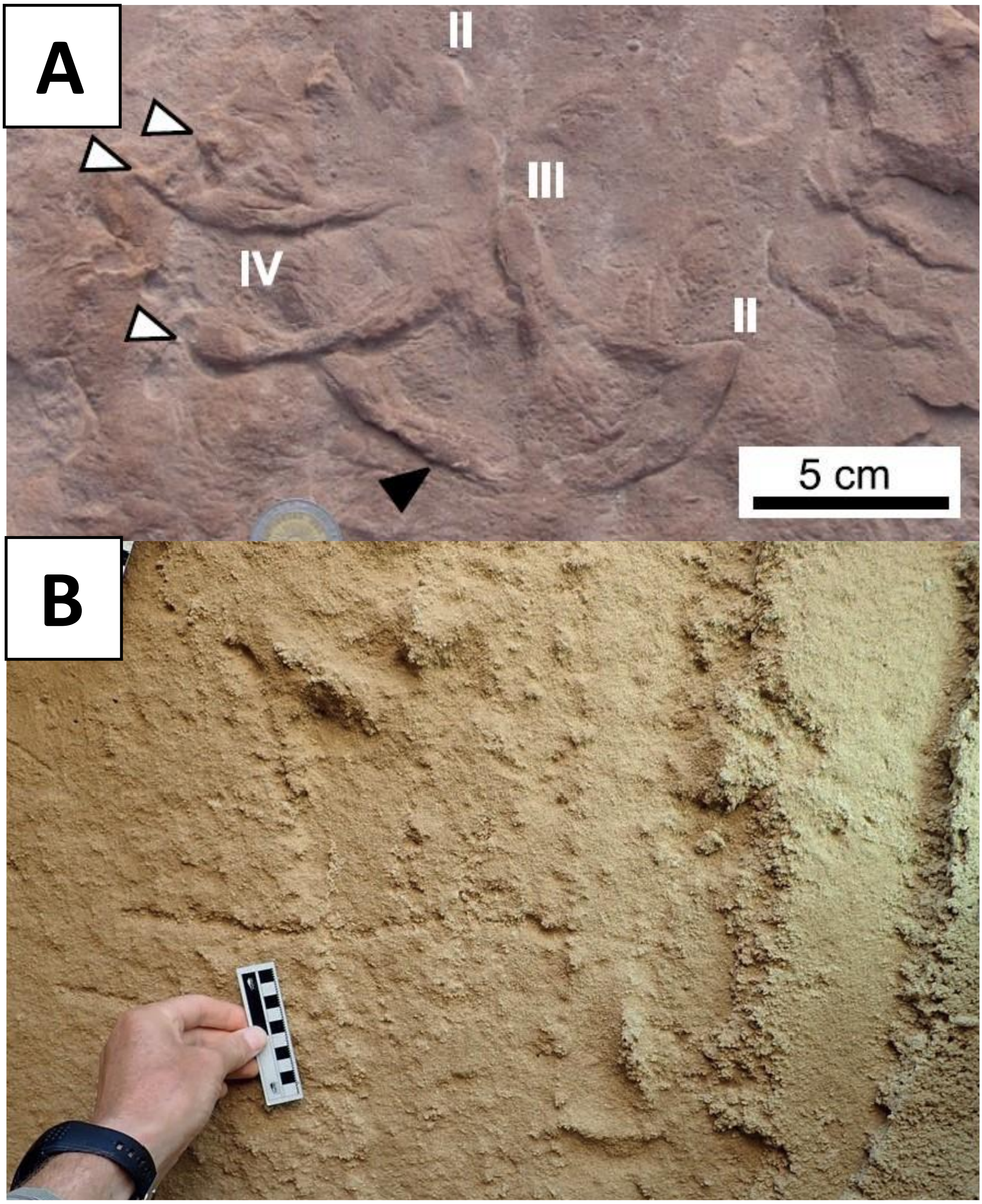

Figura 4. Traços fósseis de flamingos possivelmente associados ao comportamento de pisoteio. (A) Fotografia *in situ* de pegadas sobrepostas (hiporrelevo convexo) de *Phoenicopterichnum* isp. (Formação Vinchina, Argentina, Mioceno Tardio); seta preta indica uma pegada do autopódio direito quase completo, setas brancas indicam pelo menos três pegadas parciais (extraído de Melchor *et al.*, 2012). (B) Fotografia *in situ* de uma pista parcial (hiporrelevo convexo) atribuída a forrageio de flamingos pelo método do pisoteio, Formação Waenhuiskrans, África do Sul, Pleistoceno Tardio (extraído de Helm *et al.*, 2020).

A presente tese aborda este aspecto da neoicnologia dos flamingos, investigando o potencial de preservação das estruturas de pisoteio e a sua distribuição espacial conforme diversos fatores ambientais. Para contribuir com estas questões, realizou-se observações de campo tanto para registrar o comportamento dos flamingos quanto para avaliar a produção e o potencial de preservação das estruturas registradas, juntamente com uma extensa revisão bibliográfica e análise de vídeos de vida selvagem em plataformas eletrônicas de ciência cidadã.

2. OBJETIVOS

2.1. Objetivo geral

Analisar a neocinologia dos flamingos conforme o comportamento de pisoteio rotatório e suas estruturas biogênicas derivadas, comparando-os com o registro fóssil de modo a obter aplicações paleoambientais.

2.2. Objetivos específicos

- Descrever as estruturas derivadas do comportamento de pisoteio rotatório produzidas por flamingos chilenos (*Phoenicopterus chilensis*) em ambiente natural;
- analisar o comportamento de registro dos flamingos e sua interação com o substrato;
- fornecer descrições morfológicas detalhadas das estruturas;
- investigar os processos tafonômicos e as alterações morfológicas relacionadas;
- construir um modelo para a sua hipotética preservação no registro fóssil;
- elaborar uma sinopse sobre a ocorrência do comportamento de pisoteio dos flamingos e das estruturas biogênicas resultantes em função de uma série de contextos e controles ambientais, retirados da literatura, observações de campo e registros de vídeos online;
- revisar o contexto paleoambiental dos vestígios fósseis da linhagem dos flamingos, comparando-o com o contexto moderno para incrementar a acurácia das interpretações paleoambientais.

3. ESTADO DA ARTE

3.1. Flamingos modernos: diversidade, adaptações e ecologia

Os flamingos são aves aquáticas altamente especializadas a uma dieta filtradora, com notáveis adaptações morfológicas e comportamentais ao seu estilo de vida único entre as aves e muito raras nos restantes vertebrados, fósseis ou existentes (Stejneger, 1885). Estas aves possuem pernas e pescoço longos, bico arqueado com lamelas córneas internas que filtram o alimento da água ou do sedimento, e uma língua musculosa e hipertrofiada que funciona como um pistão (Allen, 1956; Jenkin, 1957; Rooth, 1965; Sanderson & Wassersug, 1990, 1993; Zweers *et al*., 1995). Este aparato filtrador de bico e língua possibilita aos flamingos se alimentarem de diminutos a microscópicos organismos que habitam tanto a coluna d'água quanto o substrato (Allen, 1956; Jenkin, 1957). Os flamingos habitam águas rasas e calmas, principalmente em corpos d'água salinos, desde regiões costeiras tropicais até lagos alto-montanos de clima frio (Allen, 1956; Rooth, 1965; Del Hoyo *et al*., 1992). Embora anatomicamente especializados, os flamingos são versáteis o bastante para explorar grande parte da diversificada gama de condições ambientais nos diversos ecossistemas aquáticos que ocupam. Os flamingos podem lidar com a variação ambiental através da plasticidade no comportamento de forrageio, dispondo de alta mobilidade para o encontro de áreas promissoras e alternando entre distintas técnicas conforme a variabilidade na distribuição e abundância de presas (Arengo & Baldassarre, 1998, 1999; Gihwala *et al*., 2019; Frias-Soler *et al*., 2022).

Frequentemente os flamingos exploram habitats aquáticos extremos, caracterizados por alta concentração de sais e elevada alcalinidade, onde muitas vezes compreendem a maior parte da biomassa aviana (Vareschi, 1978). Esta alta densidade, aliada aos seus modos gregários de forrageamento e reprodução, faz com que os flamingos tenham um grande impacto nos ecossistemas onde habitam, configurando um exemplo clássico de "engenharia do ecossistema" (Laing *et al*., 2022). Do ponto de vista icnológico, esta engenharia se traduz na modificação radical das propriedades topográficas e sedimentares dos terrenos bioturbados pelos flamingos. Caso preservadas como traços fósseis, estas modificações podem ser interpretadas e utilizadas para inferir as propriedades dos paleoambientes habitados por flamingos ancestrais.

Apesar de compartilharem um plano corporal bastante homogêneo, as diferentes espécies de flamingos coronais também exibem distintas adaptações anatômicas e estratégias de forrageio (Mascitit & Kravetz, 2002) (Figura 5). Podem ser reconhecidos dois grupos monofiléticos entre os flamingos, divididos conforme suas características morfológicas e comportamentais (Torres *et al.*, 2014). O primeiro grupo abrange as espécies de "quilha rasa" ou “quilha baixa” (“shallow-keeled” ou “low-keeled flamingos”), composto por três espécies do gênero *Phoenicopterus*: flamingo-chileno (*Phoenicopterus chilensis*), distribuído pela América do Sul austral, da Patagônia até o sul do Equador, reproduzindo-se no altiplano andino e invernando em altitudes até o nível do mar, em ambos os oceanos Atlântico e Pacífico (Johson *et al.*, 1958; Romano *et al.*, 2017); flamingo (*Phoenicopterus ruber*), de distribuição centrada no Mar do Caribe, Golfo do México e costa setentrional da América do Sul (Frias-Soler *et al.*, 2014 Torres-Cristiani *et al.*, 2020); e flamingo-comum (*Phoenicopterus roseus*), da África subsaariana, costas atlântica e pacífica da África, Mediterrâneo, Península Arábica, Ásia Central e Meridional (Johnson, 2000; Geraci *et al.*, 2012). Neste grupo, a anatomia do aparelho filtrador é considerada simples, com bico compacto (em corte transversal), de maxila comparativamente baixa e maior espaçamento entre as lamelas internas (Jenkin, 1957; Zweers *et al.*, 1995; Mascitti & Kravetz, 2002) (Figura 6).

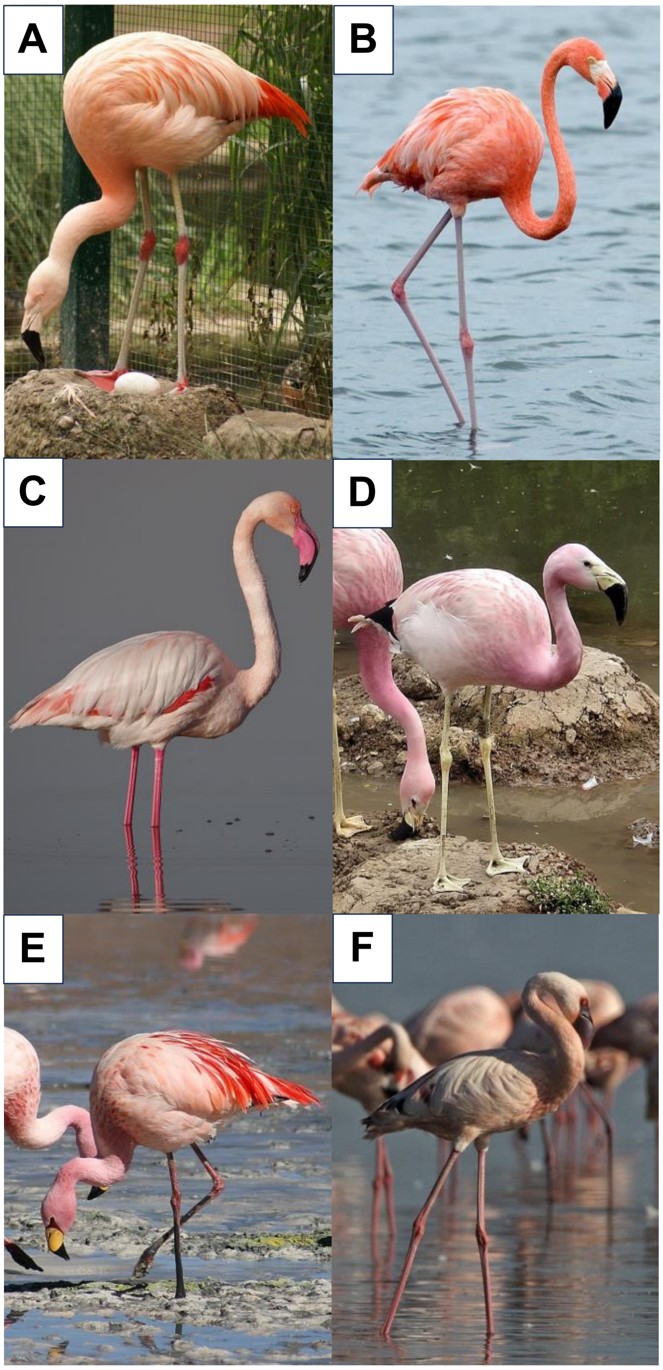

Figura 5. Exemplos de espécies de flamingos coronais: (A) flamingo-chileno (*Phoenicopterus chilensis*), fonte: Tragopan, https://commons.wikimedia.org/w/index.php?curid=4623752; (B) flamingo (*Phoenicopterus ruber*), fonte: Paul Asman and Jill Lenoble, https://commons.wikimedia.org/w/index.php?curid=26486207; (C) flamingo-comum (*Phoenicopterus roseus*), fonte: Elgollimoh, https://commons.wikimedia.org/w/index.php?curid=39979672; (D) flamingo-dos-andes (*Phoenicoparrus andinus*), fonte: Adrian Pingstone, https://commons.wikimedia.org/w/index.php?curid=2986460; (E) flamingo-da-puna (*Phoenicoparrus jamesi*), fonte: Valdiney Pimenta, https://commons.wikimedia.org/w/index.php?curid=6233369; (F) flamingo-pequeno (*Phoeniconaias minor*), fonte: Lip Kee, https://commons.wikimedia.org/w/index.php?curid=23288888.

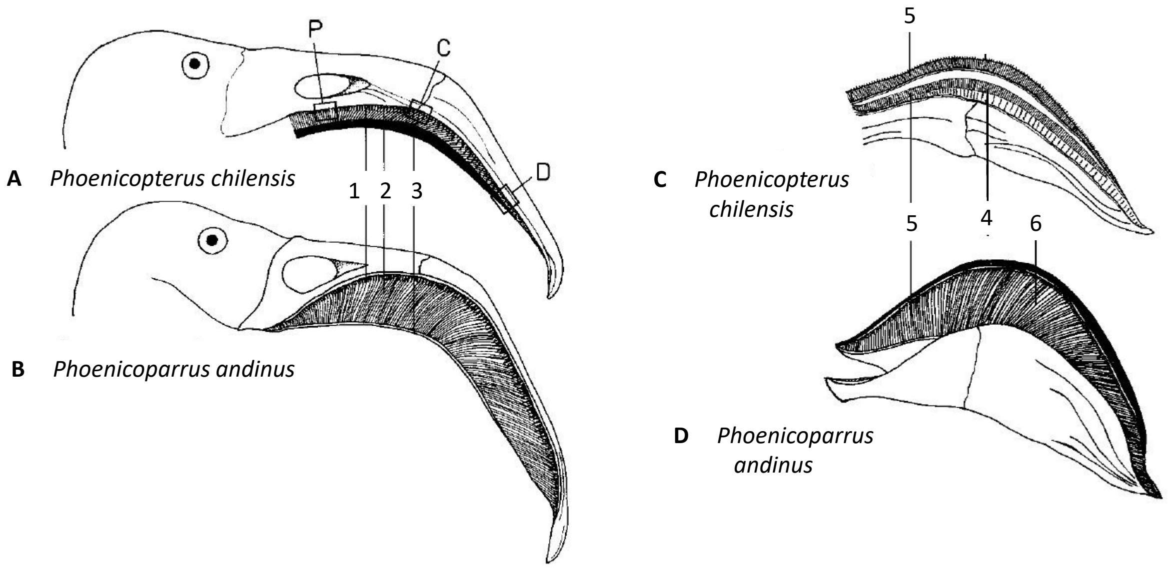

Figura 6. Esquema em vista lateral do aparelho filtrador nas espécies de quilha baixa (A, C) e de quilha alta (B, D). Números: (1) lamelas marginais, (2) quilha coberta por fileiras de lamelas submarginais, (3) borda livre da quilha, (4) fileiras submarginais externas serrilhadas, (5) fileiras submarginais internas, (6) borda expandida e dobrada do maxilar inferior. As letras indicam regiões do bico: (P) proximal, (C) curvatura, (D) distal. Adaptado de Mascitti & Kravetz (2002).

O segundo grupo compreende as espécies de "quilha profunda", compreendido pelos flamingos do gênero *Phoenicoparrus* e *Phoeniconaias*. *Phoenicoparrus* contém duas espécies: flamingo-dos-andes (*Phoenicoparrus andinus*), ocorrente nos picos andinos desde o sul do Peru até o norte da Argentina e do Chile, migrando nos meses frios para a Argentina central; e flamingo-da-puna (*Phoenicoparrus jamesi*), restrito a uns poucos lagos alto andinos no sul do Peru, oeste da Bolívia e extremo norte de Chile e Argentina (Caziani & Olivio, 2007). O flamingo-pequeno (*Phoeniconaias minor*) é a única espécie atual do seu gênero, embora estudos moleculares recentes levem alguns autores a incluí-lo como uma terceira espécie de *Phoenicoparrus* (Torres *et al.*, 2014; Frias-Soler *et al.*, 2022); distribui-se pela África subsaariana e Índia ocidental. Comparado aos flamingos do gênero *Phoenicopterus*, as espécies do grupo de grupo de quilha baixa são caracterizadas pela morfologia derivada do aparelho filtrador, exibindo bico bulboso em corte transversal, maxila comparativamente alta e maior número de fileiras de lamelas internas com menor espaçamento entre elas (Figura 6).

As espécies do gênero *Phoenicopterus* possuem uma dieta generalizada composta de organismos bentônicos e/ou livre-natantes como microcrustáceos, moluscos, vermes, larvas e pupas de insetos aquáticos e sementes (Del Hoyo *et al*., 1992) Este grupo é considerado plesiomórfico em relação aos demais flamingos coronais (Torres *et al*. 2014), inferindo-se então que a dieta do ancestral comum dos atuais Phoenicopteridae incluísse itens de maior tamanho, em conformidade com o tamanho do aparelho filtrador. Já a morfologia do aparelho filtrador dos flamingos de quilha alta permite que eles capturem organismos de menor tamanho, minúsculo a microscópico, tais como cianobactérias e diatomáceas (Jenkin, 1957; Hurlbert, 1982; Mascitti, 1998; Mascitit & Kravetz, 2002).

As marcadas diferenças anatômicas que redundam em estratégias de forrageio e em dietas distintas permitem com que espécies diferentes de flamingos possam coabitar os mesmos ambientes através da partição de nicho (Caziani & Derlindati, 2000; Mascitti, 2001; Polla *et al*., 2018). Ressalta-se que apenas as diferenças morfológicas entre os grupos não explicam a complexa simpatria observada, havendo outros fatores influentes como interações sociais intra- e interespecíficas, sazonalidade e padrão circadiano de atividade (Caziani & Derlindati, 2000; Mascitti & Castañera, 2006; Caziani et al., 2007).

3.2. Comportamento de forrageio

Embora muitos autores tenham previamente descrito vários comportamentos alimentares de flamingos selvagens (*e.g*., Gromme, 1930; Klingel, 1942; Gallet, 1949; Allen, 1956; Jenkin, 1957), a primeira tentativa de uma categorização completa dos comportamentos alimentares destas aves foi feita por Rooth (1965), que distinguiu sete métodos para *Phoenicopterus ruber* em Bonaire. Estes métodos foram agrupados de acordo com o modo de locomoção (estacionário, caminhando, correndo, pisoteando, nadando) e a utilização do bico (como filtro ou como pinça) utilizado pela ave que se alimenta (Figura 7). Em seu esquema, Rooth (1965) descreve ainda as posturas corporais, algumas estruturas biogênicas resultantes, os substratos explorados e os recursos alimentares associados a cada método. A seguir, descreve-se os diferentes tipos de comportamento de alimentação dos flamingos e das estruturas biogênicas associadas a cada tipo, acrescida de modificações por autores posteriores (*e.g*., Delfino & Carlos, 2021):

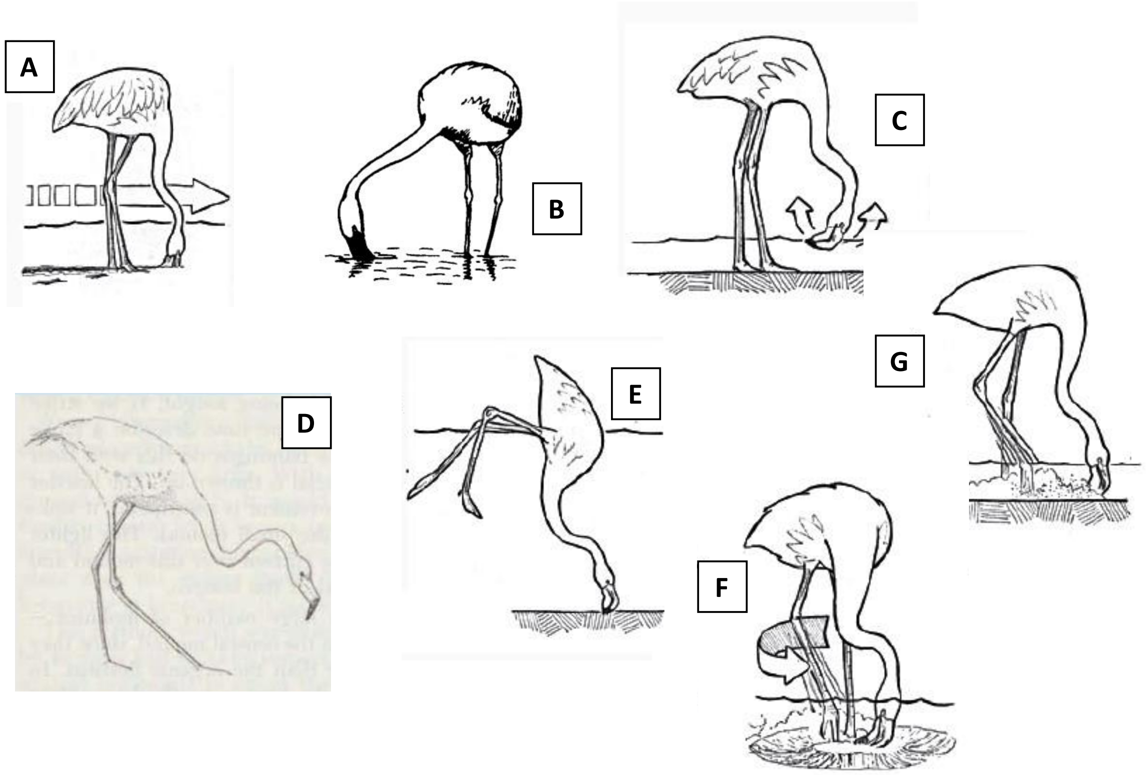

Figura 7. Técnicas de forrageio utilizadas pelos flamingos. (A) caminhada; (B) varredura; (C) escumar; (D) corrida; (E) mergulho incompleto; (F) pisoteio estático; (G) pisoteio rotatório. Adaptado de Rooth (1965) Johnson & Cezilly (2008) e Ridley *et al*. (1955).

(A) Caminhada. A ave anda enquanto forrageio com o bico no substrato, empreendendo leves movimentos laterais do pescoço, que registram um traço ondulado acompanhado por pegadas em pista (Figura 7A). Traços deste tipo foram relatados por Rooth (1965) e Hunt & Lucas (2007) (Figura 8).

Figura 8. Traços lineares de alimentação com pegadas associadas produzidos por flamingos-chilenos (*Phoenicopterus chilensis*) em forrageio de caminhada, no Parque Nacional da Lagoa do Peixe, Brasil (crédito Heitor Francischini).

(B) Varredura. Com o bico invertido, a ave filtra o sedimento com movimentos laterais do pescoço, traçando uma estrutura arqueada descrita como "semelhante a um canal" por Gihwala *et al*. (2017, 2019). O bico não é profundamente inserido no substrato, pelo que se trata de estruturas pouco profundas nos sedimentos superficiais, em geral acompanhadas por pegadas da ave em forrageio (Figura 9). A ave pode forragear neste modo tanto em condições subaéreas quanto subaquáticas, em lâmina d’água de até 1 m de profundidade (Figura 7B).

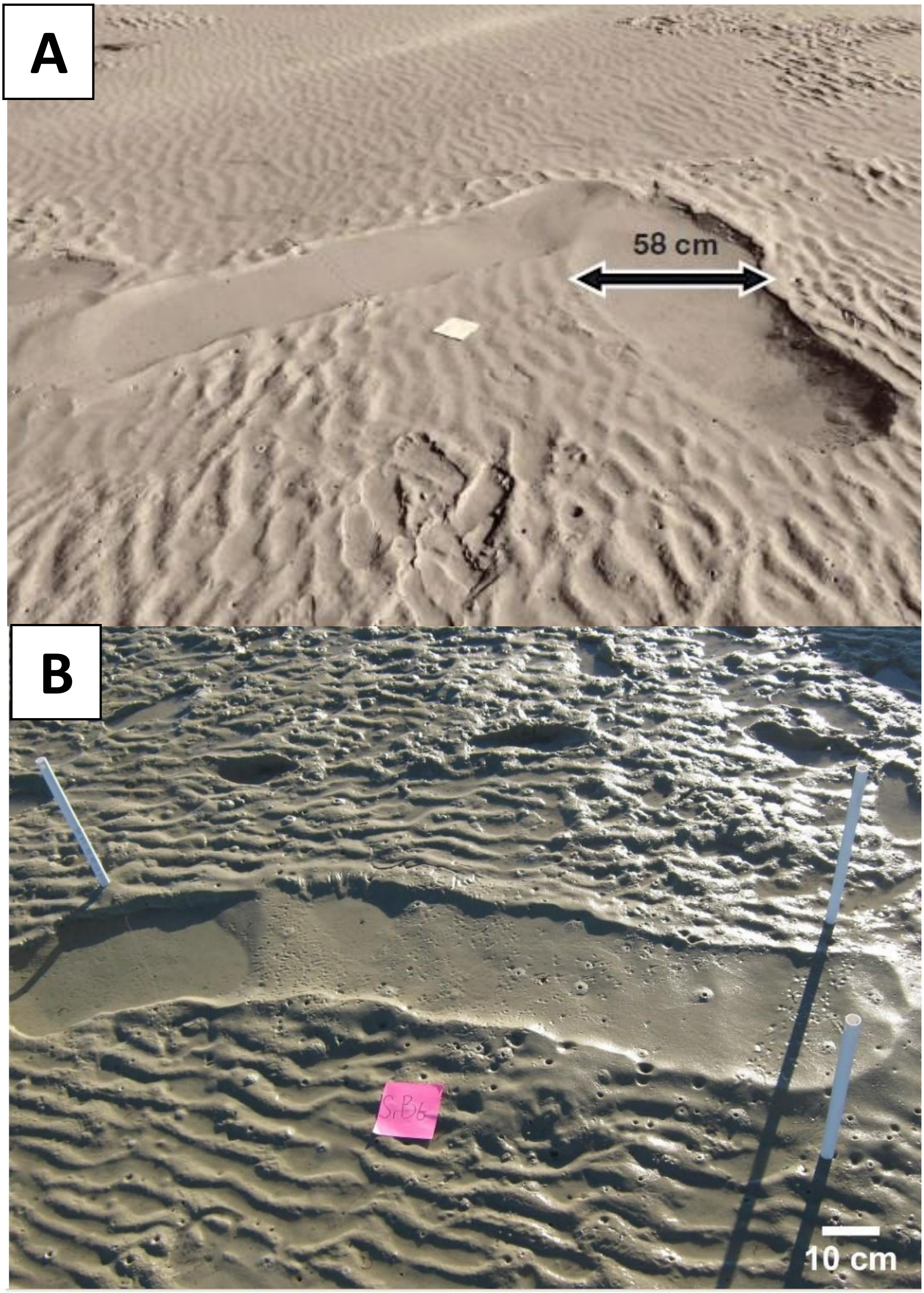

Figura 9. Estruturas de varredura no substrato, feitas por flamingos-comuns (*Phoenicopterus roseus*) na África do Sul, em ambiente tidal. (A) Extraído de Gihwala et al. (2017); (B) extraído de du Plessis (2018).

(C) Escumar. Semelhante à varredura, mas a ave movimenta o bico de um lado para outro dentro d’água, sem tocar no substrato. Assim, não há traços do bico no sedimento (Figura 7C).

(D) Corrida. Em ambiente subaéreo ou subaquático muito raso, uma vez que a corrida em ambiente aquático exige um elevado dispêndio de energia para obter energia alimentar suficientemente compensatória. Empregado para capturar presas móveis relativamente grandes, como caranguejos, utilizando o bico como uma pinça (Voous, 1957; Macnae, 1960; Rooth, 1965). O resultado desta atividade são traços de deslocamento dificilmente distinguíveis de uma caminhada ou corrida sem fins alimentares (Figura 7D).

(E) Mergulho incompleto. Quando em águas profundas o bastante para fazer a ave boiar, o flamingo em forrageio submerge cabeça, pescoço e a metade anterior do tronco, deslocando-se por movimentos de natação dos pés enquanto mantém a metade posterior do corpo horizontalmente emersa. Nesta modalidade, é provável que apenas traços do bico sejam registrados, embora tais estruturas sejam desconhecidas tanto no registro fóssil quanto no registro atualístico (Figura 7E).

(F) Pisoteio. A ave agita ritmicamente o substrato com as duas patas, suspendendo-o enquanto gira em torno do eixo do corpo (Rooth, 1965; Cifuentes, 2007; Johnson & Cézilly, 2007; Delfino & Carlos, 2021, 2022) (Figura 7F). Esta técnica produz estruturas biogênicas dicotômicas constituídas por um monturo de sedimentos empilhados delineado por uma trincheira circular onde podem estar registradas as pegadas dos flamingos (Figuras 3 e 10). Aparentemente, esta técnica permite desalojar a meiofauna e capturar os organismos que acabam suspensos na água (Allen, 1956; Macnae,1960; Bildstein *et al.*, 1991; Jonhson & Cezilly, 2008; Béchet *et al.*, 2017). Outras variações do pisoteio ocorrem quando a ave permanece na mesma orientação (pisoteio estático) (Figura 7G), ou se desloca para a frente ou para trás (pisoteio em deslocamento). Estas variações precedem por vezes a rotação completa caraterística do pisoteio rotatório (Ingraham, 1896; Cifuentes, 2007), possivelmente como fases exploratórias anteriores ao movimento de rotação. Também as estruturas formadas por cada variação diferem: no pisoteio estático, a ave escava uma depressão rasa (Allen, 1956; Cifuentes, 2007) (Figura 11A), enquanto no pisoteio em deslocamento a ave produz uma escavação alongada e rasa ou uma pista de pegadas sobrepostas (Cifuentes, 2007), de comprimento equivalente à distância percorrida pelo animal. Ambas as formas de pisoteio podem culminar no pisoteio rotatório (Figura 11B).

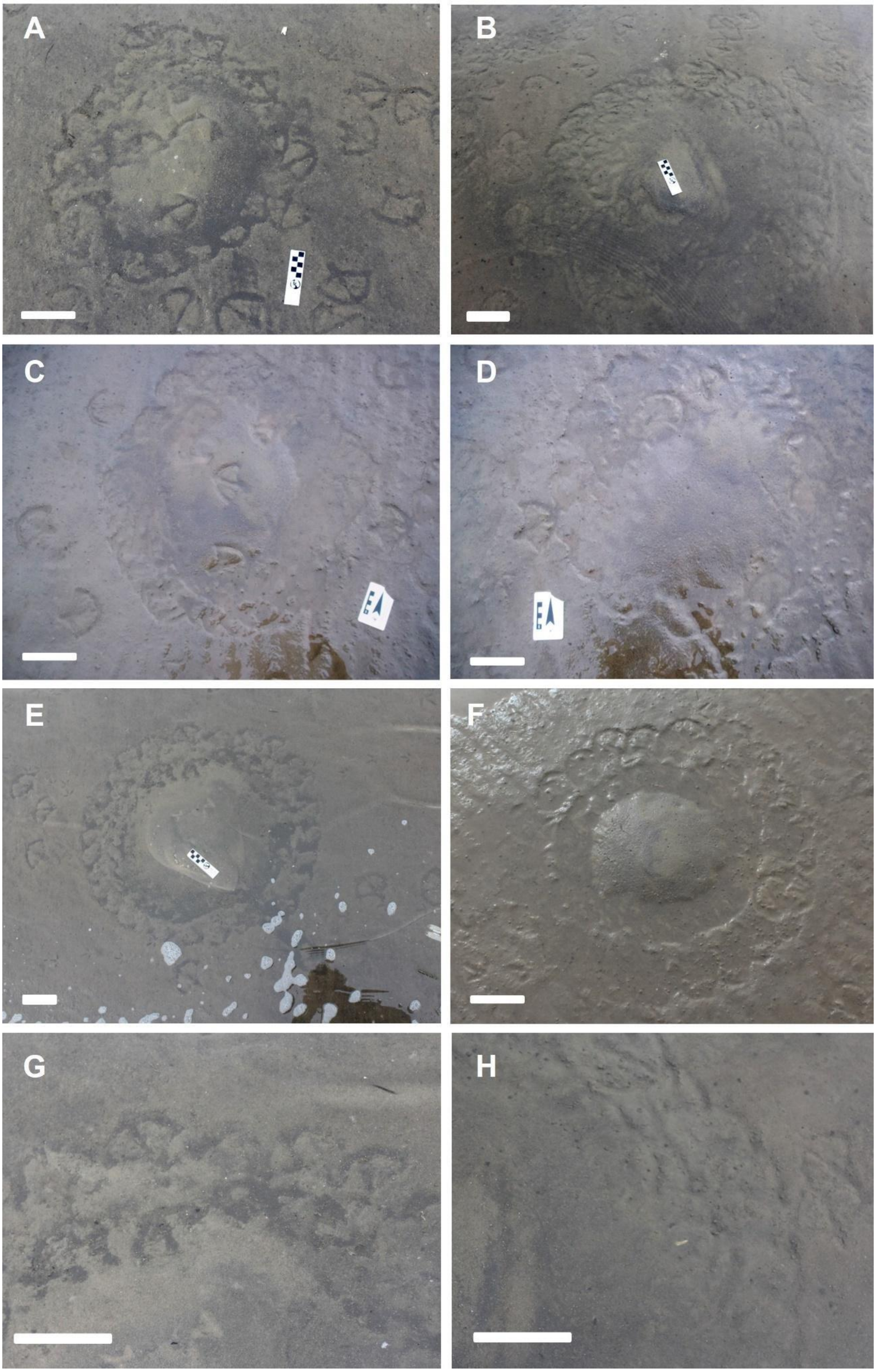
A
B
C
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Figura 10. Exemplos da gama de variação morfológica das estruturas de pisoteio rotatório recém-produzidas por flamingos-chilenos (*Phoenicopterus chilensis*) no Parque Nacional da Lagoa do Peixe, Brasil, em agosto de 2018. (A-B) Estruturas totalmente submersas, (C-E) semi-submersas e (F) totalmente emersas. (G) Detalhe das pegadas na trincheira periférica da Figura 9E, ilustrando a deposição de sedimentos mais finos e escuros, acentuando a definição da impressão dos dígitos. (H) Detalhe da figura 9B, mostrando pegadas progressivamente apagadas na trincheira periférica. Escala 10 cm.

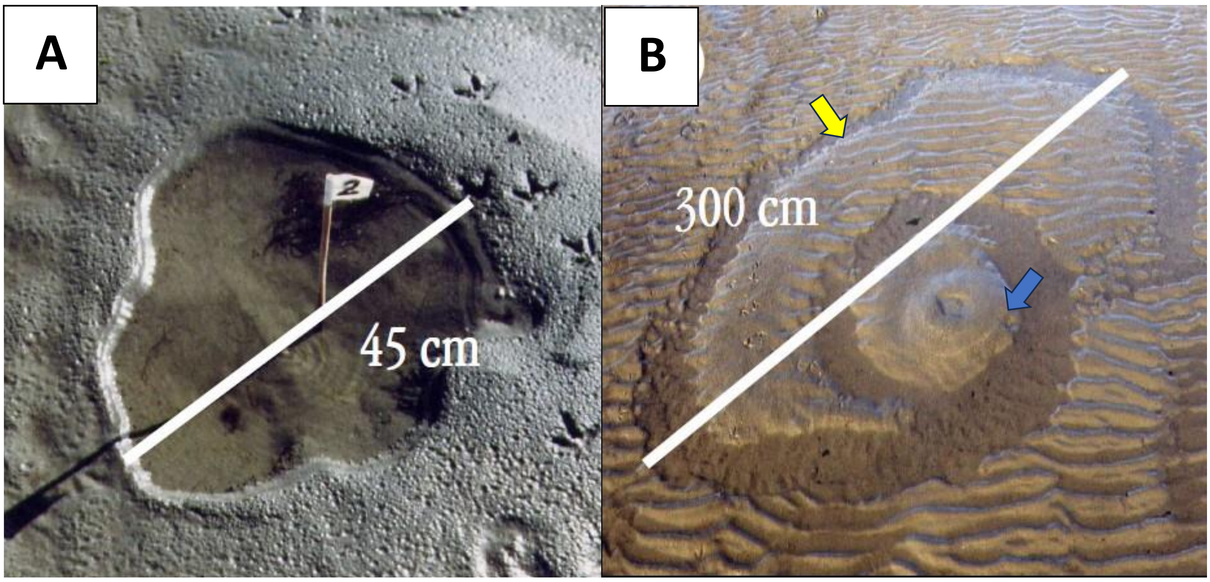

Figura 11. Exemplos de estruturas compostas por pisoteio estático (A) e pisoteio em deslocamento (seta amarela) culminando em pisoteio rotatório (seta azul) (B), registrados por flamingos-chilenos (*Phoenicopterus chilensis*) na Baya Caulín, Chile. Extraído de Cifuentes (2007).

A primeira menção ao comportamento de pisoteio foi realizada por Buffon (1781), em um tratado geral sobre os flamingos. O relato de Buffon descreve duas características do pisoteio: o movimento para cima e para baixo das pernas e a posição da cabeça orientada para o substrato. Buffon não fez quaisquer observações sobre a rotação do corpo, deixando em aberto se ele descreve o pisoteio estacionário ou o pisoteio rotatório. Rooth (1965) supôs que o relato de Buffon se referia pisoteio estacionário, mas pensamos que a descrição de Buffon foi breve e continha elementos comuns a ambas as variedades de pisoteio; o movimento rotatório, por sua vez, é tão notável que se pode supor que a um naturalista habilitado como Buffon não escaparia este pormenor, uma vez observado.

Cerca de um século mais tarde, num estudo sobre *Phoenicopterus roseus* de Camargue (costa mediterrânea da França), Clarke (1895) forneceu a primeira descrição claramente reconhecível do pisoteio rotatório. Logo após, Ingraham (1896) relatou pela primeira vez as estruturas derivadas do pisoteio rotatório, desta vez para *Phoenicopterus ruber*. Porém, a descrição de Ingraham é incompleta, tratando somente do monturo central, sem mencionar a trincheira periférica. Mais tarde, Chapman (1905) foi o primeiro a relatar a provável natureza instintiva deste comportamento, observando a sua execução por filhotes de *Phoenicopterus ruber* com apenas dez dias, acrescido da observação de que os adultos não procuram alimento perto do ninho e, portanto, não criam uma situação modelo que as crias possam imitar. Evidências posteriores confirmaram que a prática do pisoteio, ou pelo menos os seus movimentos básicos, é inata em *Phoenicopterus roseus* (Brown, 1958), *Phoenicopterus ruber* (Rooth, 1965) e *Phoeniconaias minor* (Bony, 2020). A expressão inata do pisoteio em *P. minor* indica que este comportamento tem uma origem anterior à divergência entre os grupos de quilha alta e quilha baixa, sugerindo então o Mioceno Tardio como data mínima para o surgimento deste comportamento e, consequentemente, para o encontro das estruturas dele derivadas no registro fóssil.

3.3. História evolutiva e registro somatofossilífero

A história e afinidade evolutivas dos flamingos foi objeto de farta discussão e discordância, algo esperado de acordo com o grau extremo de especialização morfológica destas aves. No passado, quase todas as outras grandes linhagens de aves aquáticas foram propostas como proximamente afins aos flamingos. Com base em um diversificado conjunto de caráteres morfológicos, bioquímicos, comportamentais, reprodutivos e parasitológicos, linhagens tão variadas como Anseriformes (patos, gansos, cisnes), Gruiformes (grous, saracuras), Charadriiformes (maçaricos, gaivotas) e Ciconiiformes (cegonhas) foram aventadas como as mais aparentadas aos flamingos (ver resenhas em Olson & Feduccia 1980). A polêmica permaneceu ao longo do século XX sem uma aparente resolução ou consenso mínimo, até que Van Tuinen *et al*. (2001), utilizando dados moleculares (DNA mitocondrial e hibridização DNA-DNA), propuseram uma imprevista afinidade com os mergulhões (Podicipediformes, Podicipedidae) (Figura 12). Posteriormente, novas análises moleculares, acompanhadas de estudos morfológicos mais refinados, consolidaram o status dos mergulhões como grupo-irmão de Phoenicopteriformes

(Mayr, 2004, 2006;). Esta relação entre mergulhões e flamingos atualmente é estabelecida como um consenso ornitológico, levando à proposição do clado Mirandornithes, contendo Podicipediformes, Phoenicopteriformes coronais e formas extintas afins (Mayr, 2004; Sangster, 2005; Manegold, 2006).

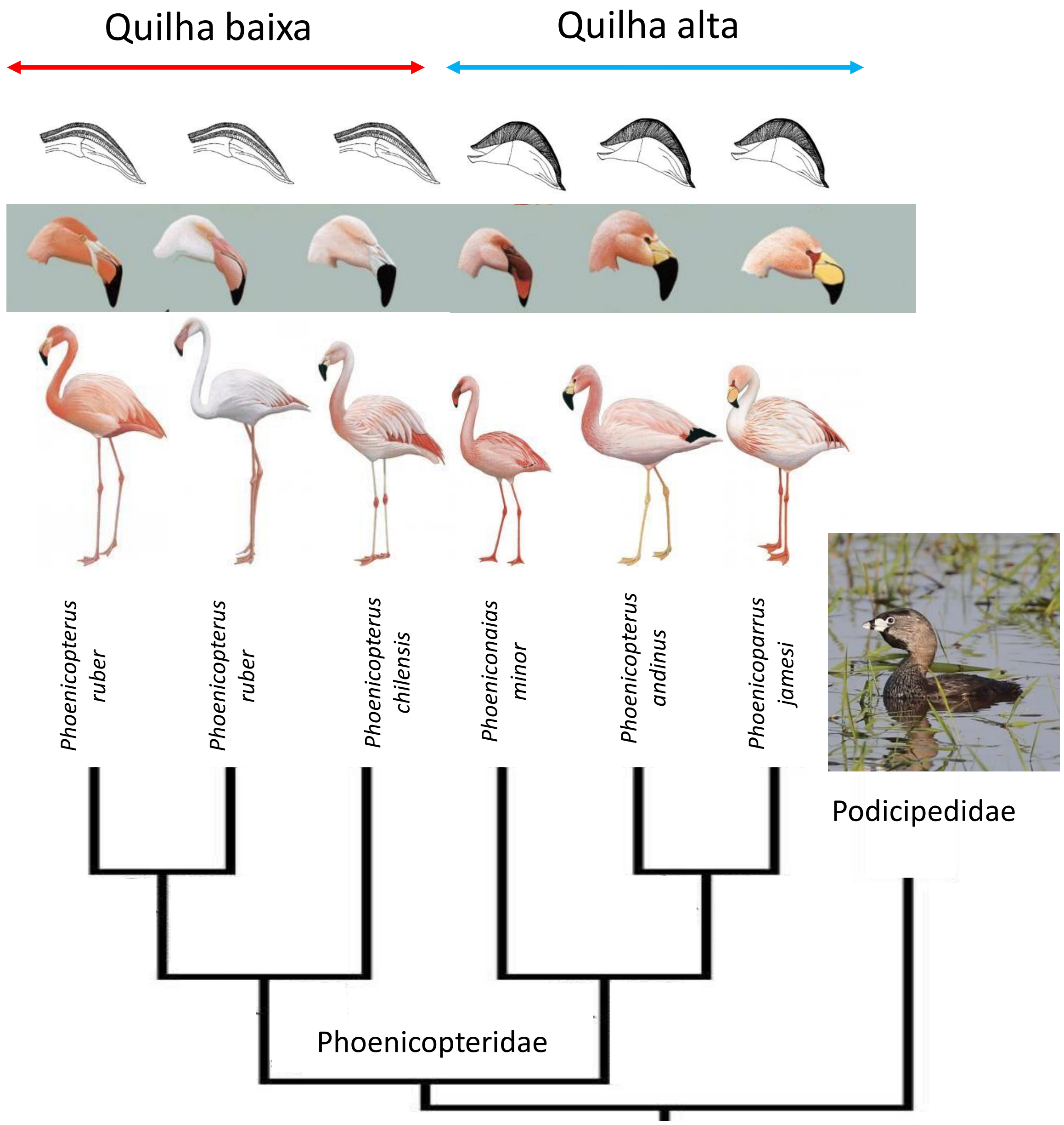

Figura 12. Filogenia simplificada de Mirandornithes, com ênfase na linhagem dos flamingos coronais (Phoenicopteriformes, Phoenicopteridae). Imagens de Phoenicopteridae extraídas de Del Hoyo (1992) e de Mascitti & Kravetz (2002). Imagem de Podicipedidae (mergulhão-caçador, *Podilymbus podiceps*), cortesia de Carlos Eduardo Agne.

Os estudos moleculares disponíveis diferem quanto às datas de origem e diversificação dos flamingos coronais. Conforme Torres *et al*. (2014), a divergência entre os dois clados ocorreu entre 3,9–1,7 Ma (transição Plioceno-Pleistoceno), e o ancestral comum de todas as seis espécies modernas (Phoenicopteridae coronal) viveu por volta de 6,5–3 Ma (transição Mioceno-Plioceno), tornando os flamingos atuais um dos grupos de mais recente diversificação entre as aves não-passeriformes. Por sua vez, o mais recente estudo molecular sobre a filogenia dos flamingos atuais (Frias-Soler *et al*., 2022) foi baseado na calibração da divergência mergulhões-flamingos no Eoceno Médio, conforme datado por Mayr (2014), calculando assim datas mais antigas de divergências entre os dois subclados de Phoenicopteridae vivos, cujo ancestral comum teria existido por volta de 13,5 Ma no Mioceno Médio (margem do cálculo 18–9 Ma). A divergência de *Phoeniconaias* e *Phoenicoparrus* foi datada em ~6,6 Ma (Messiniano, Mioceno Tardio, margem de 9,3–4 Ma), enquanto os dois *Phoenicoparrus* divergiram há ~4,5 Ma (Zanclean, Plioceno Inicial, margem de 7,6–3 Ma). No clado dos flamingos de quilha baixa, a linhagem de *P*. *chilensis* diverge dos outros dois *Phoenicopterus* no Messiniano (Mioceno Tardio, 6,9 Ma, margem de 10–4 Ma), seguida pela divergência entre *P*. *ruber* e *P*. *roseus* há cerca de 4,4. Ma (Zanclean, Plioceno Inicial, margem 6,6–2,4 Ma).

A linhagem dos flamingos conta com uma representação fóssil comparativamente rica, tanto em restos corporais quanto em traços. Entretanto, a maior parte dos restos fósseis de flamingos correspondem a elementos ósseos isolados ou fragmentados, principalmente no que diz respeito ao registro do Paleógeno. Alguns fragmentos datados do Cretáceo Tardio foram relacionados aos flamingos, mas nenhum com total segurança pois estes fragmentos possuem pouco valor comparativo (Brodkorb, 1963; Olson & Feduccia, 1980) além de constituírem registros extemporâneos ao intervalo hoje admitido de evolução dos flamingos no Cenozoico.

Os registros de Mirandornithes mais antigos provêm de rochas paleocênicas da Ásia Central, onde já se encontram diversificados em pelo menos dois morfotipos diferenciados pelo tamanho. Se não estiverem relacionadas com o dimorfismo sexual, estas duas formas (uma grande e outra menor) do Paleoceno Tardio (Thanetiano, 58,7–55,8 Ma) do sul da Mongólia (Membros Naran e Zhygden da Formação Naran Bulak) representam os registos mais antigos da linhagem de flamingos + mergulhões. A semelhança morfológica geral levou à identificação incorreta de alguns somatofósseis de Mirandornithes como Anserimorphae-Presbyornithidae. Originalmente descritos como representantes de *Presbyornis* (Kurochkin & Dyke, 2010), estes restos fragmentários foram reatribuídos a representantes basais de Mirandornithes por Zelenkov (2021). Um fragmento de quadrado procedente da Formação Naranbulag (Bumbaniano, Eoceno Inicial, ~ 55 Ma) na Mongólia foi considerado como um Mirandornithes estemático por Hood *et al*. (2019), podendo representar o registro mais antigo do clado. O gênero *Juncitarsus*, por sua vez, conta com uma completude que permite uma boa reconstrução de sua anatomia e paleobiologia. Duas espécies foram descritas para o Eoceno Médio da América do Norte (Olson & Feduccia, 1980; Ericson, 1999) e da Europa (Peters, 1987). *Juncitarsus* foi inicialmente interpretado como um membro basal da linhagem dos flamingos (Olson & Feduccia, 1980), mas trabalhos recentes colocam-no como um Mirandornithes basal ou como grupo-irmão de Mirandornithes (Mayr, 2004, 2014). Assim como os flamingos coronais, *Juncitarsus* apresenta fossas para glândulas de sal, situadas nos ossos frontais (Olson & Feduccia, 1980), indicando a adaptação muito antiga da linhagem a ambientes de maior salinidade. Diferentemente dos flamingos atuais, *Juncitarsus* possui o dígito pedal I alongado o bastante para poder produzir pegadas tetradáctilas. Entretanto, na ausência de tecidos moles preservados, não é sabido se *Juncitarsus* possuía membrana digital, o que o apontaria como um provável produtor das pegadas de *Presbyorniformipes*, cuja autoria é disputada (Yang *et al*., 1995).

A ordem Phoenicopteriformes inclui os flamingos coronais da família Phoenicopteridae, alguns Phoenicopteriformes (e.g., *Agnopterus*) e Phoenicopteridae basais (“paleoflamingos” *sensu* Grellet-Tiner *et al*., 2012) e a família extinta Palaelodidae. *Agnopterus* é o mais antigo representante de Phoenicopteriformes, conhecido por três espécies do Eoceno Tardio e Oligoceno Tardio da Europa, Cazaquistão e Brasil (Milne-Edwards, 1867-1871; Lydekker, 1891; Tugarinov, 1940). Entretanto, o material das três espécies é fragmentário e dificulta a compreensão de suas afinidades filogenéticas.

A família Palaelodidae teve uma vida longa, desde o Oligoceno Inicial até ao Pleistoceno Inicial (Brodkorb, 1961; Mayr & Smith, 2002), diversificando-se em três gêneros (*Adelalopus*, *Palaelodus* e *Megapalaelodus*; Sangster *et al*., 2022) e quase vinte espécies reconhecidas. Possuíam tarsometatarsos longos, embora não tão longos como nos flamingos modernos (Worthy *et al*., 2010), significando que a condição pernalta possa ser plesiomórfica em Mirandornithes, já que *Juncitarsus* também possuía tarsometatarso alongado e esguio. Porém, ao passo que *Juncitarsus* poderia representar uma ave vadeadora, ocupante de águas baixas e margens de corpos d’água, a anatomia dos autopódios indica que Palaelodidae provavelmente representa uma radiação adaptada a um nicho de águas abertas, empregando maior natação (Olson & Feduccia, 1980; Cheneval, 1983; Cheneval & Escuillié, 1992), permitindo supor que possam ter utilizado a técnica de mergulho incompleto com maior frequência do que o empregado pelos flamingos atuais. A anatomia das falanges pedais indica que Palaelodidae possuía membrana interdigital, e, portanto, produzia pegadas palmípedes. Porém, as falanges ungueais eram conservadoras ao formato geral das aves, diferindo das unhas achatadas dorso-ventralmente encontradas tanto nos mergulhões como nos flamingos. Assim, possivelmente *Palaelodus* produzia pegadas palmípedes similares as de anatídeos ou de gaivotas (no caso de ter membranas do tipo inteiras) ou as das demais aves aquáticas semipalmípedes. Palaelodidae também possui fossas cranianas para alojar glândulas nasais de sal. Grellet-Tiner *et al*. (2012) postularam uma série adaptativa iniciando com Mirandornithes, de dieta piscívora em ambientes dulcícolas, retida em Podicipedidae e modificada em Palaelodidae para uma dieta filtradora primitiva em ambientes salobres e posteriormente a exploração de ambientes de maior salinidade pelos Phoenicopteridae.

O registo fóssil paleogênico de flamingos “verdadeiros” (Phoenicopteridae estemáticos), é escasso e as afinidades de algumas espécies não estão bem estabelecidas. *Elornis littoralis*, do Oligoceno Inicial da França, foi descrito com base em vários ossos pós-cranianos muito fragmentados, incluindo um tarsometatarso alongado e delgado (Olson, 1978). Segundo Olson & Feduccia (1980), a afinidade filogenética de *Elornis* é de difícil precisão, especialmente porque o paradeiro dos espécimes é desconhecido. Além disso, Mlíkovský (2002) aponta que o tibiotarso figurado difere em muito da morfologia dos Phoenicopteriformes.

Do Oligoceno Superior/Mioceno Inferior da Formação Etadunna, Austrália, Miller (1963) descreveu duas espécies alocadas em Phoenicopteridae: *Phoeniconotius eyrensis* e *Phoenicopterus*(?) *novaehollandiae*. Ambas são conhecidas por ossos da perna, presumindo-se que tinham um hálux mais desenvolvido do que os flamingos atuais (Mayr, 2022). *Leakeyornis aethiopicus*, do Mioceno Médio do Quênia, e *Harrisonavis* ("*Phoenicopterus*") *croizeti*, do Oligoceno

Tardio e no Mioceno Inicial de França (23–16 Ma), são conhecidos por abundante material, de morfologia muito semelhante aos Phoenicopteridae coronais. Apenas fragmentos de bico de *Leakeyornis* são conhecidos, sendo pouco informativos de sua morfologia em vida. Já *Harrisonavis* possui material suficiente para uma reconstrução adequada de seu bico, o qual não é tão inclinado quanto o dos flamingos atuais, lembrando o formato exibido por juvenis de flamingos atuais com poucas semanas de idade (Harrison & Walker, 1976; Torres *et al*., 2015). Tal plesiomorfia indica que *Harrisonavis* está fora do clado coronal de Phoenicopteridae, sugerindo que a divergência dos flamingos atuais é tão recente quanto o início do Neógeno (Mayr, 2022).

Diferenças nas estimativas de divergência estão provavelmente relacionadas com a data escolhida para calibrar a primeira divergência entre Phoenicopteridae e Podicipedidae, estabelecida no Oligoceno Inicial por Torres *et al*. (2014) e no Eoceno Médio por Frias-Soler *et al*. (2022). Dentre as duas estimativas, a mais concordante com o registro fóssil é a de Frias-Soler *et al*. (2022). Por exemplo, a estimativa de divergência *Phoenicopterus*/*Phoenicaparrus* + *Phoeniconaias* em ~13,5 Ma por Frias-Soler *et al*. concorda com a registro somatofossilífero de Phoenicopteridae basais, não claramente atribuíveis a nenhum dos gêneros coronais (Grellet-Tiner *et al*., 2012).

3.4. Neoicnologia e registro icnofossilífero dos flamingos

Grandes quantidades de substrato são mobilizadas pelas diferentes atividades dos flamingos, originando diversos tipos de estruturas sedimentares biogênicas, tais como pegadas, ninhos e variados traços de alimentação produzidos por diferentes modalidades de forrageio. Os traços fósseis atribuídos aos flamingos são limitados quando comparados ao conjunto de pegadas avianas no Cenozoico, compreendendo, em sua maioria, pegadas e superfícies de pisoteio (repichnia). Menos frequentes são os ninhos (callichnia) (Grellet-Tiner *et al*., 2012; Scott *et al*., 2012), superfícies de pisoteio coletivo com poros de bolhas (Scott *et al*., 2012) e supostos traços de forrageio (fodinichnia) (Helm et al. 2020).

Uma das principais razões para a escassez de traços fósseis de flamingos pode ser o desconhecimento da gama de estruturas biogênicas produzidas pelos flamingos atuais, as quais podem auxiliar na identificação de traços análogos no registro fóssil. Durante o forrageio, os flamingos atuais interagem com o substrato caminhando (quando as patas originam pegadas e pistas), peneirando (o bico origina perturbações) ou agitando o substrato com movimentos repetidos das patas. As atividades de procura de alimento predominam sobre outras atividades, como o repouso, a higiene, os cuidados parentais, a corte e a exibição social (Del Hoyo, 1992; Bildstein *et al*., 1991; Arengo & Baldassarre, 1995). Como tal, espera-se que o registo paleoicnológico da linhagem do flamingo contenha muitos vestígios de locomoção e alimentação - ou repichnia e fodinichnia, respectivamente. Uma vez que diferentes comportamentos alimentares são empregues de acordo com diferentes condições ambientais, uma tipologia abrangente de vestígios de alimentação de flamingos modernos e fósseis pode contribuir para a interpretação de paleoambientes e da história adaptativa do grupo.

Flamingos modernos possuem tridactilia funcional, como em *Phoenicopterus*, ou tridactilia absoluta, como em *Phoenicoparrus*. Em *Phoenicopterus*, o dígito I está presente, porém reduzido e incumbente (isto é, não toca o substrato); em *Phoenicoparrus* o dígito I é ausente. Outra característica pedal nos flamingos é a área de membrana interdigital unindo os dígitos II-III-IV, porém sem cobrir a totalidade do espaço interdigital, deixando livre o terço distal do dígito III. Ademais, os flamingos são das poucas aves com falanges unguais planas e achatadas dorsoventralmente – uma das características que os une aos mergulhões Podicipedidae no clado Mirandornithes (Manegold, 2006). Desta forma, os flamingos modernos produzem pegadas relativamente grandes (acima de 7 cm de comprimento), tridáctilas, semipalmadas, de perímetro posterior tipicamente arqueado, dígitos com alta divaricação e extremidade distal rombuda (Figura 13). Tal combinação de caráteres permite o pronto reconhecimento da autoria de pegadas de flamingos em ambientes atuais, e serve como analogia para o reconhecimento da autoria por flamingos de pegadas similares no registro fóssil. O icnogênero *Phoenicopterichnum* (Aramayo & Manera de Bianco, 1987) foi descrito com base em pegadas fossilizadas do Pehuén-Có (Província de Buenos Aires, Argentina), cujas icnotaxobases são similares aos caráteres anatômicas citados acima (Figura 4A, Figura 14). Segundo Alonso (2012), as espécies sul-americanas simpátricas produzem pegadas distintas em tamanho e morfologia: pegadas largas e grandes são características do flamingo-chileno; pegadas estreitas, de tamanho médio, caracterizam o flamingo-andino; e pegadas estreitas e pequenas são produzidas pelo flamingo-da-puna. Porém, o autor não fornece imagens diagnósticas ou morfometrias comparativas que evidenciem estas diferenças. Diferenças de tamanho são ao menos previsíveis, em razão do tamanho distinto entre as três espécies.

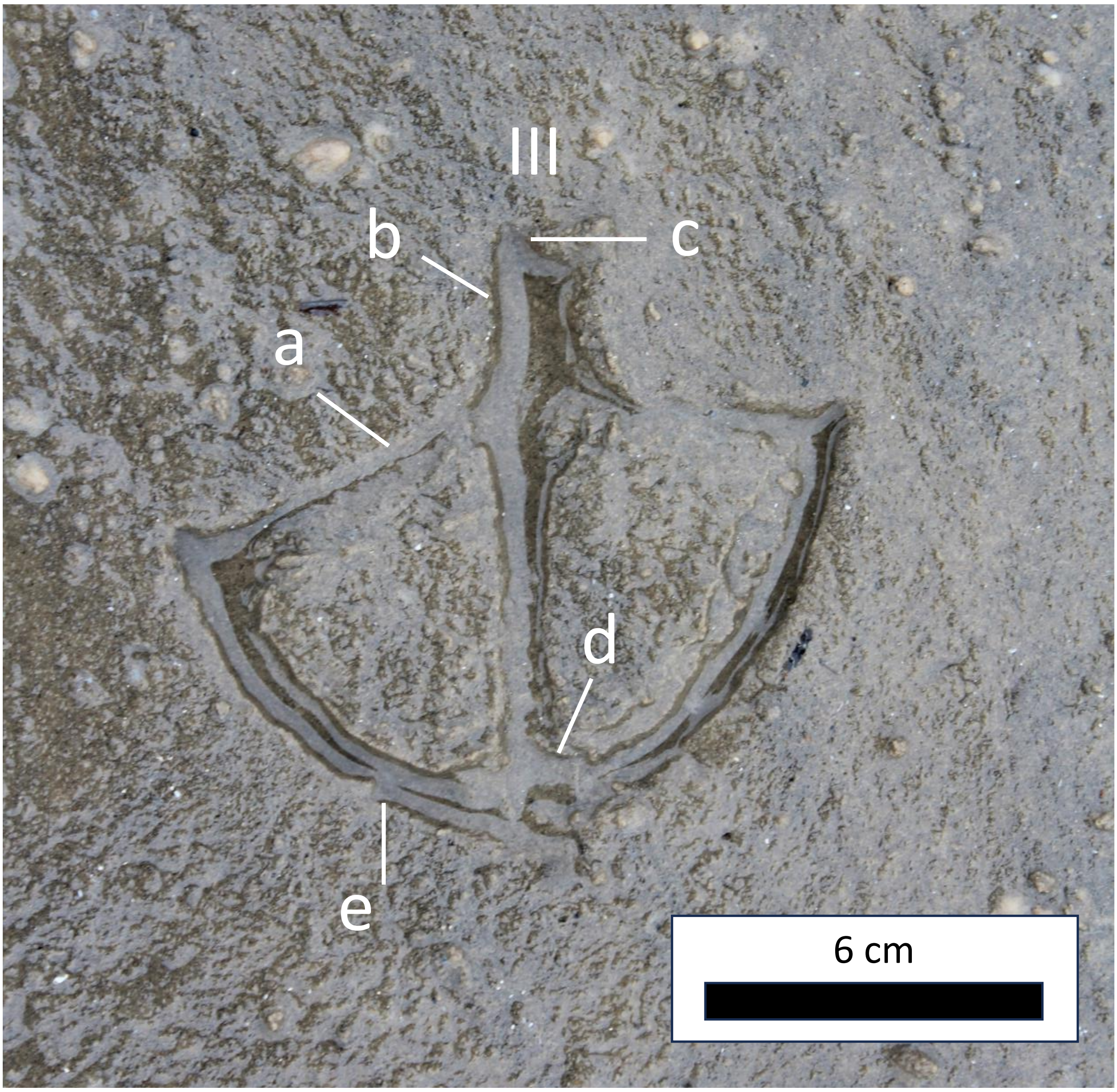

Figura 13. Pegada de flamingo-chileno (*Phoenicopterus chilensis*) no Parque Nacional da Lagoa do Peixe, Brasil. Notar a membrana interdigital (a) deixando livre o terço distal do dígito III (b), dígitos de extremidade distal rombuda (c), alta divaricação (d) e perímetro posterior alongado (e).

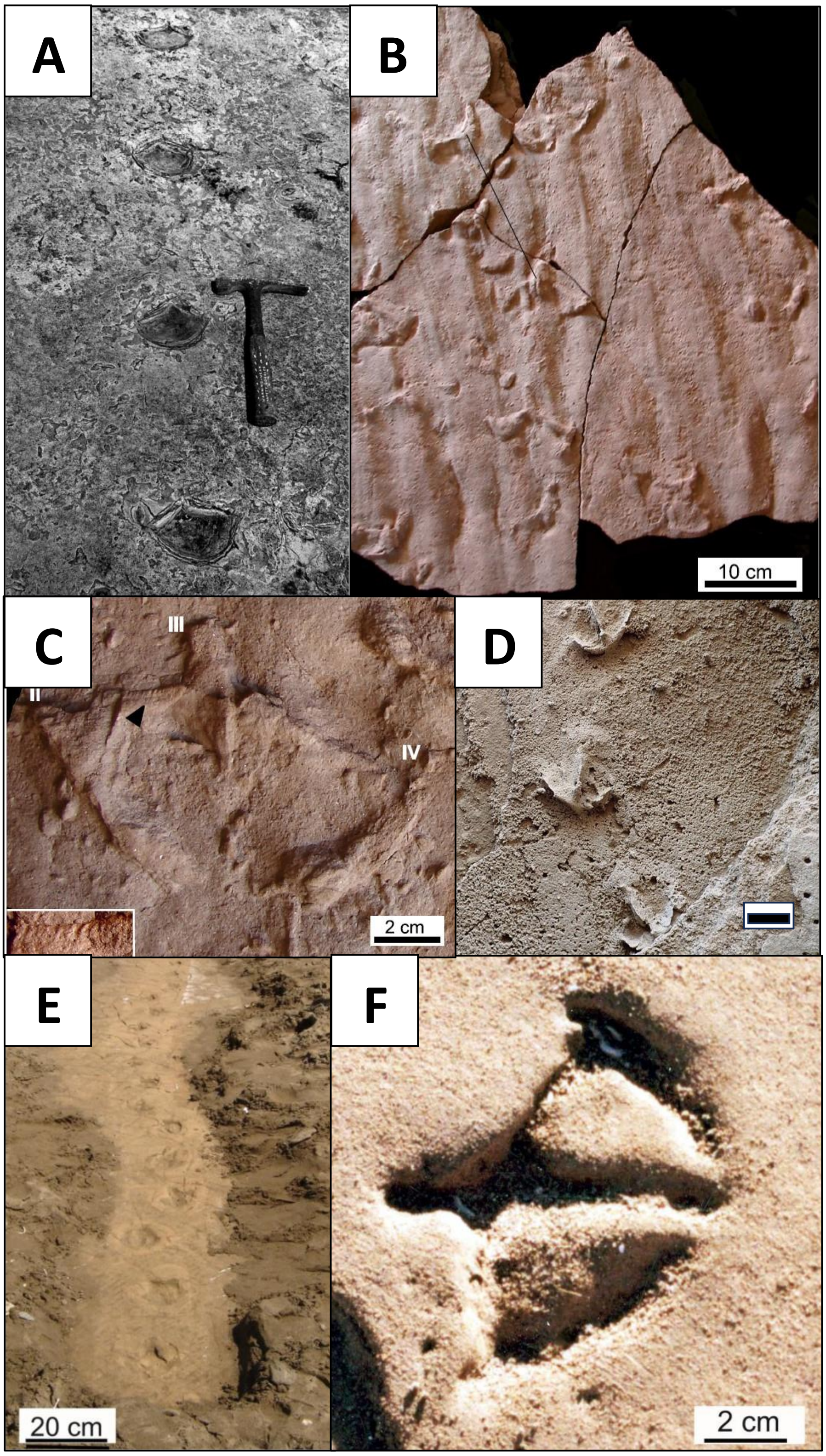

Figura 14. Exemplos de pegadas fósseis de *Phoenicopterichnum*. Mioceno: (A) Formação Río Negro, Argentina, extraído de Aramayo (2007); (B) Formação Vinchina, Argentina, extraído de Melchor *et al*. (2012); (C) Formação Vinchina, Argentina, extraído de Melchor *et al*. (2012). Pleistoceno: (D) Formação Waenhuiskrans, África do Sul, extraído de Helm *et al*. (2020); (E) Formação Pehuen-Có, Argentina, extraído de Aramayo *et al*. (2015); (F) Formação Pehuen-Có, Argentina, extraído de Aramayo *et al*. (2015).

Pistas (repichnia) são o tipo de preservação ideal para inferir o comportamento dos produtores, pois permitem interpretar aspectos como orientação e velocidade do deslocamento. Como animais filtradores, o rol de técnicas empregadas pelos flamingos é dominado por comportamento de caminhada, enquanto o animal filtra os organismos do substrato ou da água. Entretanto, na ausência de traços do bico, é difícil afirmar a partir de uma pista se o produtor estava em deslocamento de alimentação (forrageio), ou simplesmente caminhando de um ponto para outro, sem se alimentar. Melchor *et al*. (2012) observaram que, em *P. chilensis* na natureza, o tamanho da passada diferia quando a ave se alimentava e quando apenas se deslocava. Através de análises de vídeo, os autores calcularam o ângulo entre os tibiotarsos ao nível do ventre: este ângulo diminuía na medida em que a ave diminuía sua velocidade para se alimentar, e aumentava durante o deslocamento sem forrageio. Assim, pistas com baixa distância entre pegadas sucessivas pode ser um bom indicativo de comportamento alimentar em flamingos ancestrais. Entretanto, estudos adicionais precisam verificar a abrangência da relação direta entre tamanho da passada, distância entre pegadas e comportamento. É possível, por exemplo, que tal distâncias menores entre pegadas também possam indicar deslocamento em águas profundas, já que esta situação impõe restrições biomecânicas aos flamingos em deslocamento, que necessitam aumentar a elevação da articulação tibiotarsal-tarsometatarsal para vencer a maior resistência da coluna d´água, conforme demonstrado por Palecek *et al*., (2021), o que também implica em diminuição da passada e consequente redução da distância entre pegadas.

O registro fóssil de pegadas afins aos flamingos predomina em camadas do Mioceno, concentrando-se no Mioceno Superior da Argentina, principalmente em depósitos evaporíticos (Alonso, 1987; Leonardi, 1994; Zavala & Freije, 2001; Contreras, 2006; Aramayo, 2007; Melchor *et al*., 2012; Alonso, 2012; Farina *et al*. 2019). As localidades de ocorrência destas pegadas, em sequência:

Sedimentos marinhos costeiros da Formação Upper Red, Mioceno iraniano, associadas a pegadas de mamíferos carnívoros e de aves tridáctilas e tetradáctilas (Abbassi & Shakeri, 2005).

Formação Horse Spring, Nevada, Estados Unidos. Serravaliano, Mioceno Médio, 13,86–12,73 Ma (Lamb *et al*., 2020). Travertino arenoso formado em lago raso.

Pegadas medianamente preservadas atribuídas a Anseriformes e Phoenicopteriformes (Alonso, 2012).

Membro Monte Amarillo, Formação Sijes, Salta, Argentina. Torniassian, Mioceno Tardio, ~7,5 Ma (Alonso, 1987, 1992; Leonardi, 1994). Bacia endorreica continental, paleoambiente lacustre alimentado por águas termais, em clima árido/semiárido e vulcanismo ativo. Estratos de argilitos verdes a pardos ritmicamente alternados com evaporitos de borato e gesso e tufos vulcânicos (Pingel *et al*., 2020). As pegadas ocorrem em fácies associadas a gretas de contração, marcas de gotas de chuva e numerosas pegadas atribuídas a aves aquáticas de diferentes grupos. As fácies evaporíticas lacustres boratíferas da Formação Sijes (Mioceno Tardio) preservam, além de Phoenicopteriformes, pegadas de aves atribuídas a Anseriformes, Charadriformes e Passeriformes (Alonso, 1987, 1992; Leonardi, 1994).

No Membro superior da Formação Río Negro da Argentina (Mioceno Tardio) pegadas de flamingo ocorrem em fácies interdunares, formada por lâminas finas de carbonato contendo bivalves unionídeos (Zavala & Freije, 2001; Aramayo, 2007).

Membro Carbonate, Formação Copper Canyon, California, Estados Unidos. Tortoniano, Mioceno Tardio, 10 a 7 Ma (Scrivner & Bojter, 1986). A figura 3B em Scrivner & Boiter (1986) é denominada *Avipeda* sp. [*sic*] B, porém lembra a Phoenicopteridae no formato geral e no tamanho, embora não possua impressão da membrana interdigital.

Formação Blanca Lila, Salta, Argentina. Pleistoceno, 1,6–0,16 Ma (Pingel *et al*., 2020). Paleossalar de fácies aluviais, arenosas, praias lamosas e evaporitos halíticos. Pegadas mal preservadas correspondentes a Anseriformes, Phoenicopteriformes e Charadriformes (Alonso, 2012).

Prováveis pegadas de flamingo ocorrem também no Conglomerado Gila (Plioceno Tardio, Arizona, EUA; Thrasher, 2007), em depósitos lacustres alcalinos e salinos. Originalmente comparadas com pegadas de cisnes, Melchor *et al*. (2012) sugeriram uma forte semelhança com pegadas de flamingo atuais. As pegadas do icnogênero *Presbyorniformipes* (Eoceno Tardio, Green River Formation, EUA) lembram também a dos flamingos atuais, embora tenham o dígito I impresso, o que poderia remeter a *Juncitarsus*. Entretanto, *Presbyorniformipes* é tradicionalmente atribuído à Presbyornithidae, família de Anseriformes que conta com abundante registro somatofossilífero no Paleógeno (Yang et al., 1995). De fato, *Presbyornis* exibe tantas semelhanças com os flamingos atuais que antigamente se pensava que pudessem estar envolvidos na ancestralidade dos Phoenicopteridae (Feduccia 1977). Inclusive, estão preservadas pistas deste icnogênero associadas com traços de forrageio vagamente similares aos produzidos por flamingos em forrageio de caminhada (Figura 8).

Outrossim, pegadas produzidas em sedimentos de baixa umidade podem não registrar a membrana interdigital (Melchor *et al*., 2012). Portanto, pegadas não palmadas originalmente produzidas por flamingos podem estar sendo erroneamente interpretadas como sendo originadas por outros tipos de aves aquáticas (Melchor *et al*., 2012).

O predomínio de pegadas de flamingos em um intervalo restrito do Mioceno corresponde a um dos períodos também restritos de formação dos depósitos evaporíticos de borato nesta mesma época (Alonso, 2012). Esta associação também teria um potencial de aplicação econômica na identificação de sequências boratíferas (Alonso, 1987, 2012; Melchor 2015)

Uma das características marcantes dos flamingos modernos é a construção de ninhos de monturo (Figura 15A), feitos principalmente com material plástico como lama saturada, que a ave empilha e molda com o bico até adquirir a geometria final de um cone invertido (ou colunar) com uma câmara incubatória rasa no topo (Allen, 1956; Rooth, 1965; Del Hoyo, 1992), podendo haver variações deste modelo básico (More *et al*., 2020). Os flamingos são estrategistas-K extremos, incubando apenas um ovo de tamanho relativamente grande (raramente dois ovos). Nidificam em colônias de dezenas até milhares de indivíduos, em superfícies topográficas ligeiramente acima do nível de base e isoladas por grandes corpos d’água onde os adultos (que se revezam na incubação e trato do ninhego), podem forragear, prevenindo assim a perda da ninhada tanto por inundação quanto por predação (Frias-Soler *et al*., 2022). Tal estratégia de nidificação contrasta com aquela adotada pelo grupo-irmão Podicipedidae, que constrói ninhos flutuantes de matéria vegetal, onde incuba ninhadas de dois a sete ovos pequenos (Llimona & del Hoyo, 1992).

Grellet-Tiner *et al*. (2012) descreveram um ninho fossilizado contendo restos vegetais e cinco ovos – cuja casca possui microestrutura similar à dos flamingos e diferente da dos mergulhões – em depósitos lacustres levemente salinos datados do Mioceno Inicial da Formação Tudela, Espanha (~18,3 Ma) (Figura 15B). Estes vestígios estão associados com fragmentos de tibiotarso e tarsometarso, cuja morfologia é diagnóstica de Phoenicopteridae (basal). Isto indica que os flamingos ancestrais, embora anatomicamente similares aos flamingos coronais, tinham uma estratégia reprodutiva homóloga à dos mergulhões, a qual seria a condição plesiomórfica para Mirandornithes (Grellet-Tiner *et al*., 2012); infere-se assim que a evolução do ninho em monturo ocorreu associada à colonização de ambientes salinos e hipersalinos de escassa vegetação, revelando-se uma estratégia reprodutiva bem sucedida desde pelo menos o Mioceno Tardio, que é o intervalo estimado de origem dos flamingos coronais (Frias-Soler *et al*., 2022).

Scott *et al*. (2012) relatam ninhos fossilizados de flamingos nas margens dos lagos Bogoria e Magadi, no Quênia, datados do Pleistoceno Tardio e Holoceno Inicial (Figura 15C). Estes ninhos estão associados a superfícies enrijecidas pelo pisoteio constante dos flamingos ao redor das colônias de nidificação, sendo caracterizadas pelo adensamento de pegadas e presença de poros de bolhas originados pela movimentação constante dos flamingos sobre substratos saturados. As flutuações do nível dos lagos desgastam as camadas externas dos ninhos, que são mais friáveis, mas o restante interno da estrutura é resistente e de fácil preservação, podendo inclusive ser destacado da superfície do terreno e transportado em enchentes posteriores (Scott *et al*., 2012). Covas rasas provocadas pela retirada de substrato para a construção do ninho podem ser preservadas circundando o monturo de nidificação (Figura 15C), conferindo à estrutura uma aparência similar ao ROT – algo para futura investigação sobre a presença dos ROTs no registro fóssil.

Apesar de não serem considerados icnofósseis, o registro de ovos fósseis atribuídos a Phoenicopteriformes será brevemente abordado a seguir, dada a sua íntima associação com estruturas de nidificação. Além do registro de Grellet-Tiner *et al*. (2012), doze outros ovos são conhecidos do Quaternário do México (Del Campo, 1944; Cruz *et al*., 2023).

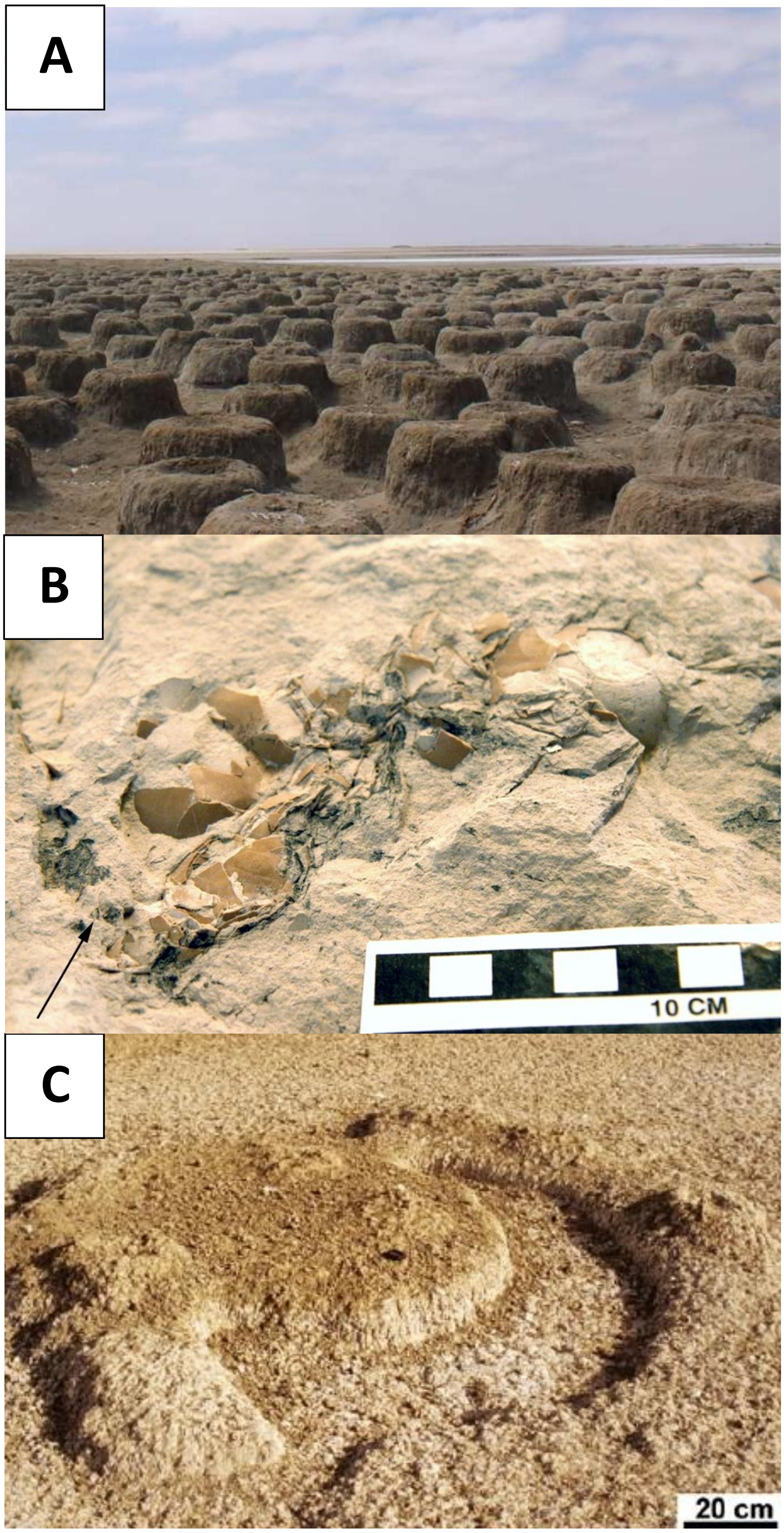

Figura 15. (A) Ninhos em colônia reprodutiva de flamingos-chilenos (*Phoenicopterus chilensis*) no norte do Peru; extraído de More *et al*. (2020). (B) Ninho de Phoenicopteriformes do Mioceno Inicial da Espanha (Formação Tudela), com cinco ovos preservados; a seta indica material vegetal preservado, possivelmente Fabaceae; extraído de Grellet-Tiner *et al*. (2012). (C) Ninho degradado de flamingo-pequeno (*Phoeniconaias minor*) no lago Bogoria, Quênia; notar o ninho degradado como monturo de baixa altura e a trincheira circundante escavada para a construção do ninho, conferindo à estrutura uma aparência similar aos ROTs; extraído de Scot *et al*., (2012).

4. MATERIAL E MÉTODOS

4.1. Observações de campo (Artigo 1)

O estudo do comportamento de pisoteio e das estruturas originadas ocorreu no Parque Nacional da Lagoa do Peixe (PNLP, 31◦14'49″ S, 50◦57'19” W), durante o inverno austral, nas datas de 30 de agosto e 15 de setembro de 2018, período correspondente ao pico local de abundância do flamingo-chileno (Delfino & Aldana-Ardila, 2020) (Figura 16). O comportamento dos flamingos foi registrado por meio de fotografias e gravações de vídeo. As estruturas biogênicas foram fotografadas, medidas em campo e, durante a campanha de setembro de 2018, observadas para acompanhar a ação dos agentes tafonômicos influenciando sua destruição, alteração ou preservação. A permissão de pesquisa no PNLP foi concedida pelo Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio, através da “Autorização para atividades com finalidade científica Número: 62203-1”, disponível no Anexo 1.

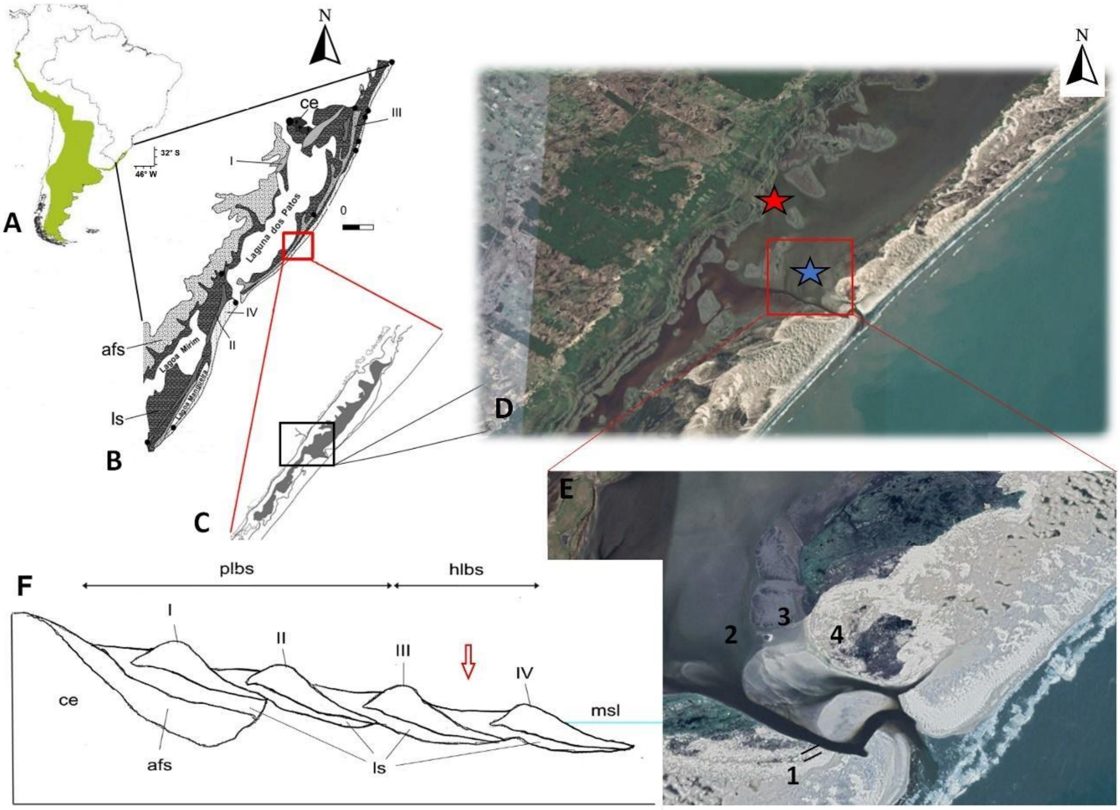

Figura 16. Mapas e imagens da distribuição geográfica do flamingo-chileno (*Phoenicopterus chilensis*) na América do Sul (modificado de BirdLife International, 2022) (A) e localização da Planície Costeira no estado do Rio Grande do Sul, sul do Brasil (B); afs: sistema de leques aluviais, ce: embasamento cristalino, ls: sistema lagunar, hlbs: sistema lagunar-barreira do Holoceno, plbs: sistema lagunar-

barreira do Pleistoceno, msl: nível do mar moderno, I: Barreira I, II: Barreira II, III: Barreira III, IV: Barreira IV; C) Lagoa do Peixe na Planície Costeira central; D) porção central da Lagoa do Peixe na Barra da Lagoa, mostrando os locais nos lados leste (azul) e oeste (vermelho) onde foram registrados flamingos em pisoteio rotatório (altura do ponto de vista 11. 94 km do Google Earth, setembro de 2018); E) vista ampliada da (1) Barra da Lagoa, (2) canal da Barra da Lagoa, (3) planície arenosa de retrobarreira e (4) campos de dunas transgressivo (altura do ponto de vista 2. 87 km do Google Earth, setembro de 2018); e F) seção transversal de sistemas deposicionais de leque aluvial e lagunar-barreira no leste do Rio Grande do Sul; a seta vermelha indica a posição da Lagoa do Peixe entre as Barreiras III e IV (modificado de Tomazelli & Villwock, 2000).

4.2. Área de estudo (Artigo 1)

O Parque Nacional da Lagoa do Peixe é uma área úmida no Litoral Médio do Rio Grande do Sul, de importância internacional na conservação de aves migratórias de ambos os Hemisférios (Figura 16). A região tem um clima subtropical húmido (Cfa) (Alvares *et al*., 2013), com 3-5 ◦C de temperatura mínima no inverno, 32-34 ◦C temperatura máxima no verão, 19,7 ◦C de temperatura média anual e precipitação média anual de 1.569 mm durante o período de amostragem, conforme dados obtidos na estação meteorológica localizada perto da cidade de Mostardas (INMET, 2021). Os ventos de norte e nordeste predominam durante todo o ano, enquanto os ventos de sudoeste predominam de abril a agosto (outono/inverno austral) (Fonzar, 1994). Os ventos de sudoeste estão associados à passagem de sistemas frontais (frentes frias) que aumentam a precipitação, favorecem a ocorrência de tempestades e forçam o mar em direção à costa, elevando o nível d’água na laguna (Delaney, 1962; Tomazelli, 1993).

A Lagoa do Peixe (Figura 16) é o principal corpo d'água do PNLP, a qual nomeia o Parque. Trata-se de uma laguna salobra pouco profunda (36 km comprimento, 1 km de largura e até 60 cm na sua profundidade máxima), cuja salinidade diminui de 30% na zona mais próxima do oceano para 5% no seu interior (Arejano, 2006). A Lagoa do Peixe é praticamente isolada do Oceano Atlântico por uma península arenosa, conectando-se ao oceano apenas por uma enseada chamada "Barra da Lagoa" (WHSRN, 2022) (Figura 16E), local onde ocorreram as observações das estruturas biogênicas. Influenciado pela mistura de água doce e salgada, esse ecótono é altamente produtivo, favorecendo uma comunidade bentônica diversificada que, por sua vez, sustenta uma elevada biodiversidade de aves aquáticas (Bencke *et al*., 2006). A área é designada como sítio RAMSAR número 603 (RAMSAR, 1997).

4.3. Espécie-focal

A elevada diversidade de habitats faz do PNLP um local promissor para investigar questões icnológicas relativas a aves e outros animais selvagens (Grangeiro & Netto, 2003; Netto & Grangeiro, 2009). A combinação variada do ciclo das marés, vento, precipitação e manejo humano expõe em grandes extensões o fundo das margens da Lagoa do Peixe, rico em nutrientes, sustentando enormes populações de aves aquáticas (WHSRN, 2022; Bencke *et al*., 2006). Duas espécies de flamingos ocorrem no PNLP: o flamingo-chileno (*Phoenicopterus chilensis*) é o mais comum e ocorre durante todo o ano como residente não reprodutor, aumentando em número durante a migração invernal a partir de suas áreas de nidificação (Antas, 1994; Delfino & Aldana-Ardila, 2020); e o muito mais raro flamingo-dos-andes (*Phoenicoparrus andinus*), ocasionalmente visto isolado ou em pequenos bandos (Bornschein & Reinert, 1996).

O flamingo-chileno é a mais comum e difundida das três espécies de flamingos endêmicas da América do Sul (Lesterhuis *et al*., 2008); distribui-se do Equador à Terra do Fogo, estendendo-se para leste (como migrante não reprodutor) até ao Uruguai e sudeste do Brasil (BirdLife International, 2022). Em algumas das suas áreas orientais, como o PNLP, a espécie pode ser encontrada durante todo o ano, com um afluxo significativo de migrantes no outono/inverno austral (Somenzari *et al*., 2018).

4.4. Compilação bibliográfica e videográfica (Artigo 2)

Para avaliar a relação entre a produção de estruturas de pisoteio e diferentes descritores ambientais, estruturou-se um banco de dados contendo registros de literatura e de arquivos eletrônicos de vídeo para todas as espécies modernas de flamingos. Para a revisão da literatura, consultou-se as bases de dados Web of Science e Google Scholar, utilizando combinações de termos associados à taxonomia (flamingo, Phoenicopteridae, *Phoenicopterus*, *Phoenicoparrus*, *Phoeniconaias*), icnologia (biogenic structures, biogenic sedimentary structures) e comportamento (feeding, foraging, paddling, stamping, stomping, treading). Alguns artigos continham apenas descrições muito genéricas sobre o pisoteio, sem mencionar a rotação caraterística do pisoteio rotatório, mas que também não especificavam se a ave permanecia no mesmo local enquanto pisoteava (pisoteio estacionário) ou se se movia para a frente ou para trás (pisoteio em deslocamento) – nestes casos, o comportamento foi registrado como pisoteio indeterminado.

Os vídeos online foram amostrados no sítio eletrônico eBird (2023), uma importante plataforma com registros de aves (listas de espécies, fotografias, vídeos) fornecidos por colaboradores de todo o mundo. O conjunto de dados do eBird cobre uma vasta área geográfica, permitindo o acesso à informação ornitológica em escala global (Smith *et al*., 2022). Foram incluídos no banco de dados apenas os indivíduos que realizaram um giro completo de pisoteio rotatório, ou um mínimo arbitrário de 5 segundos de filmagem para as outras modalidades de pisoteio.

4.5. Softwares utilizados

As fotografias de campo foram posteriormente tratadas no software de edição de imagens Paint.NET (Brewster, 2019) e suas medidas morfométricas foram calibradas no software ImageJ versão 1.53e (Rasband, 2021). Os vídeos foram utilizados para descrever a sequência de movimentos realizados pelas aves em pisoteio, isoladas em lapsos de tempo de 0,02 ms de 0,02 ms utilizando o PlayMemories Home (Sony Corporation, 2022). As análises estatísticas foram efetuadas no software de programação R versão 3.6.1 (R Core Team, 2021).

4.6. Nomenclatura

Nomes vernáculos e científicos seguem o Comitê Brasileiro de Registros Ornitológicos (Pacheco *et al*., 2021) e Costa *et al*. (2000). A nomenclatura dos termos geocronológicos e cronoestratigráficos segue Rios-Netto & Koutsoukos (1994).

5. CONTEXTO GEOLÓGICO

A descrição do contexto geológico diz respeito ao estudo empreendido no Artigo 1.

A região fisiográfica da Planície Costeira do Rio Grande do Sul abrange um conjunto de extensos sistemas deposicionais do tipo lagunar-barreira, desenvolvidos durante o Quaternário pelo retrabalhamento de depósitos de leques aluviais acumulados ao longo das elevações adjacentes de rochas pré-cambrianas interiores. Este processo ocorreu durante vários ciclos glacio-eustáticos de transgressão-regressão (Villwock & Tomazelli, 1995; Corrêa, 1996; Tomazelli & Villwock, 2000). Estes ciclos deram origem a quatro sistemas deposicionais designados por Barreiras I, II, III (Pleistoceno) e IV (Holoceno Tardio), por ordem cronológica decrescente e em direção ao mar (Dillenburg *et al*., 2009) (Figura 16F).

O atual sistema lagunar da Lagoa do Peixe situa-se num terreno de retrobarreira entre as Barreiras III e IV. A Barreira III é formada por uma sucessão de fácies praiais e marinhas rasas cobertas por depósitos eólicos, originados a ~125 Ka durante uma fase regressiva (Tomazelli, 1985). Instalada no final da última transgressão (~6–5 Ka), a Barreira IV é constituída por areias quartzosas finas a muito finas originadas pela erosão da Barreira III, com a adição de sedimentos da atual plataforma continental (Villwock, 1972; Villwock & Tomazelli, 1995). Os processos sedimentares ainda estão ativos na Barreira IV, geomorfologicamente dominada por campos de dunas barcanoides, alinhados perpendicularmente aos ventos predominantes de norte-nordeste (Dillenburg *et al*., 2009). A configuração destas barreiras restringe a fonte de sedimentos disponíveis para os processos tafonômicos na Lagoa do Peixe a uma granulometria que varia de areia fina a lama; no fundo da laguna predomina a areia fina, mais grosseira no canal de conexão da laguna com o mar (Arejano 2006).

Grandes extensões da margem leste (300 a 400 m) podem ficar expostas durante o dia devido ao aumento da intensidade dos ventos predominantes de norte-nordeste, os quais represam a massa de água em direção à margem oeste. À noite, as águas tendem a regressar aos níveis batimétricos anteriores, devido à diminuição da intensidade do vento (Arejano, 2006). A maré astronômica de baixa amplitude tem pouca influência nos processos sedimentares de maior escala, exceto nos períodos em que as tempestades amplificam os efeitos das marés (Tomazelli & Villwock, 1992; Arejano, 2006), produzindo marés meteorológicas que podem exceder as marés astronômicas em até um metro, mobilizando maior volume de sedimentos e modelando abruptamente a morfologia do sistema deposicional (Calliari *et al*., 1998).

6. ANÁLISE INTEGRADORA DOS ARTIGOS DA TESE

Estudos neoicnológicos em icnocenoses modernas podem melhorar a interpretação de vestígios produzidos por organismos antigos e esclarecer quais agentes tafonômicos operavam em seus paleoambientes. Ao final da presente tese de doutorado, demonstrou-se que os flamingos possuem um excelente potencial de abordagem como organismos-modelo para a compreensão dos mecanismos ambientais que regulam os processos de interação animal-substrato, bem como para o teste de hipóteses a respeito de associações de traços fósseis e diferentes fatores ambientais.

A origem do comportamento de pisoteio com profundas raízes filogenéticas (Rooth, 1965) e a conspicuidade e ampla distribuição das estruturas geradas apontam para a possibilidade de sua ampla distribuição lateral e vertical nas sequências sedimentares, respectivamente. Isto evidencia a questão da ausência de tais estruturas no registro cenozoico, podendo-se aventar como respostas tanto questões de ordem tafonômica quanto de viés amostral. Por serem estruturas de baixa altura e indentação pouco profunda, seu reconhecimento pode ser dificultado em razão do achatamento das camadas, quando então seriam distinguidas apenas como leves ondulações em seção transversal, ou então identificados através da característica conformação circular da pista de pegadas em vista planar. Outro provável motivo pode ser a confusão com traços fósseis com variados graus de semelhança aos ROTs, entre eles *Piscichnus* (Feibel, 1987; O'Shea *et al*., 2012), e alguns microbialitos (Kennard & James, 1986; Riding, 2011), todos produzidos nos mesmos ambientes dos flamingos. Alguns estudos neoicnológicos propõem a reinterpretação do produtor inferido para a autoria de alguns icnogêneros (*e.g*., Muñiz *et al*., 2015), podendo o mesmo ocorrer com os ROTs de flamingos. Sugere-se que estudos adicionais investiguem a similaridade morfológica entre estas estruturas por meio de, por exemplo, análises de agrupamento ou de geometria morfométrica, técnicas que se encontram em crescente uso na paleoicnologia (Ledoux & Boudadi-Maligne, 2015; Guerrero-Arenas *et al*., 2018) e na neocinologia (Rodrigues & Dos Santos, 2004; Hembree, 2016; Hembree *et al*., 2012).

Enfatiza-se a necessidade de uma revisão abrangente da evidência fóssil relativa aos flamingos, que inclua uma análise conjunta de material somato- e icnofossilífero, relacionando com a informação paleoclimática para averiguar a possível influência das sucessivas subidas e descidas do nível do mar – em especial no Mioceno – na especiação e surgimento das linhagens.

7. CONCLUSÕES

O primeiro artigo (Barcelos-Silveira *et al.*, 2023) mostra, com base em observações de campo, que em ambientes lagunares associados à lençóis eólicos, as condições ambientais são altamente favoráveis à preservação das estruturas. O trabalho evidencia também que modificações na dinâmica dos agentes tafonômicos imprimem assinaturas características às estruturas, sendo possível traçar os processos pretéritos responsáveis pelas modificações (tafofácies). As estruturas de pisoteio rotatório produzidas por *P*. *chilensis* na Lagoa do Peixe apresentaram uma variedade de morfologias relacionadas ao tipo de agente tafonômico e ao grau de alteração decorrentes. Partindo das estruturas recentemente produzidas, as alterações registradas devem-se a fatores como o movimento das marés ao nível da água, a inclinação do terreno e a atividade eólica. A erosão da estrutura foi menor nos terrenos planos e atingiu o pico nas superfícies inclinadas onde se formam riachos intermitentes. Estas observações apontam para o potencial de preservação dos vestígios modernos de flamingos e para sua importância para inferências paleoecológicas e paleobiológicas.

No artigo 2, demonstrou-se que, da mesma forma que *Phoenicopterichnum*, as estruturas de pisoteio ocorrem em ambientes lagunares, salinos e alcalinos, mas não são restritas a eles ou preferentemente a eles associadas. Os ambientes lagunares, salobros e moderadamente alcalinos predominaram no banco de dados de pisoteio e de estruturas de pisoteio; por sua vez, os ambientes lacustres foram secundariamente frequentes, seguidos pelos ambientes tidais não-lagunares. Isto pode indicar um viés preservacional para o registro de pegadas de flamingos em depósitos continentais lacustres, e um viés amostral dificultando o reconhecimento das estruturas de pisoteio em quaisquer das fácies possíveis. Uma relação entre o tipo de terreno e o tipo de estruturas biogênicas preservadas é reconhecível comparando ambientes que preservam pegadas e ambientes que preservam ninhos – nestes últimos, a escolha de locais predominantemente emersos e o constante pisoteio das aves compacta o substrato, impedindo o registro de pegadas e favorecendo a preservação dos ninhos. Grellet-Tiner *et al*. (2012) sugeriram que os ambientes de alta saturação mineral são os mais favoráveis à reprodução dos flamingos modernos, em virtude da reduzida fauna potencialmente predadora de ovos e filhotes. Assim, a associação de *Phoenicopterichnum* com fácies lacustres alcalinas e salinas pode antes indicar ambientes de reprodução do que ambientes não-reprodutivos. Por fim, este estudo atesta uma inesperada contribuição da ciência cidadã para a abordagem de tópicos e conceitos paleontológicos, geológicos e evolutivos ainda em desenvolvimento.

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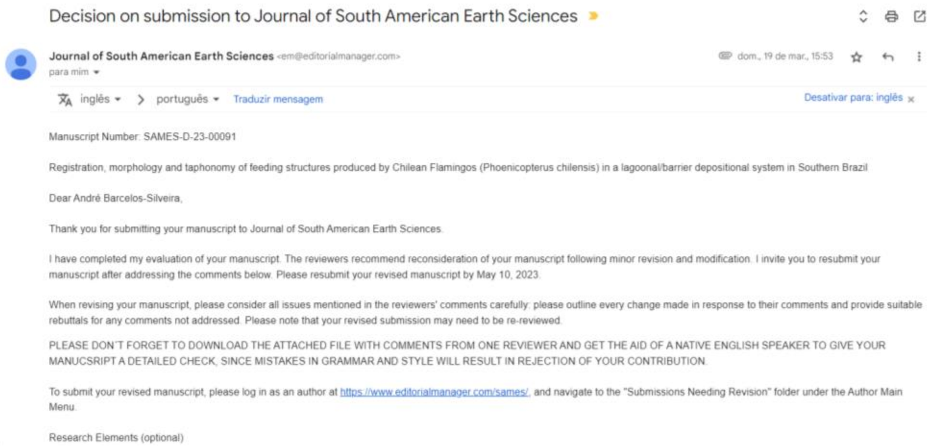
PARTE II

9. CORPO PRINCIPAL DA TESE

Nesta seção são apresentados os artigos científicos publicados e submetidos em periódicos constantes do Estrato PPGGeo, como resultados obtidos das pesquisas realizadas na presente Tese. Os textos dos artigos foram incluídos de forma integral, na mesma formatação de envio conforme as normas de cada revista. Dessa forma, a numeração de figuras, tabelas e material suplementar está restrita para cada artigo, e não seguindo a mesma ordem da Parte I desta tese.

9.1. Artigo 1

Barcelos-Silveira, A., Dentzien-Dias, P., Francischini, H. & Schultz, C.L. 2023. Registration, morphology and taphonomy of feeding structures produced by Chilean Flamingos (*Phoenicopterus chilensis*) in a lagoonal/barrier depositional system in southern Brazil. Publicado em *Journal of South American Earth Sciences*, 127: 104396 (Estrato PPGGeo N3).



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Registration, morphology and taphonomy of feeding structures produced by Chilean Flamingos (Phoenicopterus chilensis) in a lagoonal/barrier depositional system in Southern Brazil

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Registration, morphology and taphonomy of feeding structures produced by Chilean Flamingos (*Phoenicopterus chilensis*) in a lagoonal/barrier depositional system in southern Brazil

André Barcelos-Silveira [a], Paula Dentzien-Dias [b], Heitor Francischini [a], Cesar Leandro Schultz [a]

https://doi.org/10.1016/j.jsames.2023.104396

Temporal changes in land use and land cover due to retarding reservoir…
Journal of South American Earth Sciences, Volume 127…
Tâmara Bastos Silva, ..., Paulo Sávio Damásio da Silva

Orbital forcing of Upper Jurassic (Tithonian) shallow-water carbonates, Tethyan Adriat…
Palaeogeography, Palaeoclimatology, Palaeoecology, ...
Antun Husinec, ..., David B. Kemp

Fitting statistical probability distribution for evaporation in western Brazil
Journal of South American Earth Sciences, Volume 127…
Carlos José dos Reis, ..., Ivana Pobocikova

Registration, morphology and taphonomy of feeding structures produced by Chilean Flamingos (*Phoenicopterus chilensis*) in a lagoonal/barrier depositional system in Southern Brazil

André Barcelos-Silveira [a, *], Paula Dentzien-Dias [b], Heitor Francischini [a], Cesar Leandro Schultz [a]

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Highlights

- Flamingos register complex structures by differential use of both legs and bill.
- Rotating-stamping structures are prone to enter taphonomic pathways of preservation.
- Low energy tide and vicinity to aeolian sediment sources boost preservation.
- Modes of registration and preservation can enhance paleoenvironmental analysis.

ABSTRACT

Ichnological studies in modern settings can improve the interpretation of traces produced by ancient organisms and clarify which taphonomic agents operated in their paleoenvironments. This work analyzes examples from feeding structures produced by Chilean Flamingos (*Phoenicopterus chilensis*) in a lagoon/barrier depositional system in southern Brazil, describing the registration and morphology of feeding structures produced by rotating stamping, while also following taphonomic alterations. Newly registered structures consist of a central mound of piled sediment and a peripheral trench of overlapping footprints. The 52 stamping structures sampled showed a variety of morphologies related to the type of taphonomic agent and to the degree of alteration. Departing from the newly produced structures, the changes recorded are due to factors such as tidal range, current energy, terrain slope, and aeolian activity. The erosion of the structure was minor on the flat terrains and peaked at the stepper surfaces where intermittent streams form. Our observations point to the preservation potential of modern flamingo traces and to its putative importance for paleoecological and paleobehavioral inferences.

Keywords:

Neoichnology; neotaphonomy; Phoenicopteridae; bird ichnology; evolutionary taphonomy; preservation model

1. Introduction

The interpretation of biogenic structures preserved as trace fossils benefits from observing the production and preservation of traces in modern ecosystems. Such observations fall within the realm of neoichnology, a growing field in the thriving science of ichnology (Plotnick, 2012; Buynevich, 2015). Neoichnological studies help to establish a range of organism’s behaviors that are prone to registering a particular biogenic structure, as well as to clarify the taphonomic agents influencing its passing into the fossil record (Gío-Argaez et al., 2021). Instead of a purely destructive and filtering action of those less preservable remains and traces, taphonomic alteration also produces modifications that favorably creates and preserves new taphonomic elements in new taphonomic groups (or taphons), in a process called taphogenic production (Fernández-López, 2013). New taphonomic elements and taphons are the result of differential preservation of previous elements fitted to the changes of their environment (Fernández-López, 2006). As such, the observation of a range of taphonomic agents greatly increments our knowledge of how the biological information derived from biogenic production enters the fossil record as taphogenic entities, according to the interplay among taphonomic agents closing or opening the "taphonomic window" (Young and Hagadorn, 2020).

Although specialized to filter feed, the flamingos (Phoenicopteridae) show a versatile behavioral repertoire to seek different preys in different environments. Such plasticity manifests as the employment of varied foraging methods, each one adapted to specific prey types and substrate conditions (Rooth, 1965; Johnson and Cézilly, 2009; Delfino and Carlos, 2021). The stamping is a method of acquiring food where the bird agitates soft substrates at low water levels, by the means of vigorous, fast up and down leg movements, taking advantage of the large contact surface provided by its webbed feet (Hainard, 1932). In flamingos, the stamping can occur in three modes: i) in the standing stamping, the bird remains in the same place and oriented in the same direction while performing; ii) in the dislocating stamping, the performing bird moves forward or backwards; iii) finally, in the rotating stamping, the bird performs 360° turns around its body axis, with the head or feet as the pivot, turning both clockwise or counterclockwise (Rooth, 1965; Johnson and Cezilly, 2009).

Although the standing stamping can be used for similar reasons by many waterbirds (Simmons, 1961; Burger, 1988; Hendricks and Hendricks, 2006, Melnik et al., 2022), the rotating stamping appears to be specific to flamingos. Each of these behaviors produces a biogenic structure whose morphology is indicative of the original feeding mode. Those structures registered by rotating stamping are easily recognizable in the field, being elaborately architectured as a circular excavation (here called peripheral trench) surrounding a central mound of sediments (Allen, 1956). As such structures are variously dubbed in the literature (Table S1), here we suggest "rotating-stamping structure (ROT)" as a standard term to emphasize the specific mode of feeding behavior from which it originates, giving an unequivocal behavioral attribution useful to interpret eventual fossilized traces (Plotnick, 2012). As a particular structure tied to a specific behavior employed under a restricted set of environmental factors, ROTs can be used as good paleoenvironmental indicators, if they survive the taphonomical agents of destruction and become preserved in the fossil record.

ROTs were briefly mentioned in many studies (*e.g.*, Glassom, 1992; Gloe, 1998; Johnson and Cézilly, 2009; Rodríguez-Pérez and Green, 2006; Lee and Mayorga-Dussarrat, 2016; Gihwala et al., 2017), while their relevance in ecosystem engineering by flamingos was assessed in a few others (e.g., Gihwala et al., 2017; El-Hacen et al., 2019). However, we were unable to find studies on ROTs under the ichnological and taphonomic viewpoints, aside from generalized and often confusing morphological descriptions (Table S1). As such structures are ubiquitous, result in substantial reworking of the substrate and are widespread among flamingo species, they should be prone to preservation in the fossil record; however, ROTs have not yet been documented as a trace fossil (but see Helm et al., 2020 for a putative Pleistocene record). In addition, the processes regulating their preservational potential have not been evaluated. Based on field observations in a lagoonal/barrier depositional system in southern Brazil, we report the ROTs produced by Chilean Flamingos (*Phoenicopterus chilensis*), analyse the production behavior and substrate interaction, provide detailed morphological descriptions, investigate taphonomic processes and related morphological alterations and build a model for their hypothetical preservation in the geological record.

2. Study area

The Parque Nacional da Lagoa do Peixe (PNLP, 31º14'49” S, 50º57'19” W) is a 34,400-ha wetland reserve located at the central Coastal Plain of Rio Grande do Sul, the southernmost Brazilian state (Fig. 1A-C). The region has a humid subtropical (Cfa) climate (Alvares et al., 2013), with 3-5°C minimum temperature in winter, 32-34°C maximum temperature in summer, 19.7°C of mean annual temperature and mean annual precipitation of 1569 mm during the sampling period, as retrieved from meteorological station located near the city of Mostardas (INMET, 2022). North and northeast winds predominate year-round, while southwest winds become more frequent from April to August (austral autumn/winter) (Fonzar, 1994). Southwest winds are associated with the passage of frontal systems (cold fronts) that boost precipitation, favor the occurrence of storms and pile the sea towards the coast, raising the water level of the wetland (Delaney, 1965).

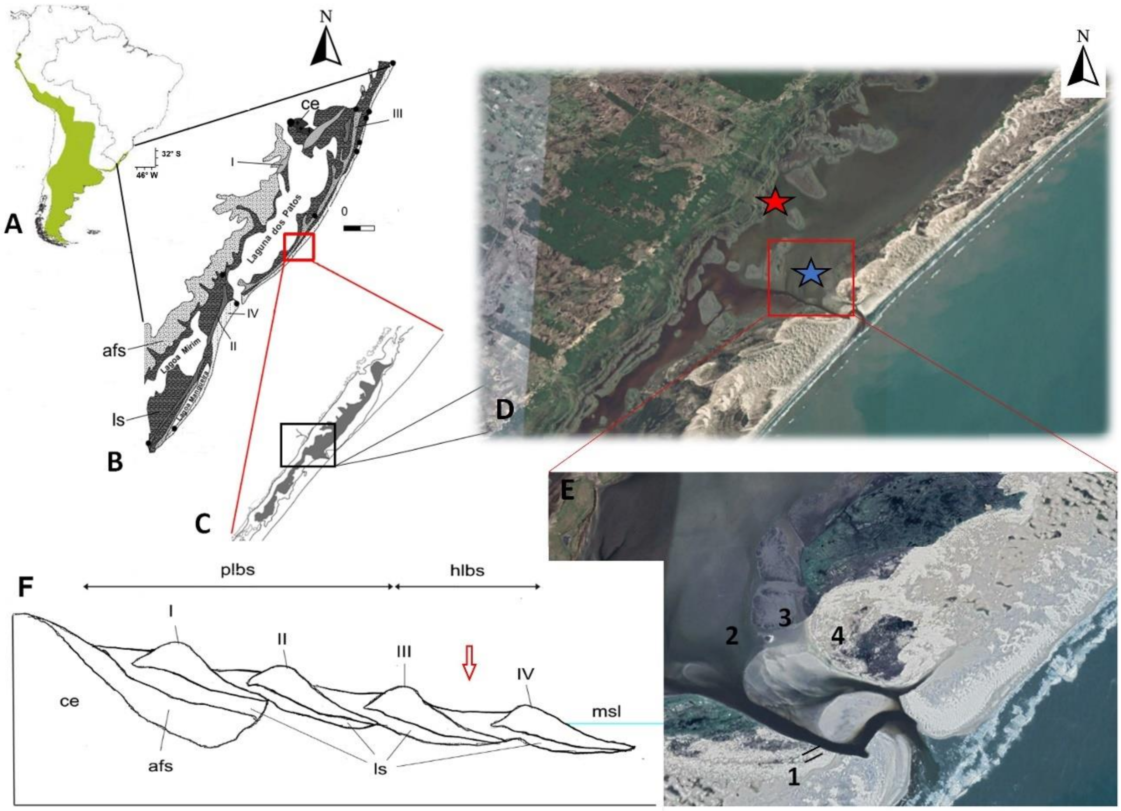

Fig. 1. Maps and images of (A) geographical distribution of Chilean Flamingo (*Phoenicopterus chilensis*) in South America (modified from BirdLife International, 2022) and location of B) Coastal Plain in Rio Grande do Sul state, southern Brazil; afs: alluvial fan system, ce: crystalline embasement, ls: lagoon system, hlbs: Holocene lagoon-barrier system, plbs: Pleistocene lagoon-barrier system, msl: modern sea level, I: Barrier I, II: Barrier II, III: Barrier III, IV: Barrier IV; C) Lagoa do Peixe at central Coastal Plain; D) central portion of Lagoa do Peixe at Barra inland, showing locations at east (blue) and west (red) sides of the lagoon where rotating stamping were recorded (viewpoint height 11.94 km from Google Earth, as taken at September 2018); E) enlarged view of the (1) Barra inlet, (2) debouchment area, with surrounding (3) backbarrier sand flat and (4) transgressive dune fields (viewpoint height 2.87 km from Google Earth, as taken at September 2018); and F) transversal section of alluvial fan and lagoon-barrier depositional systems in eastern Rio Grande do Sul, red arrow

indicates the position of the Lagoa do Peixe between Barriers III and IV (modified from Tomazelli and Villwock, 2000). [2-column fitting image]

2.1. Ecosystem settings

The Lagoa do Peixe ("Fish Lagoon", Fig. 1C) is the main PNLP water body, which names the Park. It is a shallow brackish lagoon (36 km length, 1 km width and reaches up to 60 cm in its maximum depth), whose salinity decreases from 30% in the lagoon area nearer to the ocean to 5% in its interior (Arejano, 2006). The Lagoa do Peixe is almost isolated from the Atlantic Ocean by a sand barrier peninsula and connects to oceanic waters only by an inlet dubbed "Barra da Lagoa" (WHSRN, 2022) (Fig. 1D-E), where our observations on biogenic structures were made. Influenced by the mixing of fresh and saltwater, such ecotone is highly productive, supporting a diverse benthic community which, in turn, sustains a high biodiversity of waterbirds (Bencke et al., 2006).

2.2. Geological settings

The Coastal Plain physiographic region encompasses an array of extensive lagoon-barrier depositional systems that developed during the Quaternary, by the reworking of alluvial fan deposits accumulated along the adjacent elevations of inland pre-Cambrian rocks, during several glacio-eustatic cycles of marine transgression-regression fluctuations (Corrêa, 1996; Tomazelli and Villwock, 2000). These cycles gave rise to four depositional systems called Barriers I, II, III (Pleistocene) and IV (Late Holocene), in descending chronological and seaward order (Dillenburg et al., 2009) (Fig. 1F).

The lagoonal system of Lagoa do Peixe lies on a backbarrier terrain between the Barriers III and IV. Barrier III is formed by a succession of beach and shallow marine facies covered by aeolian deposits that originated approximately 125,000 ybp during a regressive phase (Tomazelli and Villwock, 2000). Settled at the end of the last transgression (~6,000-5,000 ybp), Barrier IV is made up of fine to very fine quartzose sands originated from the erosion of Barrier III with the addition of sediments from the current continental shelf (Villwock and Tomazelli, 1995). Sedimentary processes are still active in Barrier IV, which is geomorphologically dominated by barchan dune fields, aligned perpendicular to the prevailing north-northeastern winds (Dillenburg et al., 2009). Such barriers' configuration restricts the source of sediments available for taphonomic processes at Lagoa do Peixe to a rather homogeneous granulometry ranging from fine sand to mud; in the lagoon's bottom largely predominate fine sand, coarser at the debouchment (Arejano, 2006).

Large extensions of the east bank (300 to 400 m) can be exposed during the day due to the increasing intensity of the prevailing north-northeastern winds, which dam the water mass towards the west bank. At night, the waters tend to return to previous bathymetric levels, due to the decrease in wind intensity (Arejano, 2006). The low-amplitude astronomical tide has little influence on the larger scale sedimentary processes, except in periods when storms amplify the effects of the tides, producing meteorological tides that can exceed astronomical tides by up to one meter, mobilizing greater volume of sediments and abruptly modeling the morphology of the depositional system (Villwock and Tomazelli, 1995).

2.3. Faunal settings

The high habitat diversity at the PNLP makes it a promising place to investigate ichnological issues relative to birds and other wildlife (Grangeiro and Netto, 2003; Netto and Grangeiro, 2009). The varied combination of tide cycle, wind, rainfall, and human management expose the nutrient rich mudflat at large extensions, sustaining huge waterbird populations (WHSRN, 2022; Bencke et al., 2006). Two species of flamingos occur in the PNLP: the Chilean Flamingo (*Phoenicopterus chilensis*) is the most common and occurs throughout year as a non-breeding resident, increasing in number during the winter migration of birds from their nesting areas (Antas, 1994; Delfino and Aldana-Ardila, 2020); and the much more rare Andean Flamingo (*Phoenicoparrus andinus*), occasionally seen isolated or in small flocks (Bornschein and Reinert, 1996).

3. Material and methods

3.1. Focal species

The Chilean Flamingo is the most common and widespread of the three flamingo species endemic to South America (Lesterhuis et al., 2008); it is distributed from Ecuador to Tierra del Fuego and extends eastward (as a non-breeding migrant) to Uruguay and southeastern Brazil (BirdLife International, 2022). In some of its eastern areas, as the PNLP, the species can be found year-round, with significant influx of migrants in austral autumn/winter (Somenzari et al., 2018).

The Chilean Flamingo is the smallest species of the genus *Phoenicopterus*, reaching 100-105 cm in height, with the males being slightly larger than females (Richter et al., 1991; Montalti et al., 2012). Chilean Flamingos select shallow water bodies as their ideal habitat, occupying both freshwater and saline lakes, lagoons, estuaries, and coastal flats from the sea level in Pacific and Atlantic coasts to up 4500 m in the Andes (del Hoyo, 1992; De la Peña and Rumboll, 1998). As its congeners of the genus *Phoenicopterus*, the maximum height of Chilean Flamingo’s upper jaw is lower than that of the flamingo species in the genera *Phoenicoparrus* and *Phoeniconaias* (Gray, 1860; Mascitti and Kravetz, 2002); at the same time, the thicker inner beak mesh apparatus allows to catch larger items than the high-keeled and thinner meshed *Phoenicoparrus* (Jenkin 1957; Zweers et al., 1995). Such differences are reflected in the diet preferences of each genus: *Phoenicoparrus* and *Phoeniconaias* feeds on cyanobacteria and microalgae, while *Phoenicopterus* relies on a more zoophagous diet, consuming many types of aquatic arthropods (mainly crustaceans as copepods and brine shrimps), mollusks and large foraminiferans (Olgivie and Olgivie, 1986).

The species is quite reasonably studied on its diet, ecology and behavior, and some of these works briefly mention the presence of ROTs (Cifuentes, 2007; Tobar et al., 2014; Lee and Mayorga-Dussarrat, 2016; Delfino and Carlos, 2021) – however, none of these studies were carried out under an ichnological point of view, lacking detailed descriptions of such traces or comparisons with structures made by other flamingo species. Strictly regarding ichnological studies, the Chilean Flamingo was investigated with focus on the tracks and trackways registration (Melchor et al., 2012, 2015; Alonso, 2012; Farina et al., 2019) and nest building (Johnson et al., 1958; Mascitti and Nicolossi, 1992; Sosa, 1999; Sosa and Martín, 2011; More et al., 2020).

In the PNLP, Chilean Flamingo most feed on calanoid copepods and nereid polychaetes (Aldana-Ardila and Carlos, 2021). Recently, Delfino and Carlos (2021) described the ethological repertory for Chilean Flamingo in the “Barra da Lagoa”, including brief accounts on stamping and a generalized mention of ROTs. In this way, our work expands the knowledge of stamping and ROTs for this species in the same locality.

3.2. Theoretical settings

To describe the variability in structures and better infer their preservation potential, we followed the concepts of evolutionary taphonomy by Fernández-López (2006), which view taphonomic processes not only as the destruction of biological information along its pathway to be incorporated in the geological record, but also as a creative process of new taphons. In this view, each alteration by taphonomic agents creates a new version of the anterior structure, and the different taphons are better interpreted as a series of an evolutionary taphonomic process. The theory of taphonomic evolution is an approach to explain the mechanisms of fossilization based on the original and modified architectures (composition and structure) of the taphonomic elements, the successive environmental changes and the functionality of these changes influencing its preservation potential.

3.3. Field sampling

Biogenic structures produced by Chilean Flamingos in PNLP (Fig. 2A) were studied during the austral winter, in August 30 and September 15, 2018. We found the structures by *ad libitum* searches along lagoon margins, as well as by direct observations of flamingo foraging groups and posterior investigations of the substrate after the birds take off from the foraging site. All the ROTs were assumed to be produced within 12-h interval of a tidal cycle.

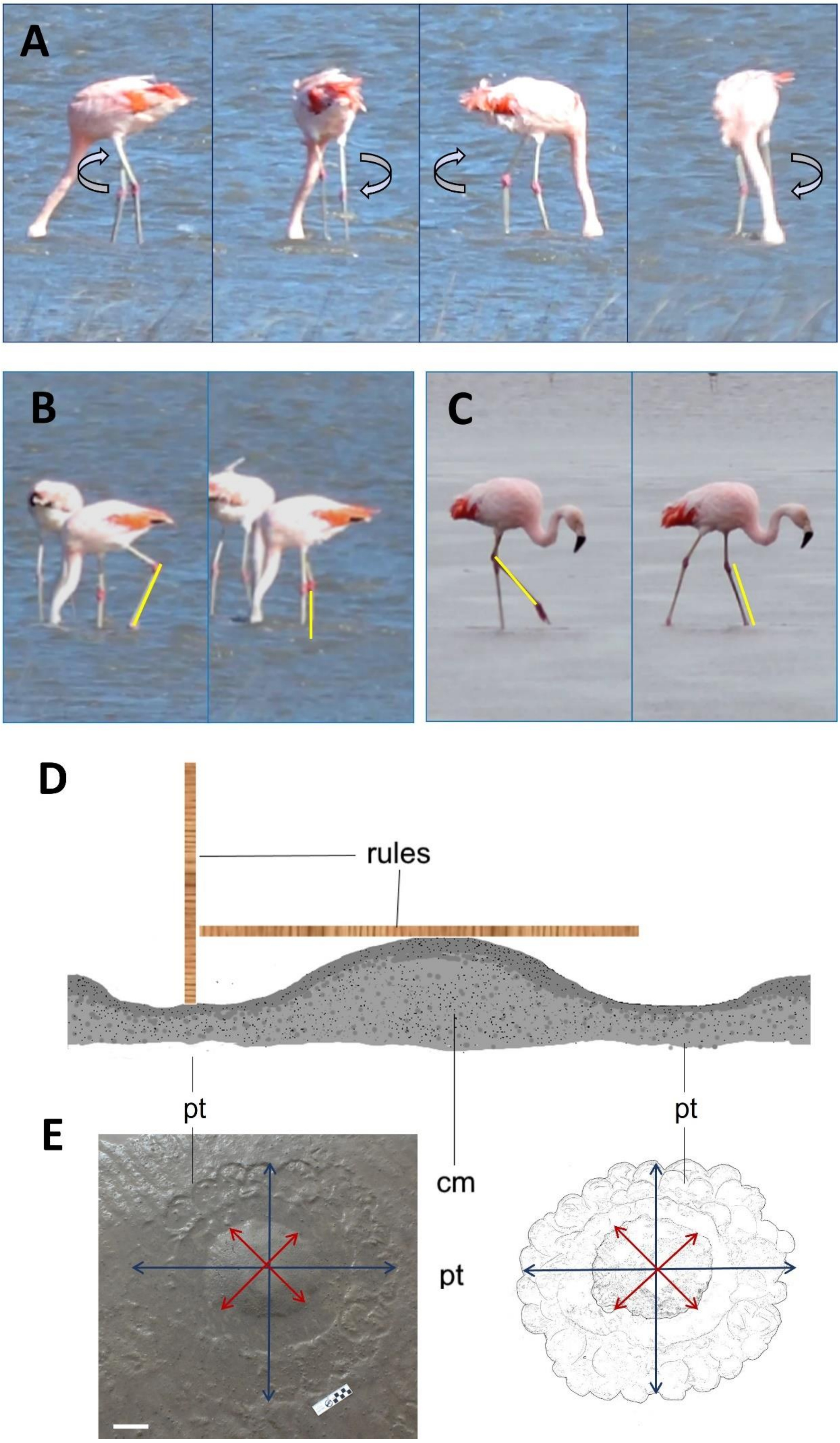
A
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Fig. 2. (A) Schematic movement sequence of a rotating-stamping Chilean Flamingo; the arrows at the level of the tibiotarsal-tarsometatarsal articulation indicate clockwise direction of the exemplified rotating-stamping individual. Foraging Chilean Flamingos at (B) west and (C) east margins of Lagoa do Peixe; the yellow bars depict the tarsometatarsus length used to calculate the water column height. (D) Height (cross section) and (E) central mound and peripheral trench diameter (plan view) measurements taken from the rotating-stamping structures. cm: central mound, pt: peripheral trench; blue arrows indicate the two measurements of the peripheral trench, red arrows indicate the two measurements of the central mound. Scale 10 cm. [2-column fitting image]

A Kodak Easyshare M530 digital camera was used for photographic and video records in field, with the following settings: 4000 × 3000 pixels, 480 dpi, ISO 80, aperture f/3.1, exposure time 1/400 seconds, focal length 6 mm; the structures were measured using a 15-m tape. The photos captured were later treated in Paint.NET image editing software (Brewster, 2019). The videos were used to describe the sequence of movements performed by stamping birds, extracted from 0.02 milliseconds time lapses using the PlayMemories Home (Sony Corporation, 2022).

3.4. Measurements

To calculate the water depth where Chilean Flamingos stomped, we estimated the fraction of tarsometatarsus submerged when supporting the body mass during stamping, then compared this fraction with tarsometatarsus lengths borrowed from literature (Miller, 1963; Richter et al., 1991), using these published adult lengths to collate a mean (as applied by Khaleghizadeh, 2010 and by Melchor et al., 2012) (Fig. 2B-C).

The biogenic structures were measured in the field using three linear morphometric measurements (central mound and peripheral trench diameters, height) and two ratio comparisons. Linear measurements provided data on size, while ratios gave information about shape. Height was calculated by placing a 30 cm ruler in the trench vertically touching the edge of the central mound and placing another 30 cm ruler on top of the mound pointed to the first ruler to touch it – the height was measured from this point of contact on the first ruler (Fig. 2D). As ROTs were not perfectly circular, each diameter measure was taken from two perpendicular lines crossing the structure E-W and N-S each line (for the almost circular structures) or by two perpendicular lines where one crossed the structure's maximal length and the second line perpendicularly intercept the first (in the case of the deformed structures) (Fig. 2E). The final diameter consists of the mean between the two perpendicular measurements in each portion. Finally, we also calculated the aspect ratio (*AR*) both for the central mound (ARM) and for the peripheral trench (ART), as the quotient of the division of the minimum diameter (d_{min}) by the maximum diameter (d_{max}) ($AR = d_{min}/d_{max}$) in each two perpendicular measures (Takashimizu and Iiyoshi, 2016). Some measurements, such as central mound height and peripheral trench diameter, were not obtained for all identified taphons mainly because they were greatly altered. All measurements were made using the software ImageJ version 1.53e (Rasband, 2021) after the photos were taken in the field.

3.5. Analysis

Size and shape data were compared through a taphogenic sequence from "fresh" to "old" and altered taphons (Fernández-López, 2006); each new taphonomic element in the sequence was given a number (e.g., T1, T2… T_x) to better view the cumulative effects of taphonomic agents. Eventual quantitative modifications of morphometrics and ratios through this sequence were analyzed by One-Way ANOVA with a posthock Tukey test performed in R software version 3.6.1 (R Core Team, 2021).

4. Results

4.1. ROT *registration and morphology*

Flamingos were recorded performing rotating-stamping behavior in two points at Lagoa do Peixe: at the East side by the lagoon's debouchment, and at the West side of the lagoon, near the swamp fields at the border of the Barrier III (Fig. 1D). In the East point the birds stomped in water depth of ~26 mm, based on a 1/10 submerged portion of a 259.04 mm tarsometatarsus mean length (data from August 30th and September 15th, 2018). At the West point, on September 15th, the flamingos stomped in higher water level, up to a 1/3 tarsometatarsus length, allowing to calculate water depth as ~86.3 mm. As the birds were farther from the margin than in the east side, we could not reach the eventual ROTs produced.

Video records show that both legs do not perform the same role during the stamping (Fig. 3, Supplementary Video 1). After selecting a foraging spot, the bird initiates the motion sequence with one leg serving as a pole, while the other leg is maintained slightly ahead of the supporting leg. As such, the non-supporting foot sinks and pushes the substrate towards the beak, where the sediment is filtered and subsequently decanted. As the substrate-shaking autopodium remains forward and slightly lower than the supporting autopodium, this forces the bird to lift higher the tibiotarsal joint of the supporting leg, while the range of motion of the stirring autopodium occurs in a plane slightly more parallel to the substrate. In this way, the supporting foot produces a well-defined footprint while the non-supporting foot registers a less defined footprint that indents an excavation in the substrate, frontal and lateral to the supporting footprint.

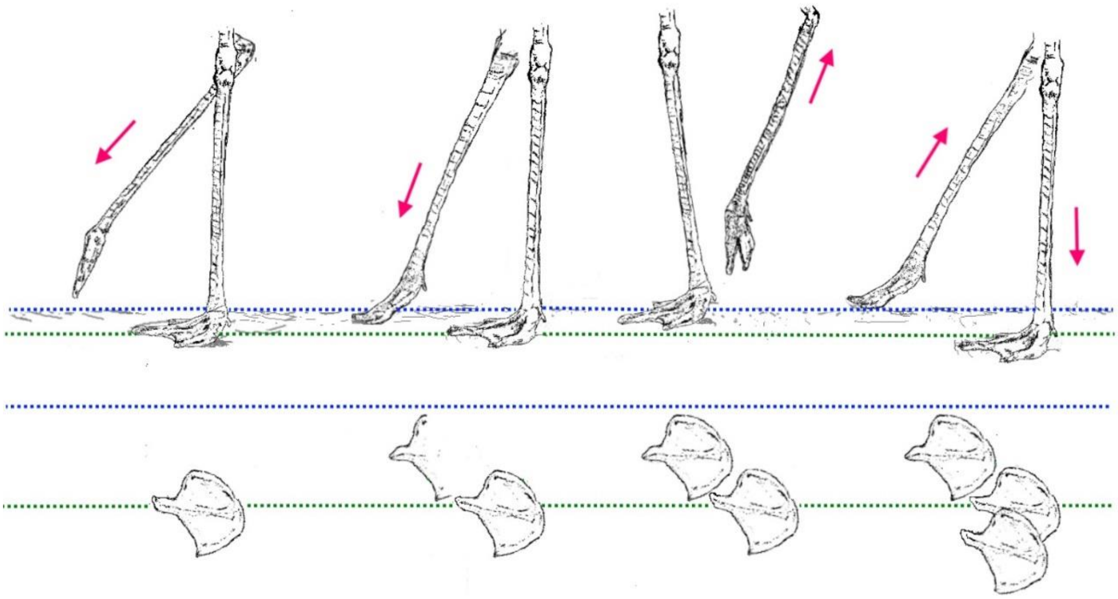

Fig. 3. Feet sequence of movement and inferred pattern of substrate bioturbation by Chilean Flamingo, with left (L) foot as shovel and right (W) foot as prop. [2-column fitting image]

Supplementary Video 1. Individual Chilean Flamingo performing rotating stamping at Lagoa do Peixe, southern Brazil.

As a result of the complex movements used during rotating stamping, the bird excavates a peripheral trench adorned with a sequence of overlapping footprints whose sagittal axes point to the center of the structure, where it accumulates the central mound (Figs. 2E and 4). This latter resembles an inverted shallow dish with a smooth and convex surface, and a visually homogeneous texture of fine grain size. Overall, the newly made structure (T1) shows a sunflower-like appearance whose “petals” are composed of up to three concentric circles of footprints, from slightly to highly overstepped (Fig. 4), indicative of the supporting role and limited range of motion of the supporting leg. T1 structures were recorded in August, setting the origin point where to attach the observed and inferred sequences of taphonomic alterations of the remaining taphonic groups recorded in August and September.

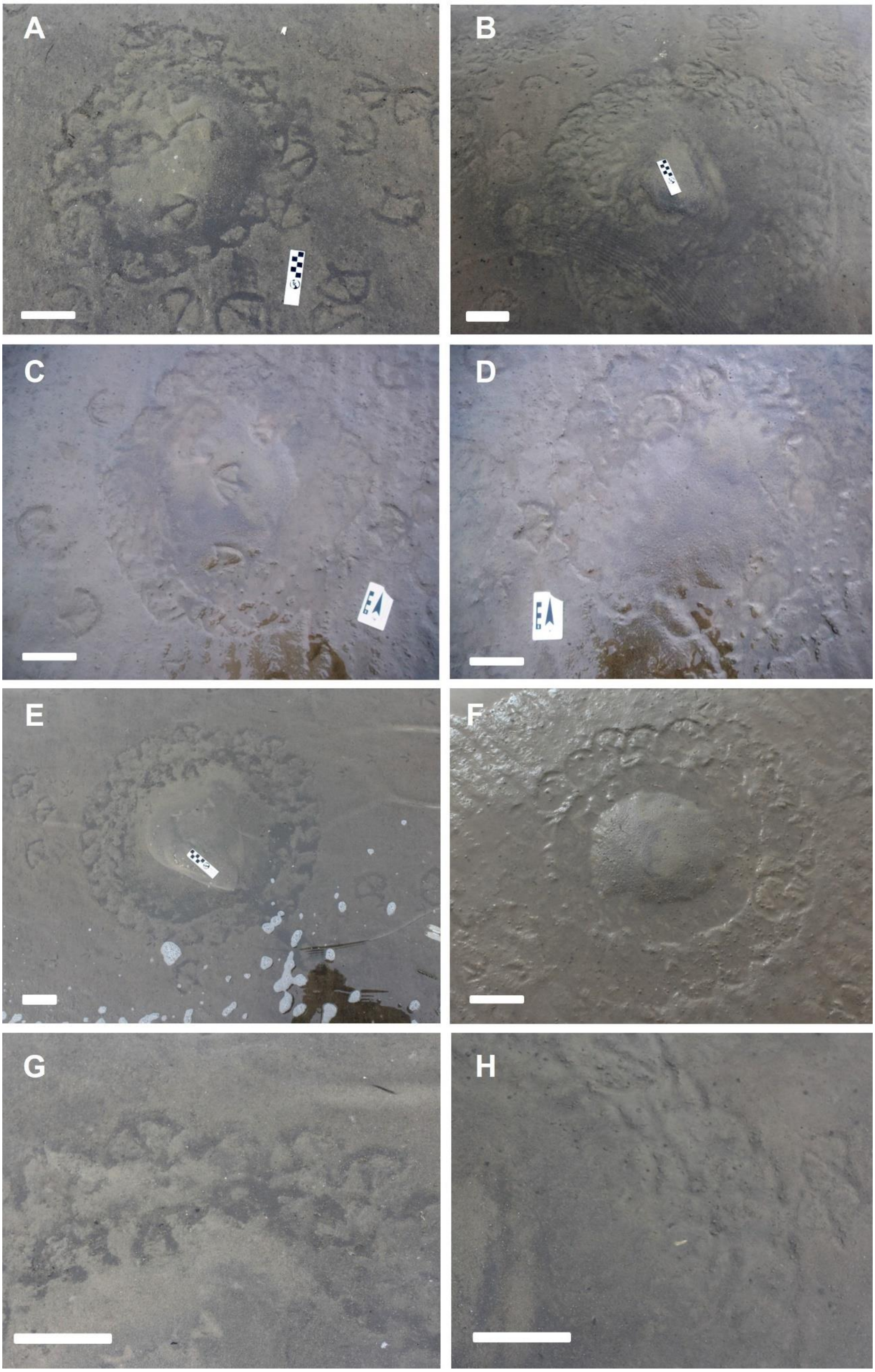
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Fig. 4. Examples of the range of morphological variation of newly produced rotating-stamping structures by Chilean Flamingos in Lagoa do Peixe, August 2018. (A-B) Fully underwater, (C-E) half immersed and (F) fully exposed structures. (G) Close-up of footprints in peripheral trench from Figure 4E, illustrating the deposition of finer and darker sediments, accentuating the definition of the deeper digit imprints. (H) Close up of Figure 4B, showing progressively faded footprints in the peripheral trench. Scale 10 cm. [2-column fitting image]

The aggregated pattern of ROT distribution over the topography of the sampled area evidenced little overlap and high evenness (Fig. 5A-C). The low frequency of overlap observed in the structures was largely restricted to the level of the peripheral trench (Fig. 5D-E), while overlap of the central mounds was less frequent (Fig. 5E-F).

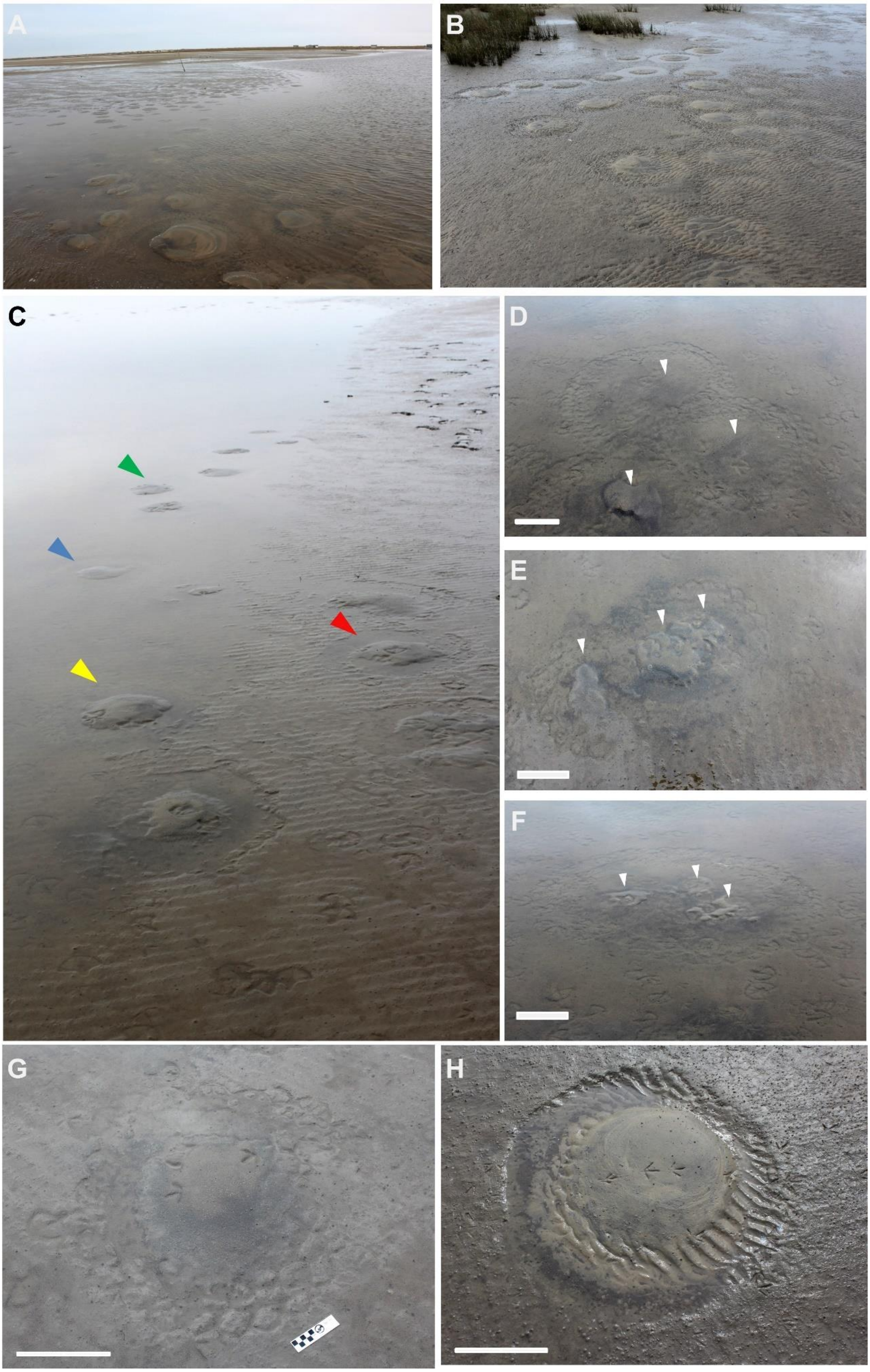
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Fig. 5. (A) Aggregate and even distribution of rotating-stamping structures, as seen during receding waters of spring tide; note the ripples orientation indicating the direction of water flux, as well as the loss of definition of footprints by erosive and burial water action. (B) Fully exposed lagoon bottom during receding tide (August 2018), showing the gradient of preservation in Taphon 2; note the increasing degree of alteration from the higher to lower terrain, ripples orientation indicating the direction of water flux, and the loss of definition of footprints by erosive and burial water action. (C) Degrees of increasing exposition of the rotating-stamping structures during receding waters of spring tide, as a function of the terrain slope (August 2018); note the gradient from immersed (blue arrow), only top central mound exposition (green arrow), full central mound exposition (yellow arrow) and full rotating-stamping structure exposition (red arrow). Examples of overlap in rotating-stamping structures: (D) Three rotating-stamping structures overlapping only at the level of the peripheral trench; (E) Three rotating-stamping structures overlapping at the level of the peripheral trench, two of them also at the level of the central mound; (F) At least three overlapping central mounds (representing three separated rotating-stamping events) surrounded by a larger peripheral trench indicating a fourth rotating-stamping event where the bird avoided the mound-overlapped surface; due to the larger scale of the rotating-stamping movement, no additional central mound were produced. Trackways made by co-occurrent bird species within Chilean Flamingo bioturbated surfaces: (G) American Oystercatcher (*Haematopus palliatus*); (H) White-backed Stilt (*Himantopus melanurus*). Scale bars 20 cm. [2-column fitting image]

4.2. Taphogenic sequence

A total of 52 ROTs were sampled. These structures can be classified in five distinct taphons, organized in two series according to its taphogenic pathway (Table

1, Fig. 6). The first taphogenic pathway conduces to increased taphonic diversity with fewer loss of morphological fidelity (Fig. 6A); the second pathway leads to higher loss of morphological fidelity and low taphonic diversity (Fig. 6B). Not all taphons were recorded in all sampling dates, so we organized them as a series of observed and inferred sequences from the "ancestral" to the "descendent" taphon.

Table 1

Sample size (N), linear measurements (in mm) and ratios of five taphon groups of rotating-stamping structures, depicted as mean ± standard deviation (minimum-maximum range).

Taphon	N	Linear measurements			Ratios	
		MMD	MTD	Height	ARM	ART
T1	11	299.43 ± 54.08 (191.28-374.41)	631.02 ± 119.82 (441.5-854.59)	Unmeasured	0.911 ± 0.08 (0.779-0.995)	0.932 ± 0.06 (0.8-0.96)
T2	10	452.08 ± 98.82 (306.11-664.48)	603.6-1146.44 (809.03 ± 153.37)	Unmeasured	0.856 ± 0.13 (0.61-0.99)	0.932 ± 0.05 (0.89-1)
T3	11	403.84 ± 61.58 (340.95-564.7)	Unmeasured	23.2 ± 2.25 (20-26)	0.903 ± 0.04 (0.79-0.95)	Unmeasured

Taphon	N	Linear measurements			Ratios	
		MMD	MTD	Height	ARM	ART
T4	10	419.75 ± 64 (300-505)	646.5 ± 122.72 (437.5-810)	29.9 ± 6.15 (20-37)	0.952 ± 0.03 (0.91-1)	0.915 ± 0.06 (0.83-1)
T5	10	507.85 ± 35.43 (440-570)	696.75 ± 42.55 (599-735)	11.6 ± 2.72 (9-16)	0.930 ± 0.06 (0.78-1)	0.931 ± 0.06 (0.79-0.99)

MMD: mean central mound diameter; MTD: mean peripheral trench diameter; ARM: aspect ratio of the central mound; ART: aspect ratio of the peripheral trench.

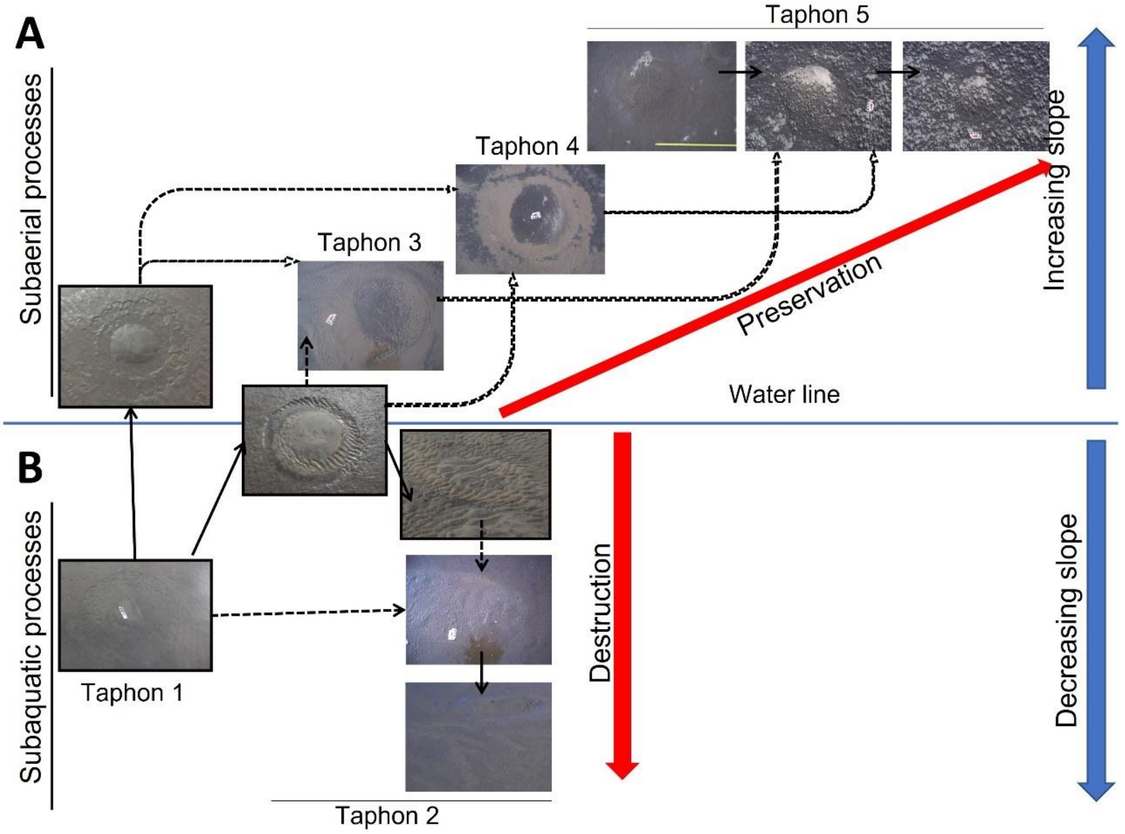

Fig. 6. Taphonomic processes, taphogenic production and inferred taphonomic pathways of (A) preservation and (B) destruction effects on taphon groups. Black arrows between taphons indicate observed (solid) and inferred (dashed) sequences

of taphonic evolution. Photographs of taphons outlined in black were sampled in August 2018, the other taphons in September 2018. [2-column fitting image]

On August 30th, structures were studied during the receding interval of the spring tide, under southwest winds reaching 18.36 km/h. Newly made ROTs (T1) already start to be buried by the decantation of finer grains at the peak of high tide (Sumner, 2017). Finer sediments can be easily recognized by its darker coloration, indicative of organic matter (Fig. 4A, E and G). The cohesiveness of these clay to mud sized particles probably contributes to the structure resistance to the dismantling by the extracting waters. Decantation ceases as the water velocity increases according to tide rhythm and terrain slope (Fig. 5B-C). At this initial phase of tide movement, environmental energy increases gently, but the first signs of erosion can be noted by the loss of detailed outlines of the footprints following the deposition of sand from the central mound, which begins to collapse (Fig. 5C-D and H). From this point onward, subaerial exposition and subaquatic erosive processes increase, altering the ROTs in varied degrees.

After the T1 original structures, the second taphonomic group (T2) includes ROTs in areas of high-water energy, as part of a destructive taphonomic pathway. Structures in this group were found both in August and September samplings. In August, morphological alterations of the T2 group were induced by ripple marks both in the peripheral trench and in the central mound (Fig. 5B and H). Further alteration of this taphon was noted in September, in areas where the topology allows the falling tidal waters to originate temporary streams with higher hydraulic energy than in the flatter areas where the water level drops more gently (Fig. 7). In both intervals, the highest energy levels dissolute flamingo footprints, fill the peripheral trench with sediments and dismantle the central mound, altering the structure to the level of destruction (Figs. 5B and 7).

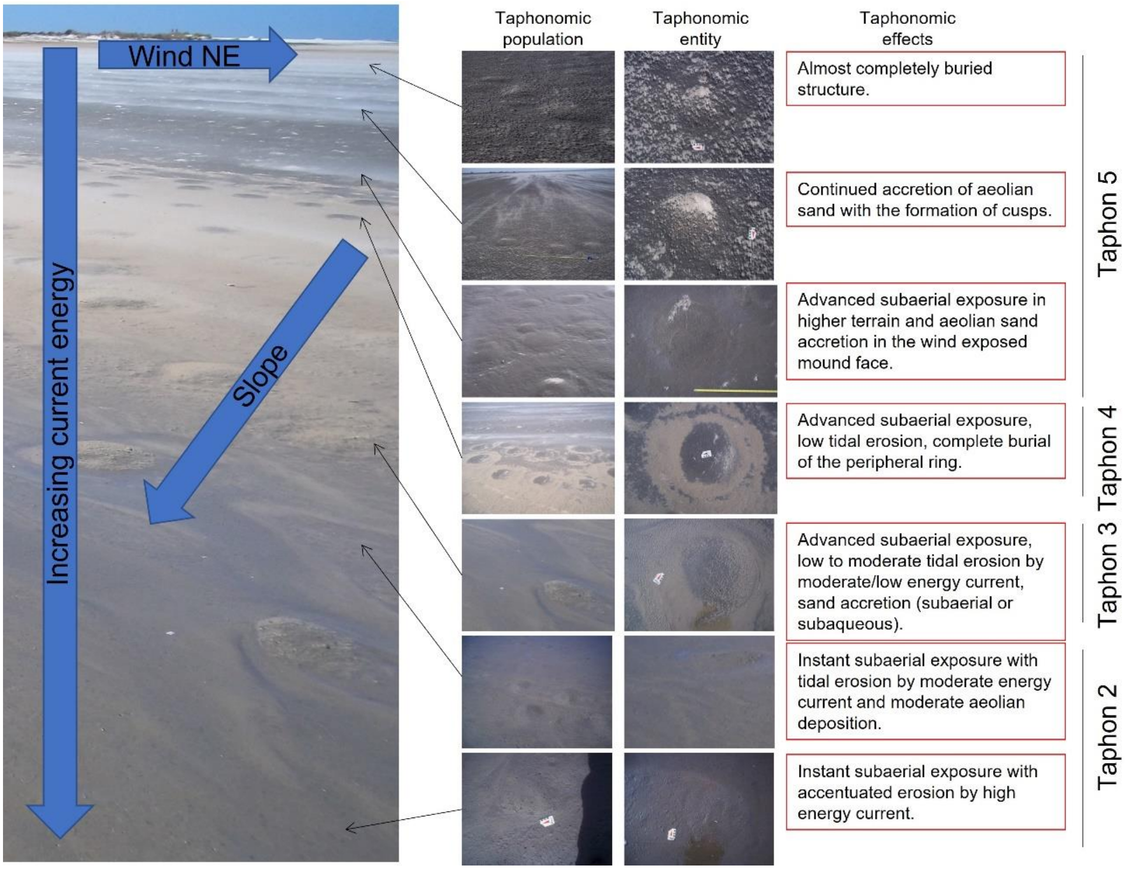

Fig. 7. Gradient of taphonomic conditions according to the interactions of wind, terrain slope and water energy, with the corresponding variation in erosion and burial of the rotating-stamping structures, as observed in September 2018. Original biogenic structures (T1) were not represented, as they were recorded only in August. [2-column fitting image]

Once the original ROTs managed to escape the destructive action of the first taphonomic pathway, they begin a second pathway which was more conducive to taphogenic production and preservation (Figs. 6B and 7). This pathway was observed on September 15th, one hour before the neap, under 23.4 km/h northeastern winds transporting massive amounts of aeolian sands from the transgressive dune fields over the now fully emerged structures in the backbarrier terrain immediately above the level of streams (Fig. 7). Also, the subaerial exposition may increase mound desiccation by sun and/or wind, incrementing its compactness. As can be seen from the third (T3) taphon onward, these processes provide the mound with more flow-resistant particles, or resistant enough to maintain the mound structure even when the peripheral trench is completely altered. As such, the central mound maintains its original morphology quasi-intact (Fig. 7).

Once exposed, the erosion action of the wind appears to be less competent to deform the compacted mound, with the aeolian sand accretion surpassing the wind erosion. When the peripheral trench is not completely dissolved, its original outline can be distinguished via different size and color of the particles deposited on the excavated terrain (Fig. 7). There also appears to be variation in the wetness of the substrate, as indicated by the coloration of the grains transported and deposited on the surface. In September, strong northeastern winds deposited sand from the transgressive dunes into the lagoon, expanding the wind sand blanket over the backbarrier flat. This process is as fast as the burial may occur in a few minutes (Fig. S1). When deposited over the structures from the third and fourth taphons, aeolian sands soak and become darker; in the fifth taphon (T5), these aeolian sands can be perfectly distinguished from the other clasts by its almost pure white coloration, indicating a drier surface over which the deposited sand forms small cusps (Fig. 7).

ROTs can suffer alteration due to trampling by walking flamingos (Fig. 4A and C-D). In this case, flamingo trackways often cross through the central mound, highlighting that the bird weight was not heavy enough to dismantle the accumulated sand heap. Also, there were alterations by some of the syntopic waterbirds species at PNLP, such as the American Oystercatcher (*Haematopus palliatus*) and the White-backed Stilt (*Himantopus melanurus*) (Fig. 5G-H).

4.3. Statistical analysis

As the first taphonomic pathway consisted of just two taphons (T1 plus T2), we do not apply the variance analysis for this sequence alone. However, although the taphons from the first taphonomic pathway were sampled at a different date from the second way taphons (August and September, respectively), we judge that they may well fit among the second pathway as a unique sequence of taphonomic evolution. The inclusion of the first taphon seems to be obligatory, as they are near to the original registration information necessary to start a comprehensible analysis of the whole taphogenic series.

The mean central mound diameter was significantly different among the treatments (F = 14.321, p = <0.0001), while Tukey test pointed to significant differences in almost all pair-to-pair comparisons. By its turn, the mean peripheral trench diameter also showed significant variation (F = 4.829, p = 0.006171), related to the greater mean of the T2 taphon (according to Tukey test). The remaining morphological parameters tested for the analysis of variance do not show significant quantative differences among the five sampled taphons (Tables 1-2, Fig. S2).

Table 2

Results of the ANOVA and Posthoc Tukey Test for five taphon groups.

	One-Way ANOVA				Posthoc Tukey Test			
Measurement	df1	df2	F	P	Between groups variability		Difference	P
MMD	4	47	14.321	**<0.0001**	T1	T2	151.65171	**<0.001**
						T3	104.40336	**0.0045618**
						T5	120.31691	**0.0011136**

Measurement	One-Way ANOVA				Posthoc Tukey Test			
	df1	df2	F	P	Between groups variability		Difference	P
						T7	208.41691	**<0.001**
					T2	T3	-47.24835	0.4773771
						T5	-31.33480	0.8230267
						T7	56.76520	0.3159793
					T3	T5	15.91355	0.9809208
						T7	104.01355	**0.0061655**
					T5	T7	88.10000	**0.0337023**
MTD	3	37	4.8299	**0.006171**	T1	T2	178.01152	**0.0068311**
						T5	15.47982	0.9902136
						T7	65.72982	0.5780534
					T2	T5	-162.53170	**0.0183072**
						T7	-112.28170	0.1581008
					T5	T7	50.25000	0.7728228
ARM	4	47	2.203	0.08303	T1	T2	-0.055342407	0.4728172
						T3	-0.007531222	0.9993524
						T5	0.041171111	0.7346810
						T7	0.019032611	0.9790463
					T2	T3	0.047811185	0.6136185
						T5	0.096513518	0.0526899
						T7	0.074375018	0.2093147
					T3	T5	0.048702333	0.5968361

	One-Way ANOVA				Posthoc Tukey Test			
Measurement	df1	df2	F	P	Between groups variability		Difference	P
						T7	0.026563833	0.9313974
					T5	T7	-0.022138500	0.9666166
ART	3	37	0.1999	0.8958	T1	T2	-0.0001894833	0.9999999
						T5	-0.0170089623	0.9134999
						T7	-0.0005833746	0.9999959
					T2	T5	-0.0168194791	0.9211315
						T7	-0.0003938913	0.9999988
					T5	T7	0.0164255877	0.9260152
Height	3	37	0.1999	0.8958	T1	T2	-0.0001894833	0.9999999
						T5	-0.0170089623	0.9134999
						T7	-0.0005833746	0.9999959
					T2	T5	-0.0168194791	0.9211315
						T7	-0.0003938913	0.9999988
					T5	T7	0.0164255877	0.9260152

df1 = between-groups variability, df2 = within-groups variability. Significance within a 95% confidence level. Significant P values are in bold. MMD: mean central mound diameter; MTD: mean peripheral trench diameter; ARM: aspect ratio of the central mound; ART: aspect ratio of the peripheral trench.

4.4. Taphonomic model for the preservation of ROTs

The taphonomy of the stamping structures involves the interplay between different post-registration agents, namely tidal cycle, terrain gradient and wind regime.

Departing from its subaquatic registration in high tide interval (Fig. 8A), the ROT becomes progressively exposed as the tide recedes, and experiences varied levels of alteration by subaquatic erosion by wave and current rippling effects (Fig. 8B). This sequence encompasses a primarily destructive taphonomic pathway, which selects those structures located on more favorable locations in the sedimentary landscape, as areas of low-gradient and subjected to mild water movement. Indeed, the preservation of the structure can begin during the subaquatic phase, with the decantation and deposition of finer sediments when water movement almost ceases. Subsequently, fully exposed structures may be subject to massive deposition of aeolian sand, according to favorable wind regime (mostly northeastern-originated winds in the study area), which favors the structure burial (Fig. 8C). Finally, depending on the degree of burial and the resistance to dismantling, the ROT could be destroyed by tide rising or could receive new sediment deposition and then enters deeper into the taphonomic active zone (Fig. 8D).

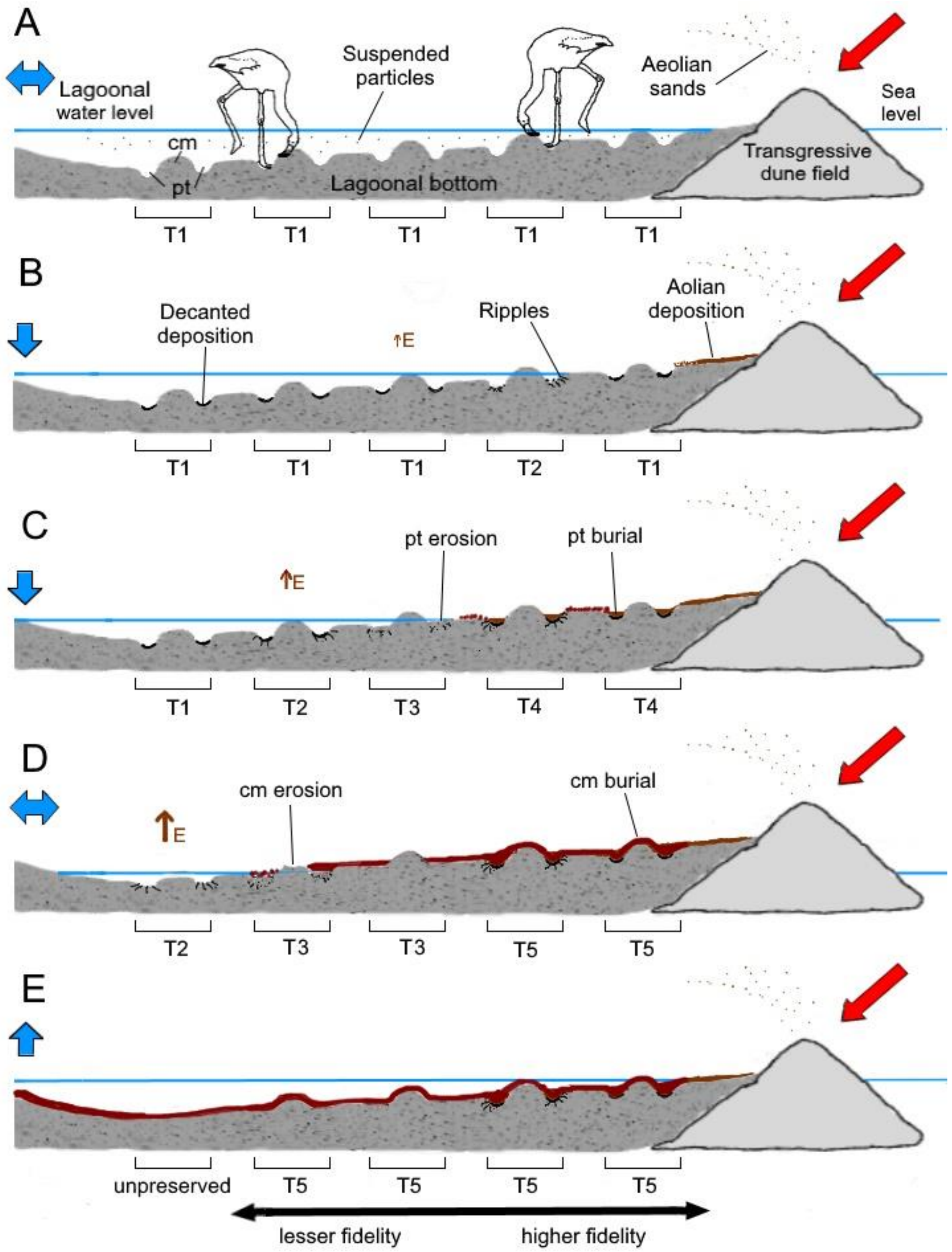

Fig. 8. Simplified taphonomic model for the preservation of rotating-stamping structures. (A) High tide with registration of rotating-stamping structures in underwater lagoon bottom; (B) Low tide with exposure of produced structures in lagoon margins, initial buring by decanted deposition; (C) deposition of aeolian sand from trangressive dunes in lagoon exposed flat, partially buring the structures; (D) Complete buring; (E)

New high tide and a new sediment layer from decanted deposition over the buried structures. cm: central mound, E: energy level, increasing arrow size indicates low, moderate and high energy; pt: peripheral trench; blue arrows indicate the direction of tidal waters; red arrows indicate the direction of the predominantly northeastern wind. [2-column fitting image]

5. Discussion

5.1. Registration behavior and substrate interaction

Both anatomical and behavioral peculiarities account for the primary morphology observed in ROTs. The mesh-like bill filter apparatus does not prevents flamingos from swallowing mud, and only the coarser sand grains are excluded by the outer lamellae, so far deposited in the center of the circle traced by the rotating-stamping motion (Jenkin, 1957). Also, the great indenting surface of the palmate feet allows the bird to register a low-deep peripheral trench which makes such dichotomous structures very conspicuous over the lagoonal flats.

In flamingos, many behaviors (including stamping) seem to be socially facilitated (Bildstein et al., 1991), when each bird triggers the same behavior in its neighbors, resulting in a flock stamping in unison (Supplementary Video 2). This contributes to the characteristic ichnofabric of quite regularly distributed structures through the topography (Fig. 5A-C). Such pattern is also found in all photographic records of ROTs found in literature for the Chilean (Lee and Mayorga-Dussarrat, 2016) and other flamingo species, as *Phoenicopterus roseus* (Glassom, 1992; Gloe, 1998; Johnson and Cézilly, 2009; Rodríguez-Pérez and Green, 2006; Gihwala et al., 2017; Salvador et al. 2022) and *Phoenicopterus ruber* (Rooth, 1965). As the overlapping occurred mainly at the level of the peripheral trench, this indicates either different individuals stamping in proximity or a sequence of explored places by a single bird;

furthermore, lower frequencies of overlapped central mounds suggests that certain places were not reworked once stamped, perhaps due to optimization by flamingos in search for unexplored and better rewarding substrates (Krebs and Davies, 1989; Bautista et al., 2001). A different pattern would be found in situations where an adult bird harasses a juvenile that initiated stamping (Bildstein et al., 1991) – in this case, the overlap among structures probably increases, indicating the resource quality of the foraging places.

Supplementary Video 2. Group of Chilean Flamingos performing rotating stamping at Lagoa do Peixe, southern Brazil.

5.2. Registration behavior and substrate interaction

After registration, the environmental conditions observed during the sampling intervals determined the fate of each taphon. Firstly, decantation and subaerial exposition assist to improve structure cohesiveness. Central mound strength can be high enough to sustain flamingo weight and permit the registration of its footprints as well as those of associated and small-bodied birds. Thus, ROTs also could work as proxies for local waterbird diversity. Such species co-occurrence recorded by tracks can be indicative of ecosystem productivity: in the Andes, the distribution of Chilean Flamingo is coincident with lakes that support a high diversity of other waterbird species, in contrast to the lakes where Puna (*Phoenicoparrus jamesi*) and Andean (*Phoenicoparrus andinus*) Flamingos inhabit (Caziani et al., 2001). Central mounds produced by Great Flamingos would even sustain a human body mass, as seen in Salvador et al. (2022).

5.2. Taphonomic processes and preservation probabilities

The water energy influences varied degrees of alterations on structures' original morphology, spanning from ripple marking until the complete dissolution. The same pattern of alteration was found for ROTs 24 h and 48 h after their registration by *Phoenicopterus roseus* in a lagoonal system of South Africa (see figure 4 in Gihwala et al., 2017).

Our observations are restricted to the pre-burial and initial burial phases of the taphonomic process. Subsequent rework may occur, mainly by weather conditions as storms from south cold fronts that can originate atmospheric tides either by elevating the ocean level near the shore, or by damming waters near the debouchment (Harrison et al., 2013). In turn, storms also can improve the sudden deposition of high quantities of sediments by overtopping seawater and subsequent rework of sand from the barrier, creating washover fans (Rodriguez et al., 2020). Also, bacteria may play a role in the sediment consolidation by creating biofilms, although we were not able to inspect such processes in the present study.

The mean diameter values of the central mound tended to increase along the alteration gradient in the taphogenic series (Fig. S2), probably as a result of substrate swelling and continued accretion of sedimentary material since the underwater phase of the taphogenesis. Also, the significant variation of the peripheral trench possibly reflects behavioral and/or anatomical variability of the tracing organism, as the Tukey test does not point to the same size variation among the other taphons, indicating the fidelity of this parameter along the taphogenic series.

5.3. Paleoenvironmental and evolutionary history significance

Given the adequate environmental conditions, which were common in the ecosystem we studied, ROTs can be used as good taphonomic elements prone to fossilization, as suggested for flamingos' nest mounds (Scott et al., 2012). When escaping the destructive taphonomic pathway, the structures can maintain its original architecture with reasonable fidelity, as the morphological variability is restricted to the linear morphometry, with a significant change occurring only with the increase in the central mound, while the total diameter of the structure is preserved along the taphogenic series.

We suggest backbarriers lagoon-barrier system as an ideal depositional system for the preservation of ROTs, primarily due to the low environmental energy derived from the sand barrier protection against the sea waves. Low energy is necessary to minimally disturb the structure morphology, composed by loose sediments of small grain sizes. Additionally, the perennial source of fine sand from the transgressive dunes contributes to the burial and further diagenesis and preservation. The current erosive processes at the intertidal region exhume Pleistocene beach sandstones from the older Barrier III, as well as peat and lagoonal mudstones from the younger Barrier IV (Arejano, 2006). We propose that the later expositions are the best to look for eventual fossilized ROTs in the PNLP region, giving the topological situation where these structures are formed today by local Chilean Flamingos. The model shown here may be valid only for the specific conditions where we worked. However, rotating-stamping behavior is not restricted to lagoonal/barrier systems, and additional studies in further environments should add more information to its taphonomic process.

Although ROTs are conspicuous, no related trace fossil have been documented; therefore, we expect that the traces recorded at PNLP could serve as a comparison material.

Biogenic structures produced by foraging flamingos are ubiquitous in many sedimentary surfaces as lagoonal, lacustrine, coastal and shore systems. As such, fossil traces associated to the flamingo lineage can provide good indicators of paleoecological conditions, but such inferences depend on accurate trace-tracemaker assignments. Observations on the morphological variation and taphonomic processes involved in the preservation potential of modern flamingo traces can improve our paleoecological comprehension of ancient environments and could also clarify the pattern of evolutionary history of flamingo adaptations to its unusual life mode.

6. Conclusions

ROTs are complex biogenic structures representative of an elaborated flamingo feeding behavior, whose morphology accurately represents the details of the movements employed. As rotating stamping is known to occur under a state of low water height and very soft substrate, such behavioral fidelity (*sensu* Plotnick, 2012) may indicate environmental characteristics with considerable accuracy. Observations carried out under two distinct weather conditions allowed for the inference that ROTs may be subject to good taphonomic circumstances for their conservation. Thus, their presence in the fossil record would seem reasonable, opening the possibility of their recognition in future studies of Cenozoic transitional paleoenvironments.

CRediT author contributions

André Barcelos-Silveira: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. Paula Dentzien-Dias: Investigation, Writing - review & editing, Funding acquisition. Heitor Francischini: Investigation, Writing - review & editing, Supervision, Visualization. Cesar Leandro Schultz: Writing - review & editing, Supervision, Funding acquisition.

Declaration of competing interest

We declare no competing interests.

Data availability

The raw morphometrics data used in this article are presented in Table S2.

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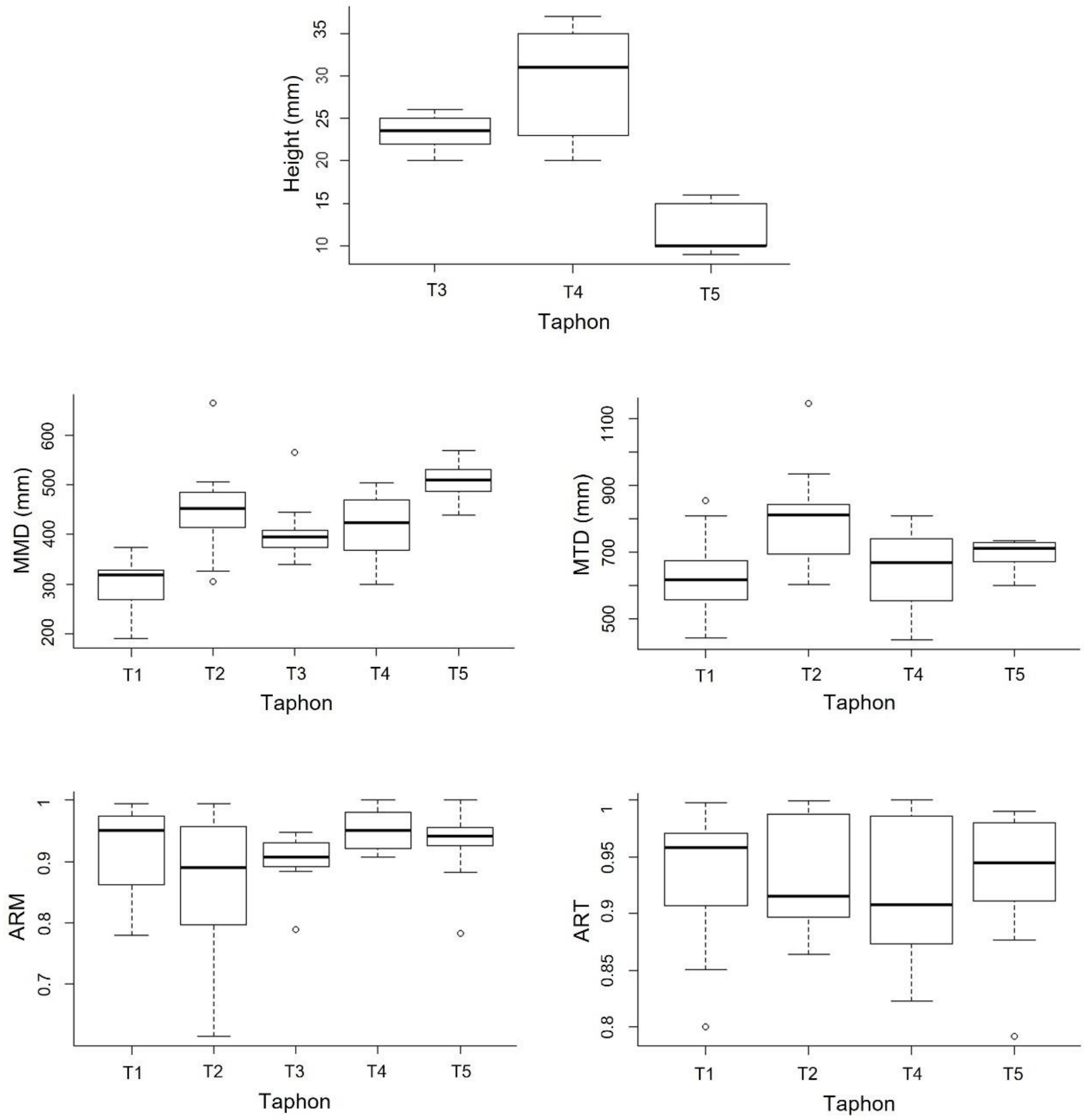
Supplementary Figure S1. Rapid burial of rotating stamping structures (1) in dark-surfaced sand flat (2) by light colored sand grains (3) transported from trangressive dune fields (4). Scale equals 150 cm. The time span from photo A to photo B equals ~1 min.



Supplementary Figure S2. Boxplot of measurement variables of rotating stamping structures classified in five taphonomic groups or taphons (T). MMD: mean central mound diameter; MTD: mean peripheral trench diameter; ARM: aspect ratio of the central mound; ART: aspect ratio of the peripheral trench.

Table S1

Summary of literature epithets for rotating-stamping structures produced by flamingos and their constitutive parts (peripheral trench and central mound).

Species	Reference	Structure designation
Phoenicopterus ruber	Ingraham, 1896	Mound
Phoenicopterus roseus	Hainard, 1932	*monticule* + *mince couche* [mound + shallow bad]
Phoenicopterus ruber	Allen, 1956	feeding mound (stamping pedestal + feeding trough)
Phoenicopterus roseus	Brown, 1958	feeding tracks, rings
Phoenicopterus roseus	Macnae, 1960	feeding rings (central mound + circular trench)
Phoenicopterus ruber	Rooth, 1965	mound + groove
Phoenicopterus ruber	Bildstein et al., 1991	circular plateaus + shallow depressions
Phoenicopterus roseus	Glassom, 1992	circular depressions, wheelies
Phoenicopterus roseus	Glassom, & Branch, 1997	Wheelies
Phoenicopterus roseus	Gloe, 1998	*Ringförmige Spuren* [ring traces]
Phoenicopterus roseus	Rodríguez-Pérez & Green, 2006	Crater

Species	Reference	Structure designation
Phoenicopterus roseus	Johnson & Cezilly, 2008	saucer-like depressions
Phoenicopterus roseus	Bensaci, 2010	*monticule au milieu* (*cône alimentaire*) + *dépression* [middle mound (feeding cone) + depression]
Phoenicopterus chilensis	Tobar et al., 2014	feeding ring
Phoenicopterus roseus	Liang, 2014	foraging pit, dome-like pit, feeding cone, wheelie
Phoenicopterus chilensis	Lee & Mayorga-Dussarrat, 2016	feeding ring
Phoenicopterus roseus	Gihwala et al., 2017	Pit
Phoenicopterus roseus	El-Hacen et al., 2019	crater, pit (bowl + hummock)
Phoenicopterus roseus	Gihwala et al., 2019	pit-like + sediment mound
Phoenicopterus chilensis	Delfino & Carlos, 2021	flamingo crater

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Table S2

Quantitative morphometric data for each rotating-stamping structure sampled at Lagoa do Peixe, southern Brazil. Values are in millimeters, except for ARM and ART.

Taphon	MiMD	MaMD	MMD	ARM	MiTD	MaTD	MTD	ART	Height
T1	319	321	320	0.99	566	666	616	0.85	-
T1	312	354	333	0.88	836	873	855	0.96	-
T1	313	323	318	0.97	563	585	574	0.96	-
T1	319	324	322	0.98	656	704	680	0.93	-
T1	242	288	265	0.84	605	686	646	0.88	-
T1	187	196	191	0.95	439	444	441	0.99	-
T1	328	421	374	0.78	654	678	666	0.97	-
T1	357	376	366	0.95	782	834	808	0.94	-
T1	270	303	286	0.89	557	558	558	1	-
T1	242	304	273	0.8	481	601	541	0.8	-
T1	242	247	245	0.98	550	563	557	0.98	-
T2	262	392	327	0.67	619	692	656	0.89	-
T2	663	666	664	0.99	1100	1193	1146	0.92	-
T2	425	486	456	0.87	730	813	772	0.9	-
T2	489	524	506	0.93	775	854	815	0.91	-
T2	233	379	306	0.62	560	648	604	0.86	-
T2	441	461	451	0.96	819	867	843	0.94	-
T2	434	438	436	0.99	659	729	694	0.9	-
T2	461	509	485	0.91	813	823	818	0.99	-
T2	367	461	414	0.8	807	807	807	1	-

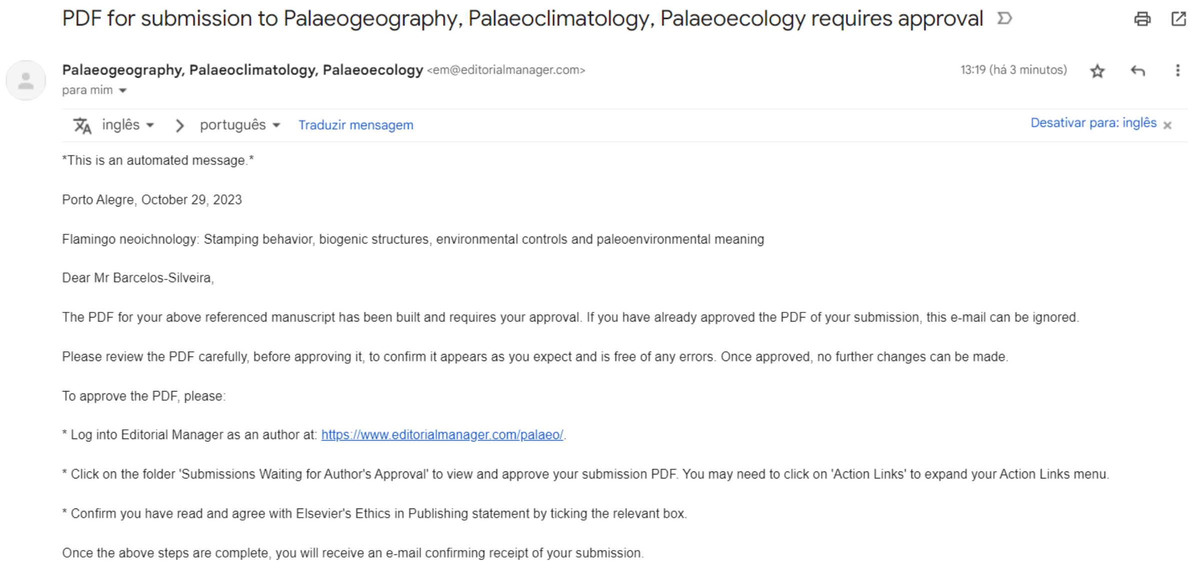
Taphon	MiMD	MaMD	MMD	ARM	MiTD	MaTD	MTD	ART	Height
T2	419	511	465	0.82	935	938	936	1	-
T3	534	596	565	0.9	916	994	955	0.92	-
T3	300	380	340	0.79	-	-	-	-	20
T3	390	430	410	0.91	-	-	-	-	20
T3	360	400	380	0.9	-	-	-	-	22
T3	370	400	385	0.93	-	-	-	-	22
T3	380	410	395	0.93	-	-	-	-	22
T3	320	360	340	0.89	-	-	-	-	25
T3	430	460	445	0.93	-	-	-	-	25
T3	360	380	370	0.95	-	-	-	-	25
T3	395	420	407.5	0.94	-	-	-	-	25
T3	380	430	405	0.88	-	-	-	-	26
T4	355	360	357.5	0.99	555	555	555	1	20
T4	300	300	300	1	395	480	437.5	0.82	22
T4	460	480	470	0.96	690	700	695	0.99	23
T4	470	510	490	0.92	690	790	740	0.87	30
T4	410	420	415	0.98	555	600	577.5	0.93	30
T4	355	380	367.5	0.93	510	510	510	1	32
T4	420	445	432.5	0.94	660	800	730	0.83	35
T4	390	430	410	0.91	610	670	640	0.91	35
T4	500	510	505	0.98	770	850	810	0.91	35
T4	430	470	450	0.91	730	810	770	0.9	37
T5	450	510	480	0.88	650	680	665	0.96	9

Taphon	MiMD	MaMD	MMD	ARM	MiTD	MaTD	MTD	ART	Height
T5	520	550	535	0.95	730	740	735	0.99	9
T5	500	540	520	0.93	610	770	690	0.79	10
T5	530	530	530	1	720	735	727.5	0.98	10
T5	500	532	516	0.94	697	765	731	0.91	10
T5	495	498	496.5	0.99	718	725	721.5	0.99	10
T5	490	520	505	0.94	690	715	702.5	0.97	12
T5	550	590	570	0.93	700	750	725	0.93	15
T5	430	450	440	0.96	575	623	599	0.92	15
T5	427	545	486	0.78	627	715	671	0.88	16

MiMD: Minimum central mound diameter, MaMD: Maximum central mound diameter, MMD: Mean central mound diameter, ARM: Aspect ratio of central mound, MiTD: Minimum peripheral trench diameter, MaTD: Maximum peripheral trench diameter, MTD: Mean peripheral trench diameter, ART: Aspect ratio of peripheral trench.

9.2. Artigo 2

Flamingo neoichnology: Stamping behavior, biogenic structures, environmental controls and paleoenvironmental meaning. Submetido à *Palaeogeography, Palaeoclimatology, Palaeoecology* (Estrato PPGGeo N3).



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Flamingo neoichnology: Stamping behavior, biogenic structures, environmental controls and paleoenvironmental meaning

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Keywords

Neoichnology, Foraging behavior, Waterbirds ichnology, Trace fossils, Paleoenvironment reconstruction

1. Introduction

Paleoenvironmental reconstructions could clarify the trends in past paleoclimate shifts and the succeeding turnovers on paleobiotas, thus in turn helping in the today rampant need to predict the future trends of the ongoing climate change (Kowalewski, 2017; Sergio et al., 2018; van Manen et al., 2020; Assumpção et al., 2022; Dillon et al., 2022). The uniformitarian principle implies that an accurate paleoenvironment interpretation should rely on multiple proxies such as lithology, paleomagnetism, isotopes, paleosols, ice cores, trace elements and fossil testimonies as charcoal, organic molecules, tree rings, leaf morphology and many other kinds of organic remains (Gornitz, 2009; Nichols, 2009; van Manen et al., 2020). Additionally, trace fossils (or ichnofossils) are indicators of syndepositional environmental conditions and taphonomic post depositional agents, since the trace registration is chiefly an autochthonous process (Sarjeant, 1975; Frey and Seilacher, 1980; Lockley, 1986; Gingras et al., 2007; Zonneveld, 2016; Marchetti et al., 2019; Shibata and Varrichio, 2020). Although not reliable indicators of depositional environments (Frey et al., 1990; Buatois and Mángano, 2011, 2020), trace fossils are better indicators of specific environmental conditions (stressors), such as salinity, oxygenation, substrate consistency, subaerial exposure, turbidity, oxygenation, and rates of sediment deposition (Seilacher, 1978; Bromley, 1996; Dashtgard, 2011; MacEachern et al., 2012). In this way, similar ancient set of environmental conditions control the type and abundance of traces, leading to the recognition of distinct ichnofacies (MacEachern et al., 2007).

The meaning of ichnofossils models for paleoenvironmental inferences is largely based on the description of the nowadays tracemakers' diversity and its associations with environmental stressors within modern environments (Hasiotis et al., 2012; Dashtgard and Gingras, 2012; Hembree, 2016). Although there is a growing body of ecological research addressing variations in bioturbators distribution and bioturbation intensity across a range of physicochemical conditions and substrate types (e.g., Levinton, 1979; Sassa and Watabe, 2008; Needham et al., 2010; O'Shea et al., 2012; Fang et al., 2021), the bulk of neoichnological studies proceeds from wave-dominated or distal marine environments, with limited knowledge coming from tidal and continental settings (Dashtgard, 2011; Desjardins et al., 2012; Hembree et al., 2012). Furthermore, vertebrate sampling is underrepresented in comparison to those of invertebrates (Frey and Seilacher, 1980; Manion and Upchurch, 2010). Such vertebrate sample is even more skewed toward few clades, predominating examples with burrowing mammals (Cameron et al., 1988; Eldridge and Rath, 2002; Eldridge and Mensinga, 2007; Dentzien-Dias and Figueiredo, 2015; Cardonatto et al., 2018; Belmontes et al., 2018; Cardonatto and Melchor, 2021, 2023), fishes (Howard et al., 1977; Gregory et al., 1979; Tweddle et al., 1998; Pearson et al., 2007; O'Shea et al., 2012; Hasiotis et al., 2012), squamates (Catena and Hembree, 2014; Hembree, 2016), and less frequently with amphibians (Brustur, 2016; Hembree 2016), and aquatic mammals (Shimek, 1977; Nelson and Johnson, 1987; Deocampo, 2002). In this context, birds constitute a minor representation (excluding nest studies), despite their abundance, megadiversity, ecological relevance and large range of habitat-types through its ~160 My of evolution (Xu et al., 2009; Lee et al., 2014; Brusatte et al., 2015; Xu et al., 2023).

Ichnology is a geological science and also an ethological science, since the production of traces occurs through the interaction between the organism's behavior and the substrate. Because the ideal subjects for ichnological studies are those organisms with great bioturbating activity in soft sediments, waterbirds traces dominate in neoichnological studies (Wietfield, 1980; Cadee, 1990; Genise et al., 2009; Melchor et al., 2012; Brewer and Falk, 2020; Melnick et al. 2022a, b). This characteristic substrate intimacy is also reflected in the predominance of shorebird walking (repichnia) and feeding (fodinichnia) traces in fossil deposits since a few million years after the arise of Avialae (Greben and Lockley, 1993; Lockley, 1993;

Lockley and Harris, 2010). Within this group, the flamingos (Phoenicopteridae) are notorious bioturbators, stirring great amounts of subaqueous substrates while feeding or nesting and producing diverse types of biogenic sedimentary structures, such as tracks, nest mounds and a set of distinctive feeding traces arising from specific feeding behaviors (Rooth, 1965; Scott et al., 2012; Brown et al., 2021). Their palmate, tridactyl footprints are analogous to flamingo-like fossil tracks grouped in the ichnogenus *Phoenicopterichnum* (Aramayo and Manera de Bianco, 1987), characteristically preserved in lacustrine, lagoonal, and other facies deposited in subaqueous settings. As the bulk of *Phoenicopterichnum* tracks proceeds from lacustrine facies, Melchor et al. (2012) proposed the recognition of the *Phoenicopterichnum* ichnosubfacies to indicate lacustrine environments of saline and alkaline water, based on the habitat selection of modern flamingos. The *Phoenicopterichnum* ichnosubfacies would insert as a unique assemblage within the “shorebird ichnofacies”, which, by its turn, is a proposed tetrapod ichnofacies indicative of shallow water bodies shorelines (Greben and Lockley, 1993; Lockley et al., 1994; Yang et al., 1995; Lockley, 2007; Lockley and Harris, 2010). However, this proposal still pending large acceptance, as even the adequacy of the tetrapod ichnofacies as a distinct concept apart from the classical, archetypical invertebrate ichnofacies has been intensely criticized (Santi and Nicosia, 2008; Buatois and Mángano, 2020).

All the six modern species of flamingos (Torres et al., 2014; Frias-Soler et al., 2022) are specialized filter-feeders of small organisms sieved from the water and from the substrate (Jenkin, 1957; Zweers, 1995; Mascitti and Kravetz, 2002), mostly in extreme habitat types, often under stressful environmental conditions (Del Hoyo, 1992). In this scenario, flamingos show behavioral plasticity as an adaptation to fully explore the limited resources of its challenging environments (Arengo and

Baldassarre, 1999; Gihwala et al., 2019). For example, flamingo could employ a set of distinct foraging techniques according to substrate consistence, depth of the water column and prey density (Allen, 1956; Rooth, 1965; Del Hoyo, 1992). Each of these behaviors could produce distinct biogenic sedimentary structures, which signal the behavior from what the structure originated. One remarkable feeding behaviors are the rotating-stamping, when the bird rhythmically agitates the substrate with both feet, suspending the substrate for filtering, while spinning around the body axis (Rooth, 1965; Cifuentes, 2007; Johnson and Cézilly, 2007; Delfino and Carlos, 2021, 2022) (Figure 1A, C). Such technique produces dichotomic biogenic structures consisting of a mound of sediment piled inside a circular trenched depression (called rotating-stamping structures [ROTs] by Barcelos-Silveira et al., 2023) (Figure 1B, D). Apparently, this technique allows to disrupt the burrows of meiofauna and capture the dislodged organisms then suspended in the water (Allen, 1956; Macnae,1960; Bildstein et al., 1991; Jonhson and Cezilly, 2008; Béchet et al., 2017).

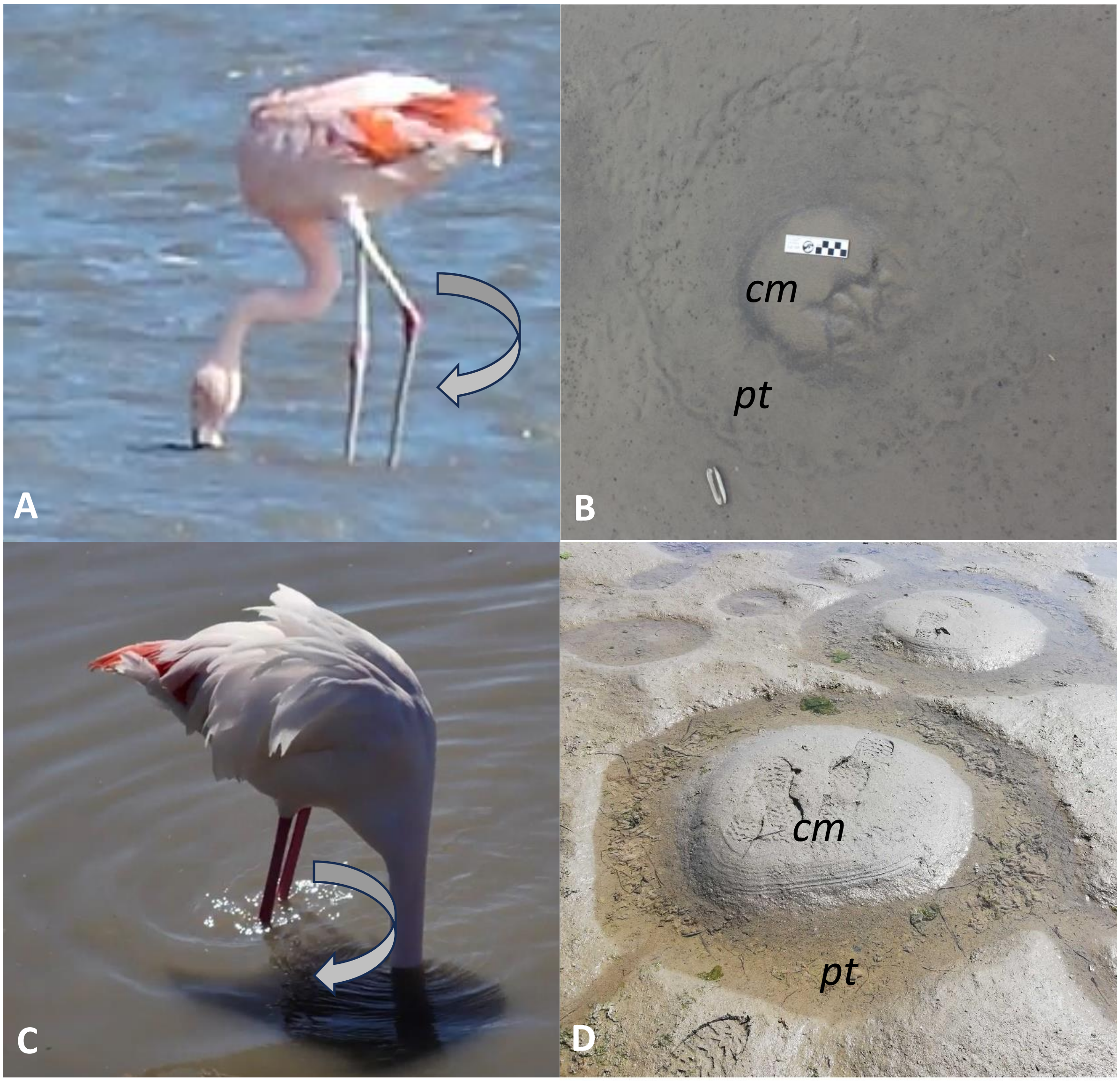

Figure 1. Rotating-stamping behavior of two flamingo species (A, C) and derived structures (B, D). Flamingo species represented: A) Chilean Flamingo *Phoenicopterus chilensis*, clockwise rotation (Lagoa do Peixe National Park, Rio Grande do Sul, Brazil); C) Greater Flamingo *Phoenicopterus roseus*, clockwise rotation (Étang du Ginès, Camargue, France; video frame from eBird contributor Josep del Hoyo, Macaulay Library ML201513421. Rotating-stamping structures registered by: (B) Chilean Flamingo at Lagoa do Peixe, Brazil, and (D) Greater Flamingo from Marano, Italy (photo courtesy of Paolo Salvador). Note the different water depths where

flamingos stamped; also note the resistance of the structures to the trampling by flamingos (B) and humans (D). Legends: cm, central mound; pt, peripheral trench.

Pending the long relating of this behavior since the end of the 18th century (Buffon, 1781), until now we lack an in-depth analysis of the full spectrum of environmental settings where this behavior is performed; therefore, an improved analysis of the occurrence pattern of stamping/ROTs per environments may improve its use as indicators of environmental conditions and also may clarify the evolution of such behavior in the flamingo lineage and their ecosystem role as bioturbators. Which environmental conditions control this behavior and the preservation of the associated structures produced in modern environments? There are species-specific patterns of behavior/environment association? Which environmental conditions could be indicated by eventual fossilized ROTs? Here we present a synopsis on the occurrence of flamingo stamping behavior and the resulting biogenic structures according to a series of environmental settings and controls, taken from published literature and online video records. We also revised the paleoenvironments from where proceeds the known body and trace fossil record of the flamingo lineage, purposing the comparison with the modern settings with stamping records to infer the probable paleoenvironments where flamingos performed stamping and leaved ROTs during the Cenozoic time span. Finally, we compare our results with the known trace fossil record of flamingo lineage and discuss them in the context of the shorebird/*Phoenicopterichnum* ichnofacies.

2. Methods

2.1. Taxonomic notes

Living flamingos are the survivors of a once more diverse lineage, with a rich fossil record dating back to the early Paleogene (Mayr, 2022). Today, there are six living species of flamingos, classified in three genera and broadly arranged in two ecomorphological groups, mainly differing by the morphology of the beak and the structure of its filter apparatuses: (i) the basal *Phoenicopterus*, encompassing the shallow-keeled group, characterized by upper and lower jaw of equal width, including Chilean (*P. chilensis*), Greater (*P. roseus*) and American (*Phoenicopterus ruber*) Flamingos; (ii) the derived deep-keeled genera *Phoenicoparrus* (Andean *P. andinus* and James's Flamingo *P. jamesi*) and *Phoeniconaias* (the Lesser Flamingo *P. minor*), sharing a higher, bulbous lower jaw that is wider than the upper jaw (Jenkins, 1957; Del Hoyo, 1992). Such dichotomy in the beak anatomy accounts for distinct prey selection in the two groups: the shallow-keeled flamingos capture larger items as insect larvae, crustaceans, seeds, molluscs and worms, while the deep-keeled group specializes in minute algae as cyanobacterias and diatoms (Mascitti and Kravetz, 2002). Despite this taxonomic arrangement in two ecomorphologies is well established, the consensus on the number of genera and species is still debated. Based on molecular data, some authors propose *Phoeniconaias minor* as a species of *Phoenicoparrus* (Torres et al., 2014; Frias-Soler et al., 2022); here, we maintain a conservative view adopted by many bird lists (e.g., Dickinson and Remsen Jr., 2013; Winkler et al., 2020; Gill et al., 2023). The taxonomic assignment of the American *P. ruber* and the Greater Flamingo *P. roseus* alternates between full specific status for both forms, or the Greater Flamingo is merged as a subspecies of the American Flamingo (*P. ruber roseus*); today, these two flamingos are widely accepted as independent species (Sangster, 1997; Collinson, 2006; Banks et al., 2008), an interpretation we adopted here. Due to genetic, morphological and oological divergence from the core *P. ruber* population, the flamingo population of the Galápagos Islands may be regarded as a geographic or subspecific variation of the

American Flamingo (*P. ruber glyphorhynchus*) (Ridgway, 1896; Salvin, 1876; Frias-Soler et al., 2014, 2022), or, less frequently, as a species per se (*P. glyphorhynchus*) (Gray, 1869); we adopted the first interpretation following the current opinion but treated this taxon as a separate taxonomic unit in our analysis.

2.2. Dataset assembling

We assembled a dataset from literature and online video archives on rotating-stamping behavior for all modern flamingo species. Further variations of rotating stamping occurs when the bird remains at one spot, either standing in the same orientation (standing stamping) or moving forward or backward (dislocating stamping). Such variations sometimes precede the full spinning characteristic of the rotating stamping (Ingraham, 1896; Cifuentes, 2007), possibly as exploratory phases prior to the spinning movement. Due to the similar adaptive meaning and possible interrelationship of the stamping-behavior variants (standing, dislocating and rotating), hereafter we treat this series collectively as stamping behavior, highlighting that for the most cases this designation refers to the specific phase of rotating-stamping. This aims to preserve the sense of a behavioral continuum involving what some researchers consider as distinct behaviors, but whose analytical separation could mask the influential environmental and biological factors under it is performed.

For the literature review, we searched the databases of Web of Science and Google Scholar, employing combinations of terms associated to taxonomy (flamingo, Phoenicopteridae, *Phoenicopterus*, *Phoenicoparrus*, *Phoeniconaias*), ichnology (biogenic structures, biogenic sedimentary structures) and behavior (feeding, foraging, paddling, stamping, stomping, treading; see the full list of similar designations in the Supplementary Data 1). Both studies on wild and captive birds were gathered, but the last was excluded from the statistical analyses. Some papers retrieved just very generic descriptions about stamping, lacking mentions of the characteristic spin of the rotating-stamping, but nor also specify if the bird remained at the same spot while stamping (standing-stamping) or if it moved forward or backward (dislocating-stamping) – in such cases, we recorded the behavior as “indeterminate stamping”.

The online videos were searched on eBird (2023), a major electronic platform with bird records (species lists, photos, videos) filled by collaborators worldwide. The eBird dataset covers a wide geographic area, enabling access to ornithological information on a global scale (Smith et al., 2022). We included in the dataset only those individuals that performed a full round of rotating-stamping, or an arbitrary minimum of 5-seconds shooting for the other stamping modalities.

To improve the number of records in the dataset, we made additional searches for localities known to harbor flamingo populations, but not represented in the stamping records of electronic literature (Google Scholar, Web of Science) and video (eBird) platforms. Video records permit to tab stamping occurrence at the bird individual level; however, this is not always the same for the literature records. Therefore, literature records were individualized by species > locality > habitat type > time, meaning that records of a given species from the same locality were dubbed as distinct only if occurred at separate habitat types and time intervals. By its turn, video records were individualized in the same way, except that many video individual archives depict more than one bird stamping: in this case, each video was treated as a single record, whatever the number of individual birds in stamping. Doing this, we aim to achieve the independence of sampling units required for the application of most of the statistical tests.

2.3. Environmental parameters

In the modern environments, the distribution of populations, their behavior and the associated biogenic sedimentary structures produced by them are controlled by a plethora of environmental factors. Accordingly, each stamping record was classified by a set of environmental factors as geography (lat-long coordinates, locality, country, elevation), depositional environment, predominant sediment, substrate, lithology (inferred according to the data from the two preceding factors), habitat type, water depth, salinity, water pH, tidal regime, climate, and season. Such parameters were selected according to those mentioned as the most influential in the relevant literature about environmental controls of bioturbating biotas and trace fossil registration (e.g., Roy et al., 2001; Dashtgard et al., 2008; Whitfield and Elliot, 2011; Dashtgard, 2011a, b; MacEachern et al., 2012; Hembree, 2016). Part of the information was taken from the original stamping-reporting references; otherwise, we consulted additional references to complete the environmental dataset when such information was not given by the specific literature on stamping. In this last case, because physicochemical parameters such as salinity and pH often vary locally and seasonally (Le Fur et al., 2018), we carefully searched data spatially and temporally coincident with the local/time where stamping were reported. However, not all localities could be searched for this level of detail, and, in this case, the gathered values are better interpreted as approximations.

Geographic coordinates and elevation values were taken directly from the referred works or were obtained with the software Google Earth version 7.3.6.9345 (http://earth.google.com) when not specified by the authors consulted. Data on climate zonation follows the update of the Köppen-Geiger climate classification by Peel et al. (2007) and Beck et al. (2018). Tidal classification follows Whitfield and Elliot (2011).

Analysis of the Earth systems is a manifold task, as the Earth surface is a mosaic of different ‘spheres’ (geosphere, atmosphere, biosphere) interplaying at multiple space-time scales. As a result, the choice of the scale for analysis can greatly impact the resulting environmental-association outcome (de Boer, 1992; Mannion and Upchurch, 2010; Ramkumar and Menier, 2017), and hierarchical schemes had been proposed for a bunch of landforms and depositional systems (e.g., Miall, 1985; Brookfield, 1977; Cullis et al., 2018). Given that, the different environmental settings were organized according a three-scale hierarchy (similar to the models developed by Gagrani et al., 2006 and Kim et al., 2021), from the broadest to the narrowest as follow: (i) first- or higher-order, corresponding to the major landforms (Boggs, 2014); (ii) second- or intermediate-order, broadly equals to the specific depositional environments within the major landforms; and (iii) third- or least-order, the narrowest systems’ classification, corresponding to discrete habitat types (Figure 2). “Habitat-type” is an umbrella term related to biophysical environment or vegetation assemblages; it differs from “habitat”, which, in its simple usage, is a species-specific term referring to the requirements of the ecological niche of a given species (Krausman and Morrison, 2016; Darracq and Tandy, 2019) – as such, it is not appliable to the physical environment of hole communities composed by populations of many species, which are the ecological level more akin to the scale of the ichnocoenoses, ichnofacies and other fossil assemblages (Buatois and Mángano, 2011). Depositional systems and habitat types were taken as two different environmental settings (sedimentological and biotic/ecological, respectively) because some habitat types can overlap with distinct sedimentary environments (*e.g.*, saline marshes in both tidal and lacustrine environments), or, alternatively, different sedimentary environments often encompass more than one habitat type (*e.g.*, tidal environment harboring marshlands, flats and seashore). Such organization aims to satisfy the premise that trace fossils and their associations (ichnoassemblages and ichnocoenoses) are not good predictors of depositional environments, but rather indicators of specific environmental conditions that could be repeated between different depositional environments or could vary according to different aspects of the same depositional system (Buatois and Mángano, 2011). By this way, we intend to perform a number of analyses in each of these levels and evaluate whom of them show significant associations with the stamping frequency.

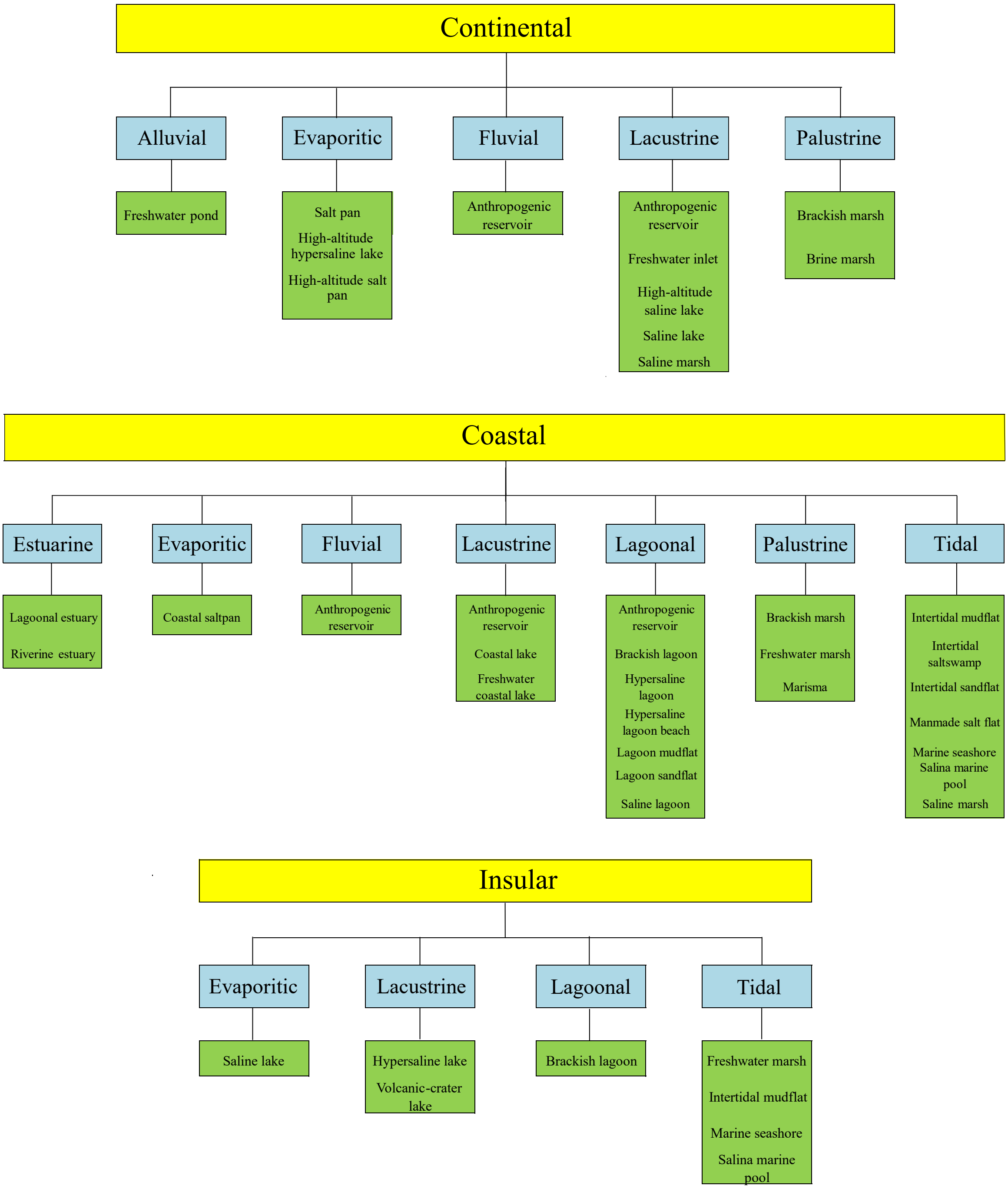

Figure 2. Flowchart of the proposed hierarchical classification scheme of first- (yellow), second- (blue) and third-order (green) environments.

Since calculating the exact water depth where a flamingo foraged is impossible from video records, we calculated this depth based on the submerged portion of the bird's hindlimb length – this technique has been applied by different authors (Sebastiani et al., 1995; Mascitti, 1998; Mascitti and Castanera, 2006; Khaleghizadeh, 2010; Gutiérrez and Soriano-Redondo, 2018). As hindlimb morphometrics can vary between flamingo species and populations (Frias-Soler et al., 2014), we calculated mean length values for tibiotarsus and tarsometatarsus of each flamingo species by compiling published measures, to derive inferred water column depths in those eBird videos where flamingos foraged by rotating stamping (Supplementary Data 2). These approximations were species-specific due to the slight size difference among flamingo species, but we do not distinguish measurements by gender, or from captive versus field records. As the tarsometatarsus length only reach full size in birds at the age of one-and-a-half year (Studer-Thiersch, 1986) and its definitive size may depend on the environmental conditions during the bird's ontogeny (Barbraud et al., 2003), we refrain calculation of water depths using morphometrics from juveniles or immatures individuals. As non-adult individuals accounted for only 10% of total records, we judged that this exclusion did not affect the analyses.

Not all papers reported grain size or sediment composition for the definition of our sediment categories, while among those that did, accuracy ranged from high (e.g., sandy mud) to low (e.g., mud). Thus, the sediment types were grouped into four broader categories: (i) mud (including silt, clay, sandy mud, sandy clay, sandy silt) (ii) sand (includes muddy sand), (iii) carbonate (carbonate mud, carbonate-siliciclastic, marl mud) and (iv) mixed (ooze, organic matter). As such, substrate type has a broader meaning than the sediment type, which is mainly defined by the grain size in the substrate. This aims to overcome the difficult to obtain more detailed information about heterogeneous areas with high sedimentary variability, and because the distinction between sediment types varies according to the discipline (geology, sedimentology, engineering). Sediment and substrate types were used as surrogates to infer lithologies where hypothetical ROTs could be found in the geological record.

2.4. Statistics

To investigate the ROTs reliability as ichnological proxies for accurate paleoecological and paleoenvironmental inferences, we analyzed the relationship of the stamping behavior and ROTs structures occurrence with the above cited parameters. We made two groups of analyses: (i) group I include all the variants of the stamping behavior, and (ii) group II encompass only the rotating-stamping performance. In each group, we analyzed each species separately and the total records of all species summed.

We used the non-parametric Pearson’s chi-square tests (χ^2) to investigate bias in the environmental parameters for the stamping performance among the flamingo taxa. The chi-square test is appropriate for data as counts of discrete objects (in our case, the stamping records) of two or more categories (e.g., the flamingo taxa). We computed chi-square in R software (The R Foundation for Statistical Computing 2023) using the function chisq.test(). Differences were considered significant if the *p*-value was less than 5% ($p \leq 0.05$).

To investigate differences in depth and pH values between flamingo species, the non-parametric Kruskal-Wallis test was used, as the data did not meet the homoscedasticity assumptions necessary for the application of parametric ANOVA. The Kruskal-Wallis test was performed using the standard kruskal.test() function in R. Subsequently, the comparison between species means was performed using Dunn's non-parametric test using the DunnTest() function from the {DescTools} library (Andri et al., 2020) implemented in R.

3. Results

3.1. Taxonomic pattern

We obtained a total of 131 stamping records (in all its variants) for five flamingo species, including literature and video records. *P. roseus* was the most recorded species (n = 75), accounting for 57% of the records (Table 1, Figure 3). The two subspecies of the American Flamingo were represented, predominating the records of the nominal subspecies *P. r. ruber* over the Galapagos subspecies *P. r. glyphorhynchus* (n = 29 and n = 3, respectively). For the Chilean Flamingo, there were 19 records, being the *Phoenicopterus* species least represented in the rotating-stamping accounts. Regarding the deep-keeled group, Lesser Flamingo and Andean Flamingo accounted for three records each. Rotating stamping was the predominant stamping mode for most species, except for the Andean Flamingo with only indeterminate stamping recorded.

Table 1. Frequency of records of stamping behaviors in five flamingo species. The first and second values in parentheses indicate the number of records from literature and online videos, respectively.

Taxon	Rotating	Standing	False	Indeterminate	Compound*
Phoenicopterus chilensis	10 (8, 2)	2 (2, 0)	2 (1, 1)	3 (3, 0)	1 (1, 0)
Phoenicopterus roseus	58 (32, 26)	16 (2, 14)	-	2 (1, 0)	-
Phoenicopterus ruber#	14 (11, 3)	9 (7, 2)	-	8 (8, 0)	1 (1, 0)
Phoenicoparrus andinus	-	-	-	3 (3, 0)	-
Phoeniconaias minor	3 (3, 0)	-	-	-	-

* Dislocating stamping + rotating stamping for the *Phoenicopterus chilensis*; standing stamping + rotating stamping for the *Phoenicopterus ruber*.

Includes *P. r. ruber* and *P. r. glyphorhynchus* subspecies.

Sixty-one references citing stamping yielded 88 records from the literature, from which *P. roseus* predominates (Table 1). Lesser and Andean Flamingos were recorded only by literature accounts. By its turn, the eBird dataset catalogued 541 videos of flamingos in foraging/feeding behaviors, from which 49 (9%) represent stamping behavior, mainly rotating-stamping behavior (N = 31, 5.73% of the 541 total). All the video records for rotating stamping depict the three *Phoenicopterus* species, mirroring the literature records by the predominance of the Greater Flamingo (26 of a total 256 videos, or 10%), followed by the American Flamingo (three of a total 90 videos, or 3.3%) and by the Chilean Flamingo (two of a total 75 videos, or 2.7%) (Table 1, Figure 3). No eBird video archive documents this behavior for *Phoenicoparrus* or *Phoeniconaias* species.

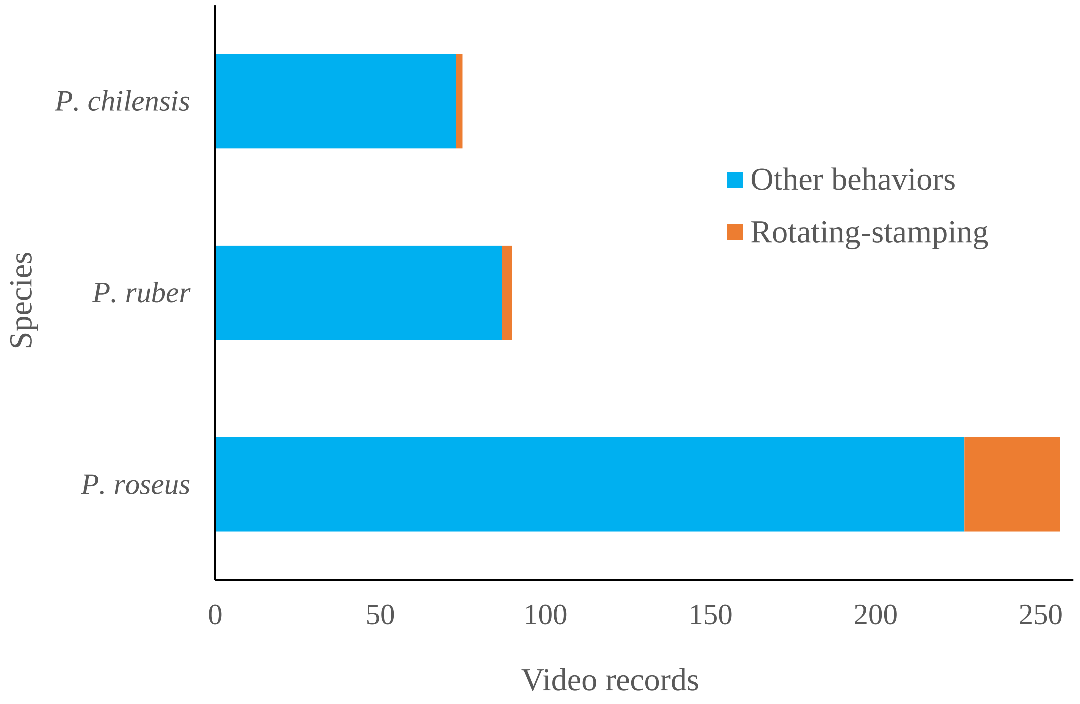

Figure 3. Frequency of the rotating-stamping and other feeding behaviors recorded in eBird videos for three *Phoenicopterus* flamingo species.

3.2. Geographic pattern

Overall, rotating-stamping records were distributed across the global range of flamingos, but were unrecorded for some regions, such as the Red Sea coast, East Asia and Southwestern Africa (Figure 4). ROT structures were present from all the regions were the rotating-stamping behavior was recorded.

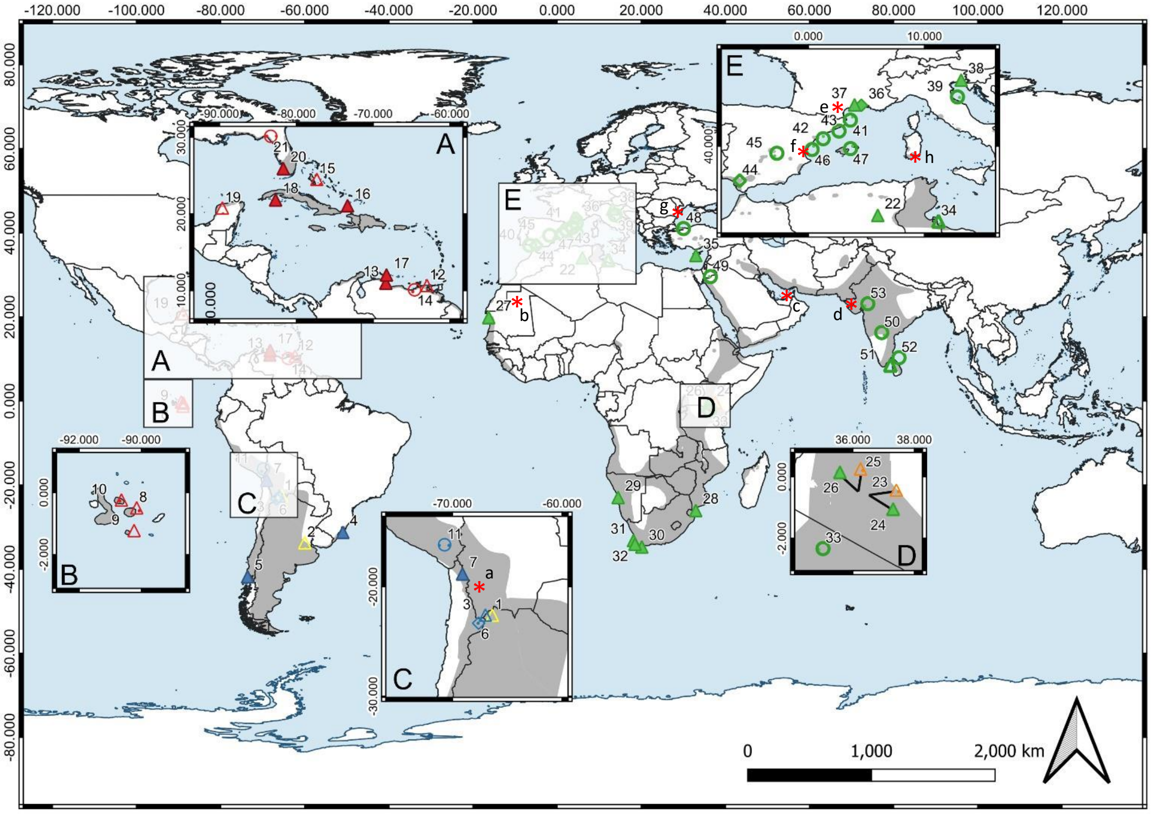

Figure 4. Field record distribution of stamping behavior and associated structures from literature (triangles), video (circles) or both sources (diamonds) for five extant flamingo species: *Phoenicopterus ruber* (red; includes *P*. *r*. *ruber* and *P*. *r*. *glyphorhynchus*), *Phoenicopterus roseus* (green), *Phoenicopterus chilensis* (blue), *Phoenicoparrus andinus* (yellow) and *Phoeniconaias minor* (orange). Full color symbols indicate records of rotating-stamping structures; open symbols indicate records of rotating-

and/or indeterminate-stamping behavior without mention of associated structures; asterisks depict localities only with other variants of stamping behavior (dislocating-, standing- and false-stamping). Grey shaded area indicates the global distribution of modern Phoenicopteridae. Localities: 1- Vilama, 2- Melincué, 3- Herrera, 4- Lagoa do Peixe, 5- Caulín, 6- Chaxa, 7- Salar de Surire, 8- Las Bachas, 9- Punta Cormorán, 10- Santiago Island, 11- Salinas y Aguada Blanca, 12- Chacopata, 13- Cuare, 14- Unare, 15- Andros, 16- Rosa (Windsor), 17- Pekelmeer, 18- Nueces Salina, 19- Celestún and Ría Lagartos, 20- Caxambas, 21- Wakulla, 22- Chott Merouane and Chott Tindla, 23-24- Elmenteita, 25-26- Nakuru, 27- Banc d'Arguin, 28- Inhaca, 29- Walvis Bay and Sandwich Harbour, 30- Heuningnes, 31- Langebaan, 32- Rondevlei, 33- Moru Kopjes, 34- Bou-Ghrara and Djerba, 35- Akrotiri, 36- Camargue, 37- Montpellier, 38- Marano, 39- Saline di Cervia, 40- Ría Formosa, 41- Aiguamolls de l'Empordà, 42- Delta de l'Ebre and Tancada, 43- Delta del Llobregat, 44- Doñana, 45- la Veguilla, 46- El Quadro, 47- Sa Roca, 48- Büyükçekmece, 49- Eilat, 50- Alamatti, 51- Koonthakulam, 52- Calimere, 53- Thol, 54- Kutch, a- Uyuni, b- Oued Souss, c- Al-Zora, d- Mandvi, e- Gard, f- L'Albufera, g- Pomorie, h- Molentargius.

3.3. Environmental pattern

Pearson's chi-square test found significant association between coastal environments and stamping for the Greater Flamingo (group I analyses, χ^2_2 = 50.25, p = 1.2 x 10-11 group II, χ^2_2= 46.211, p = 9.2 x 10-11) and for the total Phoenicopteridae (group I, χ^2_2= 39.66, p = 2.4 x 10-9; group II, χ^2_2= 36.024, p = 1.5 x 10-8). However, continental environments were comparatively representative in almost all taxonomic levels, except for the American Flamingo, whose records were restricted to coastal and island environments (Figure 5). The results of all analyses are depicted in the Table 2.

Table 2. Results of Pearson's chi-square test for environmental variables analyzed in relation to stamping behavior for three species of Phoenicopterus flamingos and for the total of Phoenicopteridae sampled. Statistically significant results at α = 0.05 are in **bold**. # Includes *P. r. ruber* and *P. r. glyphorhynchus* subspecies.

Environmental variable	*Phoenicopterus chilensis*		*Phoenicopterus roseus*		*Phoenicopterus ruber#*		Total Phoenicopteridae	
	GI	GII	GI	GII	GI	GII	GI	GII
First-order environment	χ^2_1= 49.461, *p* = 0.8084	χ^2_1= 0, *p* = 1	**χ^2_2 = 50.25, *p* = 1.2 x 10^{-11}**	**χ^2_2 = 46.211, *p* = 9.2 x 10^{-11}**	χ^2_1= 0.13333, *p* = 0.715	χ^2_1= 0.69231, *p* = 0.4054	**χ^2_2 = 39.66, *p* = 2.4 x 10^{-9}**	**χ^2_2 = 36.024, *p* = 1.5 x 10^{-8}**
Second-order environment	χ^2_3 = 0.64706, *p* = 0.8856	χ^2_3 = 1.2222, *p* = 0.7477	**χ^2_7 = 70.444, *p* = 1.2 x 10^{-12}**	**χ^2_7 = 56.825, *p* = 6.5 x 10^{-10}**	**χ^2_3 = 16.667, *p* = 0.0008275**	**χ^2_3 = 9.4615, *p* = 0.02374**	**χ^2_7= 94.968, *p* < 2.2 x 10^{-16}**	**χ^2_7 = 62.39, *p* = 5 x 10^{-11}**
Third-order environment	χ^2_5 = 5.2353, *p* = 0.3878	χ^2_4 = 1.5556, *p* = 0.8168	**χ^2_{23} = 65.333, *p* = 6.2 x 10^{-6}**	**χ^2_{21} = 46.053, *p* = 0.001257**	**χ^2_{11} = 28.4, *p* = 0.00281**	χ^2_6 = 6.9231, *p* = 0.328	**χ^2_{31} = 114.36, *p* = 1.8 x 10^{-11}**	**χ^2_{28} = 82.805, *p* =**

Environmental variable	*Phoenicopterus chilensis*		*Phoenicopterus roseus*		*Phoenicopterus ruber#*		Total Phoenicopteridae	
	GI	GII	GI	GII	GI	GII	GI	GII
								2.5×10^{-7}
Sediment type	$\chi^2_5 = 7$, *p* = 0.2206	$\chi^2_2 = 2$, *p* = 0.3679	**$\chi^2_9 = 130.06$, $p < 2.2 \times 10^{-16}$**	**$\chi^2_8 = 68.471$, $p = 9.9 \times 10^{-12}$**	$\chi^2_8 = 11.655$, *p* = 0.1673	$\chi^2_5 = 1$, *p* = 0.9626	**$\chi^2_{14} = 4.5172$, $p < 2.2 \times 10^{-16}$**	**$\chi^2_{13} = 146.21$, $p < 2.2 \times 10^{-16}$**
Substrate type	$\chi^2_2 = 5.2$, *p* = 0.07427	$\chi^2_2 = 3.5714$, *p* = 0.05878	**$\chi^2_2 = 109.76$, $p < 2.2 \times 10^{-16}$**	**$\chi^2_3 = 79.118$, $p < 2.2 \times 10^{-16}$**	$\chi^2_3 = 4.5172$, *p* = 0.2108	$\chi^2_3 = 1.3333$, *p* = 0.7212	**$\chi^2_2 = 99.637$, $p < 2.2 \times 10^{-16}$**	**$\chi^2_3 = 68.753$, $p = 7.9 \times 10^{-15}$**
Lithology	$\chi^2_2 = 3.4499$, *p* = 0.1782	$\chi^2_1 = 3.5714$, *p* = 0.05878	**$\chi^2_2 = 62.182$, $p < 3.1 \times 10^{-14}$**	**$\chi^2_2 = 46.941$, $p = 6.4 \times 10^{-11}$**	$\chi^2_4 = 9.4483$, *p* = 0.05082	$\chi^2_4 = 1.3333$, *p* = 0.8557	**$\chi^2_4 = 145.36$, $p < 2.2 \times 10^{-16}$**	**$\chi^2_4 = 103.23$, $p < 2.2 \times 10^{-16}$**

Environmental variable	*Phoenicopterus chilensis*		*Phoenicopterus roseus*		*Phoenicopterus ruber#*		Total Phoenicopteridae	
	GI	GII	GI	GII	GI	GII	GI	GII
Salinity	$\chi^2_2 = 0.4$, p = 0.8187	$\chi^2_2 = 1.1429$, p = 0.5647	$\chi^2_3 = 6.4925$, p = 0.08996	**$\chi^2_3 = 7.8462$, p = 0.0493**	$\chi^2_2 = 3.5$, p = 0.1738	**$\chi^2_2 = 7.8182$, p = 0.02006**	**$\chi^2_3 = 16.966$, p = 0.0007184**	**$\chi^2_3 = 15.603$, p = 0.001368**
Tide	$\chi^2_1 = 0.058824$, p = 0.8084	$\chi^2_1 = 0.11111$, p = 0.7389	**$\chi^2_2 = 25.583$, $p = 2.8 \times 10^{-6}$**	**$\chi^2_2 = 20.632$, $p = 3.3 \times 10^{-5}$**	**$\chi^2_2 = 29.6$, $p = 3.7 \times 10^{-7}$**	**$\chi^2_2 = 7.5385$, p = 0.02307**	**$\chi^2_2 = 38.608$, $p = 4.1 \times 10^{-9}$**	**$\chi^2_2 = 24.171$, $p = 5.6 \times 10^{-6}$**
Climate	$\chi^2_3 = 1.2667$, p = 0.7371	$\chi^2_3 = 1.5714$, p = 0.6659	**$\chi^2_9 = 106.61$, $p < 2.2 \times 10^{-16}$**	**$\chi^2_9 = 103.18$, $p < 2.2 \times 10^{-16}$**	**$\chi^2_3 = 19.867$, p = 0.0001809**	$\chi^2_3 = 7.1429$, p = 0.06748	**$\chi^2_{11} = 89.39$, $p = 2.2 \times 10^{-14}$**	**$\chi^2_{11} = 88.3$, $p = 3.5 \times 10^{-14}$**
Season	$\chi^2_3 = 1.4615$,	$\chi^2_2 = 0.25$,	$\chi^2_3 = 5.2258$,	$\chi^2_3 = 3.1667$,	$\chi^2_3 = 0.4$,	$\chi^2_3 = 2.1111$,	$\chi^2_3 = 4.64$,	$\chi^2_3 = 2.8769$,

Environmental variable	*Phoenicopterus chilensis*		*Phoenicopterus roseus*		*Phoenicopterus ruber#*		Total Phoenicopteridae	
	GI	GII	GI	GII	GI	GII	GI	GII
	p = 0.6912	*p* = 0.8825	*p* = 0.156	*p* = 0.3666	*p* = 0.9402	*p* = 0.5497	*p* = 0.2001	*p* = 0.411

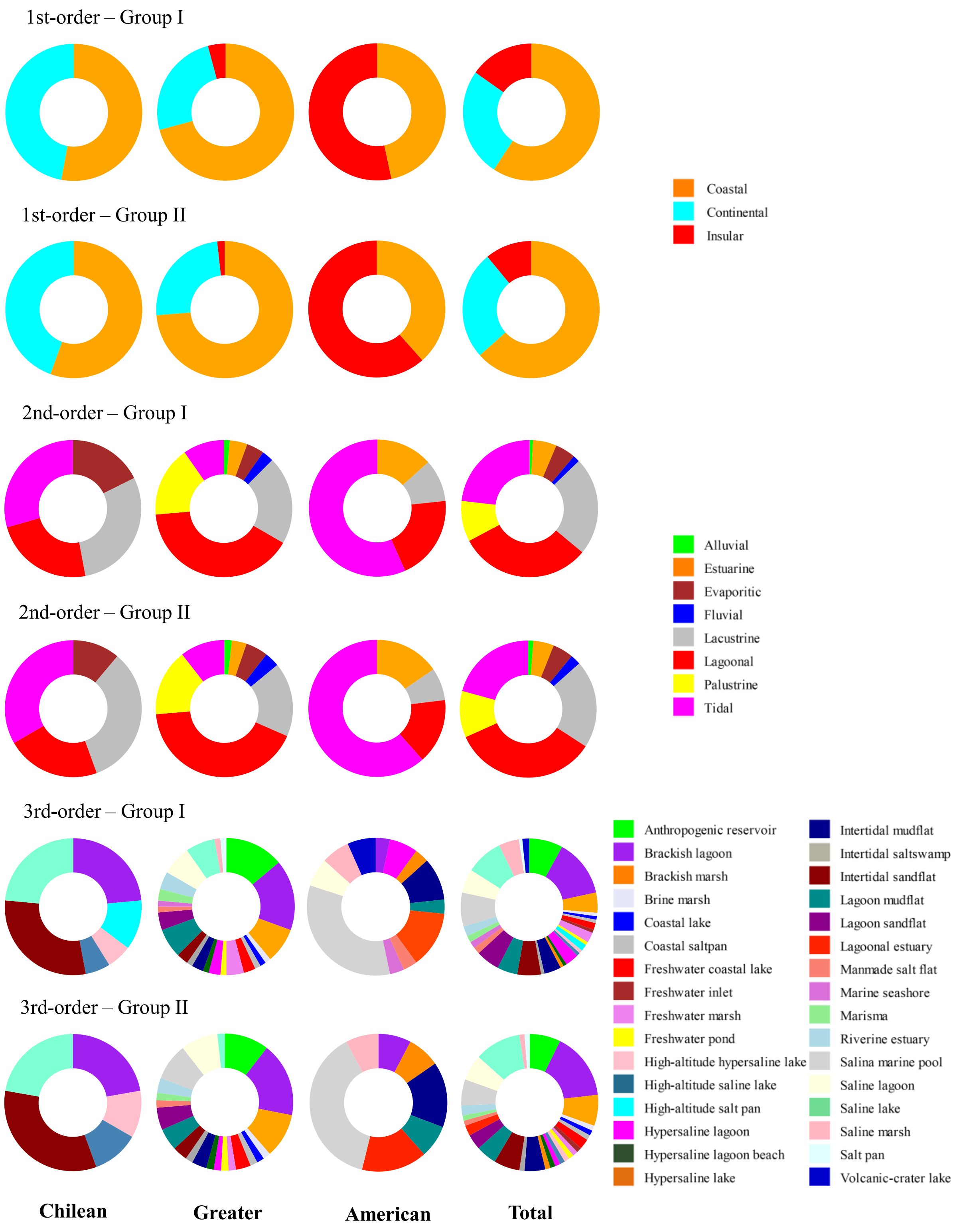

Figure 5. Frequency of stamping behavior by (A) first-, (B) second-, and (C) third-order environmental settings for five flamingo species (Chilean *Phoenicopterus chilensis*, American *Phoenicopterus ruber*, Greater *Phoenicopterus roseus*, Andean

Phoenicoparrus andinus, and Lesser *Phoeniconaias minor*) from combined literature and online video data. Andean and Lesser Flamingos had only up to three records in less than two environmental settings, so they are not showed individually but are represented in the total records. Group I includes all the stamping variants (rotating, standing, false and indeterminate); group II includes only rotating stamping.

The lagoonal depositional environment predominated among major second-order environments (Figure 5). Such association was significant for the Greater Flamingo (group I, $\chi^2_7 = 70.444$, $p = 1.2 \times 10^{-12}$; group II, $\chi^2_7 = 56.825$, $p = 6.5 \times 10^{-10}$) and for the total Phoenicopteridae (group I, $\chi^2_7 = 94.968$, $p < 2.2 \times 10\text{-}16$; group II, $\chi^2_7 = 62.39$, $p = 5 \times 10^{-11}$). A significant association with tidal environment occurred only for the American Flamingo (group I, $\chi^2_3 = 16.667$, $p = 0.0008275$; group II, $\chi^2_3 = 9.4615$, $p = 0.02374$).

Significant association was found to brackish lagoons and saline lakes habitat-types for the total Phoenicopteridae (group I, $\chi^2_{31} = 114.36$, $p = 1.8 \times 10\text{-}11$; group II, $\chi^2_{28} = 82.805$, $p = 2.5 \times 10\text{-}7$), brackish lagoons and anthropogenic reservoirs for the Greater Flamingo (group I, $\chi^2_{23} = 65.333$, $p = 6.2 \times 10\text{-}6$; group II, $\chi^2_{21} = 46.053$, $p = 0.001257$), and marine pools for the American Flamingo (only group I, $\chi^2_{11} = 28.4$, $p = 0.00281$) (Figure 5). The Greater Flamingo was the species with the higher number of environments recorded for rotating-stamping, while Chilean, Andean and Lesser Flamingos had the least environmental diversity.

The mean depth where flamingos used stamping was 22.2 cm (Table 3, Figure 6). There was a significant difference between species averages (means and medians), according to the Kruskal-Wallis test (Kruskal-Wallis chi-squared = 7.8775, df = 2, p = 0.01947). Dunn's *post hoc* test showed that the average depth of the Greater Flamingo (24.45 cm) differed significantly from the average depth of the Chilean

Flamingo (7.4 cm) but did not differ from the average depth of the American Flamingo (20.12 cm), demonstrating some species-specific particularities (Table 4).

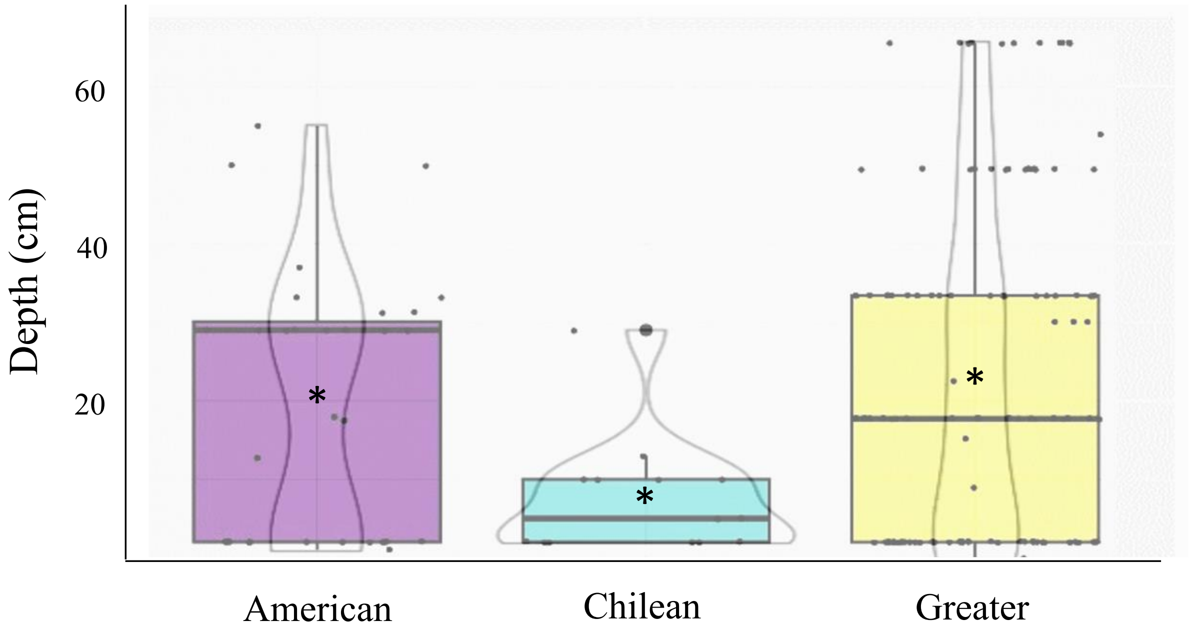

Figure 6. Distribution of the water depth measurements (in centimeters) where the three *Phoenicopterus* species displayed the stamping behavior. An asterisk indicates the mean.

Table 3. Statistical descriptors of water depth at stamping for three flamingo species.

Species	*n*	Mean	Median	Range
Phoenicopterus ruber #	31	20.12	29	1-55
Phoenicopterus chilensis	14	7.4	3.5	2-29
Phoenicopterus roseus	111	24.45	17.72	0-65.55

Total Phoenicopteridae	156	22.19481	17.72	0-65.55

Includes *P. r. ruber* and *P. r. glyphorhynchus* subspecies.

Table 4. Output from of the *post hoc* Dunn's test for water depth. An asterisk (*) indicates significance at $\alpha = 0.05$. Flamingo species: Chilean (*Phoenicopterus chilensis*), American (*Phoenicopterus ruber*), Greater (*Phoenicopterus roseus*)

Pair-pair comparison	Mean rank difference	*p*
Chilean-American	-23.3917	0.199
Greater-American	10.43069	0.2443
Greater-Chilean	33.82239	0.0205 *

We find a positive association between stamping and muddy substrates for the Greater Flamingo (group I, $\chi^2_2 = 109.76$, $p < 2.2 \times 10^{-16}$; group II, $\chi^2_3 = 79.118$, $p < 2.2 \times 10^{-16}$) and for the total Phoenicopteridae (group I $\chi^2_2 = 99.637$, $p < 2.2 \times 10^{-16}$; group II, $\chi^2_3 = 68.753$, $p = 7.9 \times 10^{-15}$) (Figure 7). These results derived from the predominance of mud-sized sediments (*e.g.*, clay, silt, sandy mud) found for all species (Figure 8).

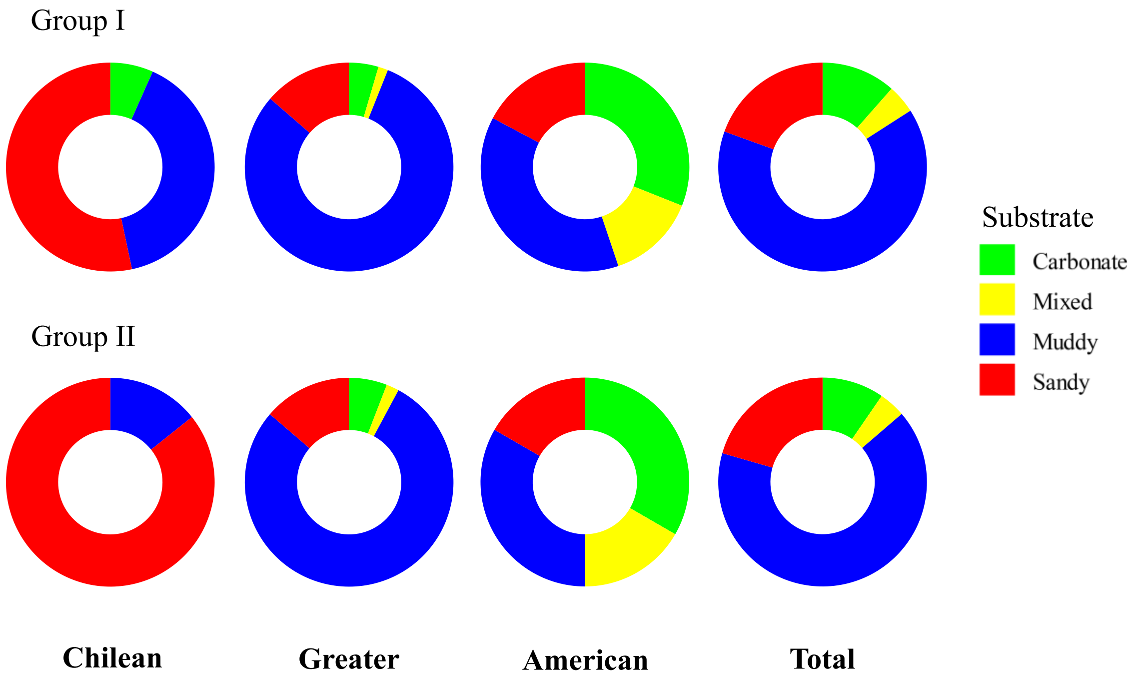

Figure 7. Frequency of stamping behavior by substrate type for five flamingo species (Chilean *Phoenicopterus chilensis*, American *Phoenicopterus ruber*, Greater *Phoenicopterus roseus*, Andean *Phoenicoparrus andinus*, and Lesser *Phoeniconaias minor*) from combined literature and online video data. Andean and Lesser Flamingos only represented in the total records. Group I includes all the stamping variants (rotating, standing, false and indeterminate); group II contains rotating stamping only.

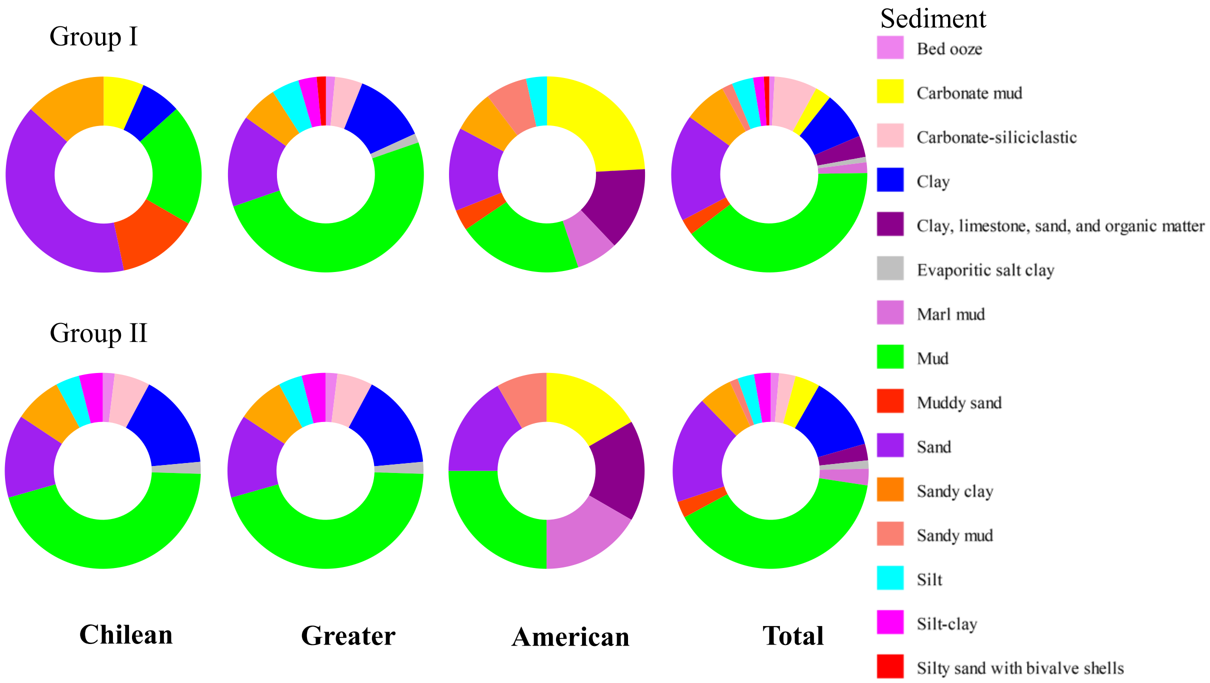

Figure 8. Frequency of stamping behavior by sediment type for five flamingo species (Chilean *Phoenicopterus chilensis*, American *Phoenicopterus ruber*, Greater *Phoenicopterus roseus*, Andean *Phoenicoparrus andinus*, and Lesser *Phoeniconaias minor*) from combined literature and online video data. Andean and Lesser Flamingos only represented in the total records. Group I includes all the stamping variants (rotating, standing, false and indeterminate); group II contains rotating stamping only.

We found significant association between mudstone lithology and stamping for Greater Flamingo (group I, $\chi^2_2 = 62.182$, $p < 3.1 \times 10^{-14}$; group II, $\chi^2_2 = 46.941$, $p = 6.4 \times 10^{-11}$) and for the total Phoenicopteridae (group I, $\chi^2_4 = 145.36$, $p < 2.2 \times 10^{-16}$; group II, $\chi^2_4 = 103.23$, $p < 2.2 \times 10^{-16}$) (Figure 9). A nearly significant association occurred for the American Flamingo (only group I, $\chi^2_4 = 9.4483$, $p = 0.05082$).

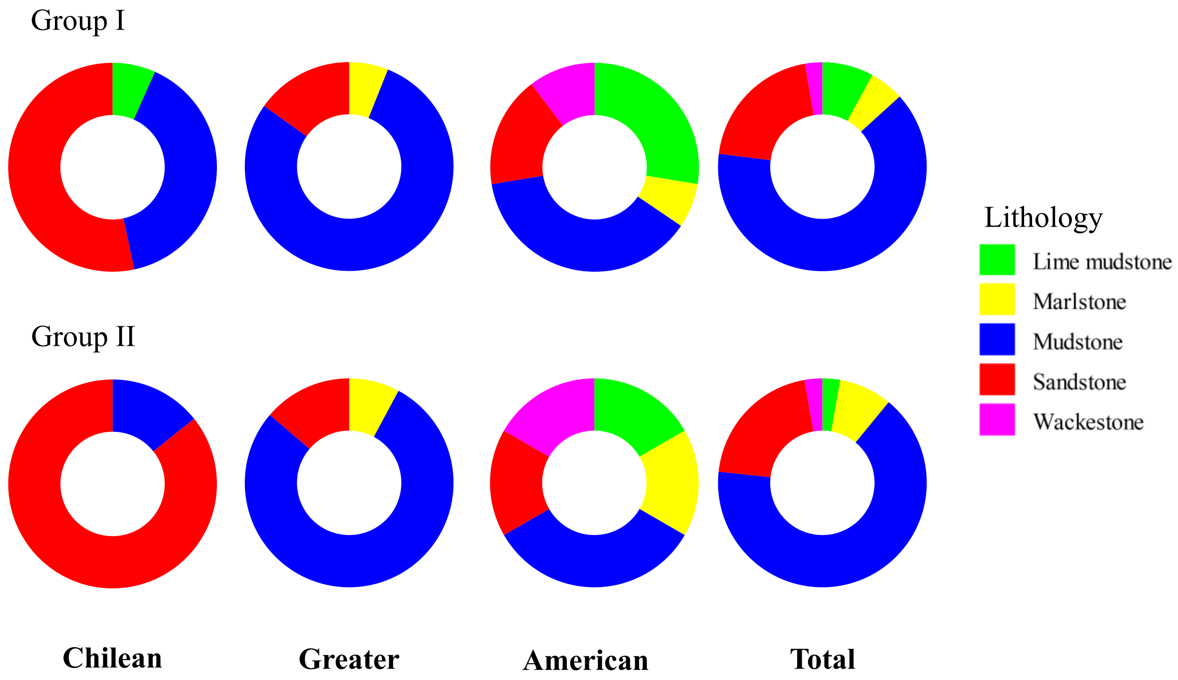

Figure 9. Frequency of stamping behavior by inferred lithology for five flamingo species (Chilean *Phoenicopterus chilensis*, American *Phoenicopterus ruber*, Greater *Phoenicopterus roseus*, Andean *Phoenicoparrus andinus*, and Lesser *Phoeniconaias minor*) from combined literature and online video data. Andean and Lesser Flamingos only represented in the total records. Group I includes all the stamping variants (rotating, standing, false and indeterminate); group II contains rotating stamping only.

Brackish and saline were equally the most frequent salinity degrees where rotating stamping was significantly performed by the Greater Flamingo (group II, $\chi^2_3 = 7.8462$, $p = 0.0493$) and the total Phoenicopteridae (group II, $\chi^2_3 = 15.603$, $p = 0.001368$), but the significance for stamping in general occurred only for the total Phoenicopteridae (group I, $\chi^2_3 = 16.966$, $p = 0.0007184$) (Figure 10). Brackish waters association with rotating stamping were also significant for the American Flamingo (group II, $\chi^2_2 = 7.8182$, $p = 0.02006$).

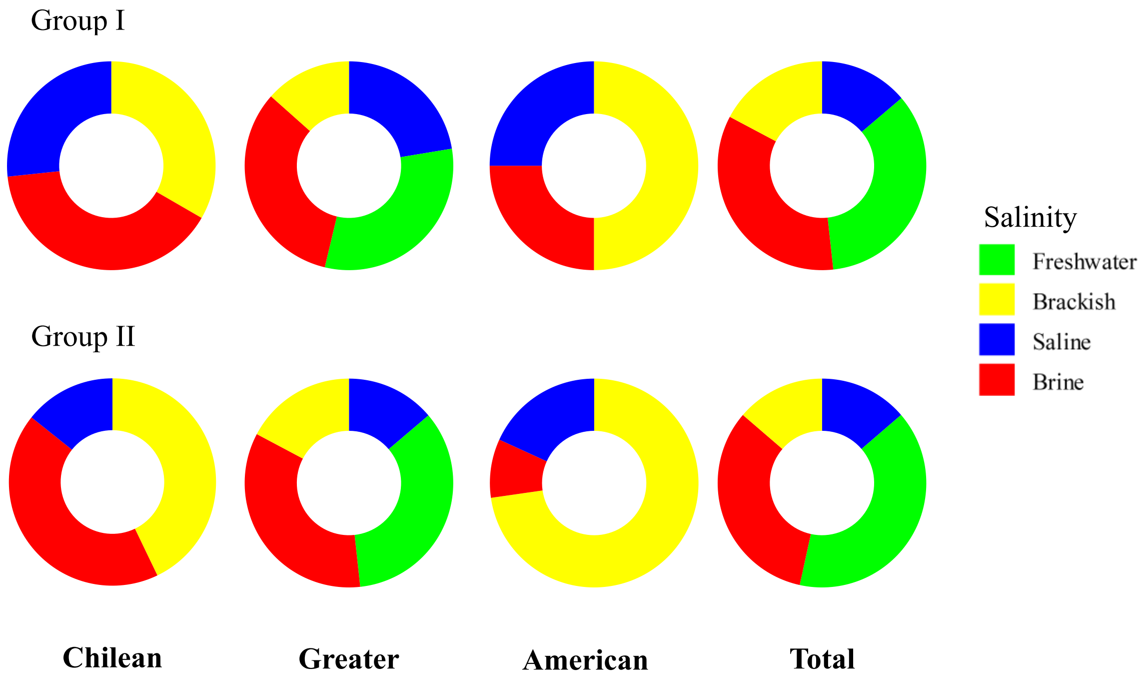

Figure 10. Frequency of stamping behavior by salinity for five flamingo species (Chilean *Phoenicopterus chilensis*, American *Phoenicopterus ruber*, Greater *Phoenicopterus roseus*, Andean *Phoenicoparrus andinus*, and Lesser *Phoeniconaias minor*) from combined literature and online video data. Andean and Lesser Flamingos only represented in the total records. Group I includes all the stamping variants (rotating, standing, false and indeterminate); group II contains rotating stamping only.

The mean pH for stamping of flamingos was 7.8 (Table 5, Figure 11). There was a significant difference between species means, according to the Kruskal-Wallis test (Kruskal-Wallis chi-squared = 16.858, df = 4, p = 0.00206). According to Dunn's post hoc test, the greatest differences occurred between pairs of deep-keeled versus shallow-keeled species, as Chilean (mean pH 7.5) contrasted to Andean (mean pH 10) and to Lesser Flamingo (mean pH 9.23) (Table 6). The contrast between shallow-keeled species was smaller, as demonstrated by Dunn's *post hoc* test (Table 6), suggesting that these species practice stamping in only slightly alkaline waters.

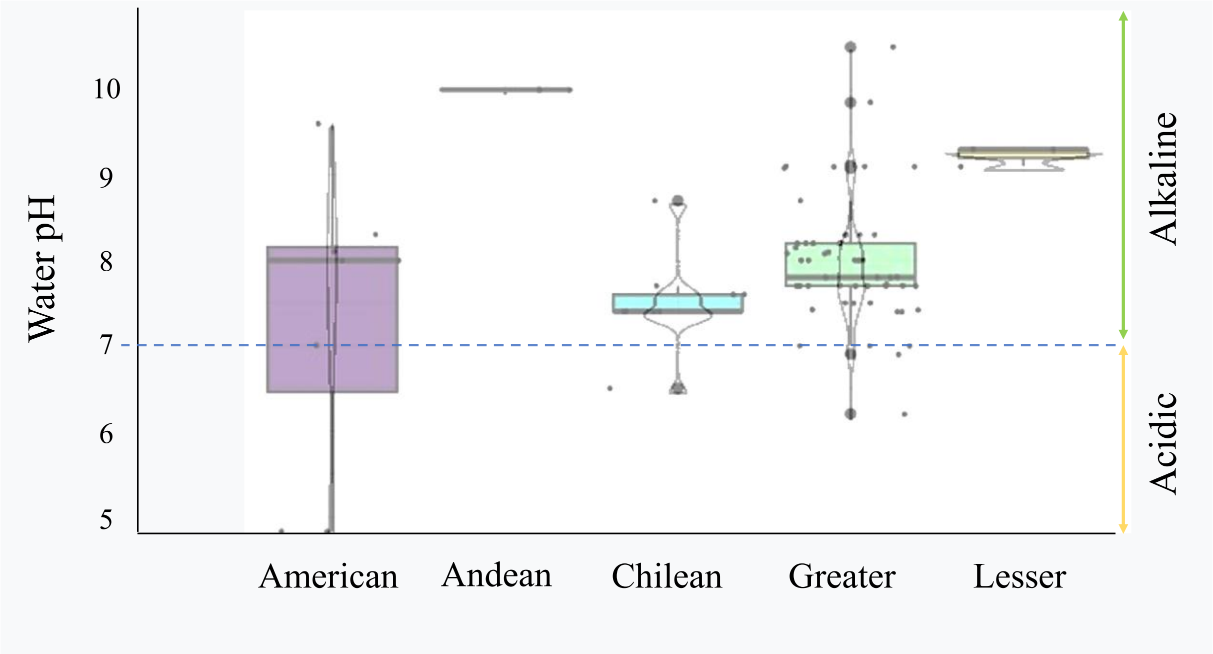

Figure 11. Distribution of the water pH values where five flamingo species displayed the stamping behavior.

Table 5. Statistical descriptors of water pH at stamping for three flamingo species.

Species	*n*	Mean	Median	Range
American#	8	7	7.7	4.8–9.6
Chilean	9	7.5	7.7	6.5–8.7
Greater	51	7.93	7.7	6.2–10.5
Andean	2	10	10	10
Lesser	3	9.23	9.3	9.1–9.3
Total Phoenicopteridae	73	7.8	7.7	4.8–10.5

Includes *P. r. ruber* and *P. r. glyphorhynchus* subspecies.

Table 6. Output from of the post hoc Dunn's test for water depth. An asterisk (*) indicates significance at α = 0.05.

Pair-pair comparison	Mean rank difference	*p*
Andean-American	38.25	0.1675
Chilean-American	-12.8056	0.6391
Greater-American	4.181373	1
Lesser-American	33.08333	0.1675
Chilean-Andean	-51.0556	0.0183 *
Greater-Andean	-34.0686	0.1675
Lesser-Andean	-5.16667	1
Greater-Chilean	16.98693	0.1675
Lesser-Chilean	45.88889	0.0114 *
Lesser-Greater	28.90196	0.1675

Results of the analyses investigating the relationship between tide regime and stamping behavior derived a significant association with microtidal and nontidal regions for the total Phoenicopteridae (group I, $\chi^2_2 = 38.608$, $p = 4.1 \times 10^{-9}$; group II, $\chi^2_2 = 24.171$, $p = 5.6 \times 10^{-6}$), nontidal for the Greater Flamingo (group I, $\chi^2_2 = 25.583$, $p = 2.8 \times 10^{-6}$; group II, $\chi^2_2 = 20.632$, $p = 3.3 \times 10^{-5}$) and microtidal for the American Flamingo (group I, $\chi^2_2 = 29.6$, $p = 3.7 \times 10^{-7}$; group II, $\chi^2_2 = 7.5385$, $p = 0.02307$) (Figure 12).

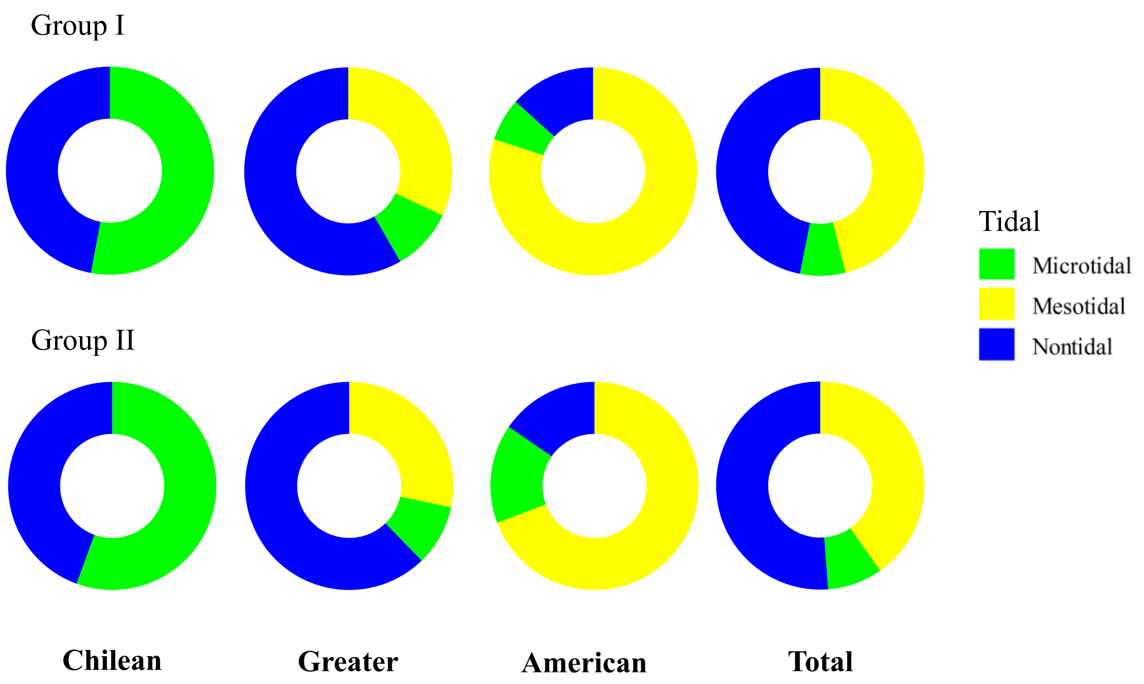

Figure 12. Frequency of stamping behavior by tide regime for five flamingo species (Chilean *Phoenicopterus chilensis*, American *Phoenicopterus ruber*, Greater *Phoenicopterus roseus*, Andean *Phoenicoparrus andinus*, and Lesser *Phoeniconaias minor*) from combined literature and online video data. Andean and Lesser Flamingos only represented in the total records. Group I includes all the stamping variants (rotating, standing, false and indeterminate); group II contains rotating stamping only.

Regarding climate, significant association was found between Mediterranean climate (Csa) and stamping for the Greater Flamingo (group I, $\chi^2_9 = 106.61$, $p < 2.2 \times 10^{-16}$; group II, $\chi^2_9 = 103.18$, $p < 2.2 \times 10^{-16}$) and the total Phoenicopteridae (group I, $\chi^2_{11} = 89.39$, $p = 2.2 \times 10^{-14}$; group II, $\chi^2_{11} = 88.3$, $p = 3.5 \times 10^{-14}$), as well as for Steppe (Bsh) and Savanna (Aw) climates for the American Flamingo (group I, $\chi^2_3 = 19.867$, $p = 0.0001809$; group II, $\chi^2_3 = 7.1429$, $p = 0.06748$) (Figure 13).

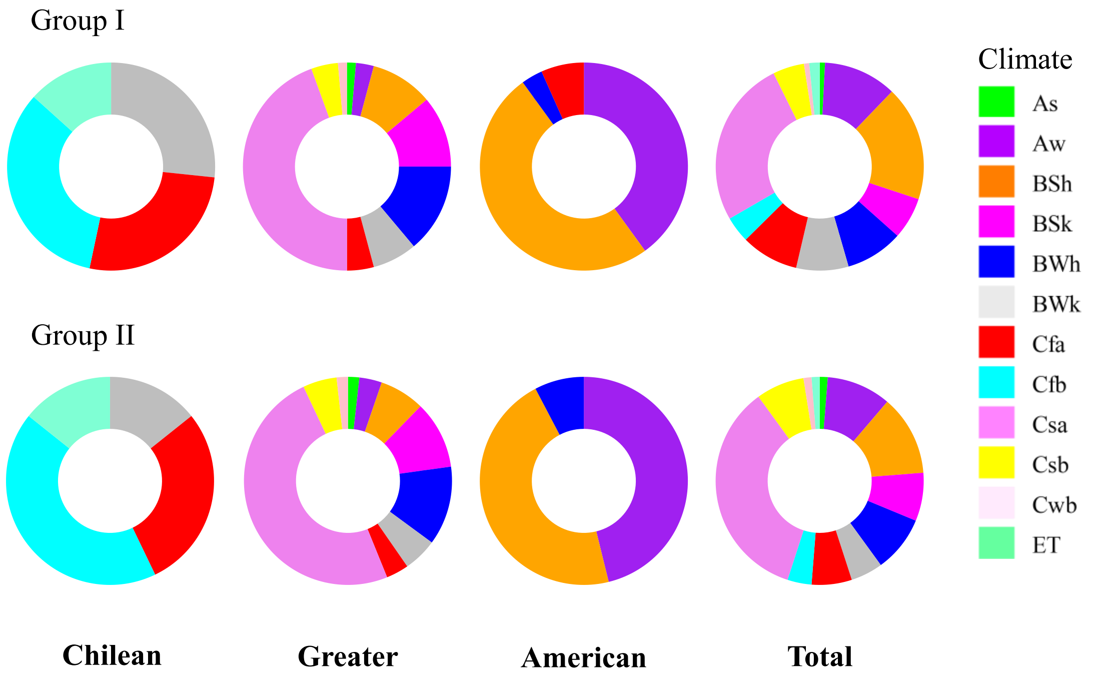

Figure 13. Frequency of stamping behavior by Köppen-Geiger climate classification for five flamingo species (Chilean *Phoenicopterus chilensis*, American *Phoenicopterus ruber*, Greater *Phoenicopterus roseus*, Andean *Phoenicoparrus andinus*, and Lesser *Phoeniconaias minor*) from combined literature and online video data. Andean and Lesser Flamingos only represented in the total records. Group I includes all the stamping variants (rotating, standing, false and indeterminate); group II contains rotating stamping only.

Finally, no seasonal preference for stamping was supported by chi-square test, neither for the Phoenicopteridae clade (group I, $\chi^2_3 = 4.64$, $p = 0.2001$; group II, $\chi^2_3 = 2.8769$, $p = 0.411$), nor for any particular species, although the raw data showed a predominance of winter records for the Greater Flamingo, which influenced the predominance of winter records for the whole Phoenicopteridae set (Figure 14).

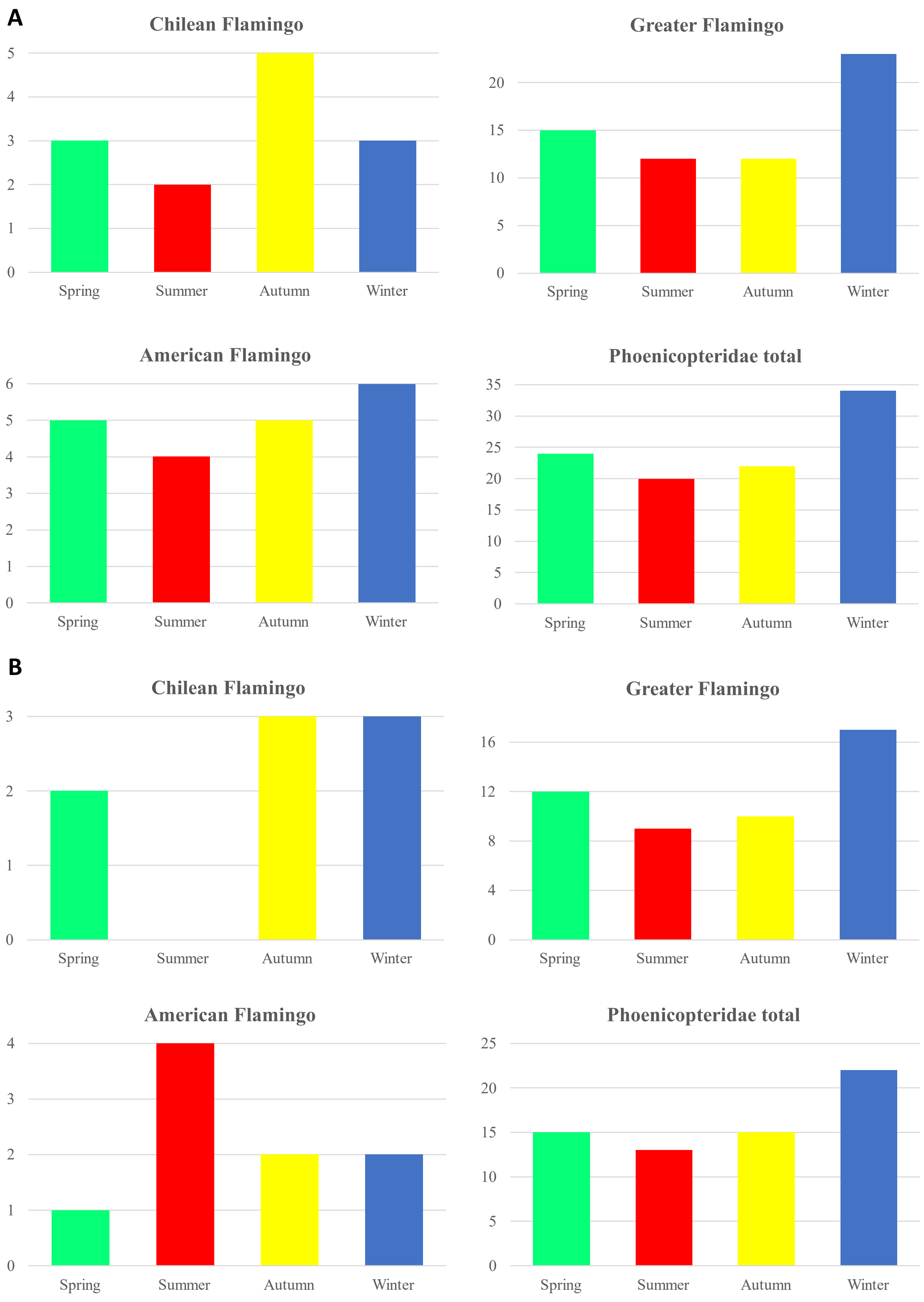

Figure 14. Frequency of stamping behavior by season for five flamingo species (Chilean *Phoenicopterus chilensis*, American *Phoenicopterus ruber*, Greater

Phoenicopterus roseus, Andean *Phoenicoparrus andinus*, and Lesser *Phoeniconaias minor*) from combined literature and online video data. (A) Group I analyses includes all the stamping variants (rotating, standing, false and indeterminate); group II analyses contains rotating stamping only.

4. Discussion

4.1. Interspecific pattern of stamping in extant flamingos

The shallow-keeled clade largely predominates as stamping-engaged, both in literature and video records, while the record of such behavior for the species in the deep-keeled clade was substantially less frequent and proceeding only from literature sources. As far as we can assessed, the stamping is unreported just for the rare and poorly known Puna Flamingo (*Phoenicoparrus jamesi*) pending if this absence represents a true lack of behavioral engagement or an effect of the little knowledge of the species. Inversely, the concentration of records on the Greater Flamingos is not surprising, as it is a widely distributed and well-studied species (Brereton and Rose, 2019; Delfino and Carlos, 2022).

The predominance of the shallow-keeled group among stamping flamingo species suggests that stamping is related to the foraging of macroscopic prey, since the filter apparatus of the deep-keeled flamingos permits only the catching of diminutive items (Jenkin, 1957). *Phoenicopterus* species are regarded as generalists (Brown and Root, 1971; Mascitti and Kravetz, 2002) because they can switch from a truly carnivorous (zooplanktonic) diet to a broader omnivore (zoo- and phytoplanctonic) diet, while the *Phoenicoparrus*/*Phoeniconaias* group are specialized in a narrower trophic spectrum, mainly consuming benthic and phytoplanktonic algae (Zweers et al., 1995; Mascitti and Kravetz, 2002; Polla et al., 2018). If the observed discrepancy in the stamping frequency of the two flamingo groups is real, then the evolution of the stamping behavior may precede the shallow/deep-keeled divergence, being maintained in the shallow group as a plesiomorphy while disappearing in the deep-kelled group. On the other hand, the use of stamping by deep-keeled flamingos, although restricted, points to the origin of this behavior at least as far back as the common ancestor of the crown flamingos, whose divergence is settled at 12.95 Mya (Middle Miocene) as most recent molecular data estimates (Frias-Soler et al., 2022).

Stamping behavior of Lesser Flamingos has been recorded a few times in the literature, but these scant records are brief and not very detailed. In a detailed study of the feeding behavior of Lesser Flamingos in the African Rift, Robinson (2015) recorded ten different feeding methods, but stamping was not recorded. As such, any bioturbation associated to stamping in fossil record – at least in the Old World – can be strongly related to the *Phoenicopterus* shallow-keeled flamingos. However, although just three records for Andean Flamingos, this species appears to engage more frequently than *Phoeniconaias* (as observed by Derlindat et al., 2014), and the scarce record of stamping is merely due to an overall scarcity of studies with South American deep-keeled species. If it is true, then eventual stamping structures (at least in South American deposits) would be referred to shallow or deep-keeled species only in basis of some morphological, species-related differences in the traces registered.

The case of the Andean Flamingo is interesting, as the only literature reference mentioning stamping in this species set the first mention as "stamp-feeding" (in opposition to "walk-feeding" behavior, Derlindat et al., 2014:321) and proceeds using the same terminology (Derlindat et al., 2014:322) until switch to adopt "stand-feeding" in the remaining of the paper (Derlindat et al., 2014:323). Both definitions are generic and, in a sense, disparate, and both can relate to the standing-stamping phase/version of the stamping behavior. However, "stand-feeding" also can indicate the sporadic stops in the foraging gait of the Andean and (more frequently) the James Flamingo, both species wading more slowly while foraging than the Chilean Flamingo (McFarlane, 1975; Hulbert, 1982). As such, without a clear statement about at least the energic feet activity suspending the substrate, it is difficult to be sure about the stamping engagement by the Andean Flamingo. In this point the video records were uninformative, as no video shoot Andean Flamingos in stamping. Overall, these uncertainties are in consonance with the still poorly known feeding behavior of the Andean Flamingo (Mascitti and Castanera, 2006; Derlindat et al., 2014).

4.2. Geographical representation of stamping behavior

Stamping records were widespread through all the global distribution of extant flamingos, including well known sites of breeding and wintering populations. Other traditional sites bearing large concentrations of flamingos, as Etosha Pan (Namibia), Makgadikgadi Pan (Botswana), Golu Lake (Turkey), and Urmia Lake (Iran) (Delany and Scott, 2006), do not rendered records of stamping, but such absence may relate to underestimate sampling rather than to legitimate non stamping.

Although current populations of most modern flamingo species are declining, (except for a few populations such as those of the Greater Flamingo due to successful conservation measures, Delany and Scott, 2006; BirdLife International, 2023), they had larger populations in the recent past (BirdLife International, 2023). Moreover, the flamingo lineage included various other species and families with similar inferred lifestyle habits to modern species, and a broader geographical distribution in the geological past that encompassed regions where flamingos do not inhabit today, such as the continental North America (Shufeldt, 1891; Miller, 1944,1950; Howard, 1955; Brodkorb, 1953, 1961, 1963; Olson and Feduccia, 1980; Webb et al., 1981; Howard, 1984; Becker, 1985; Jefferson, 1987, 1991; Emslie, 1992, 1995; Olson and

Rasmussen, 2001; Kloess and Parham, 2017; McDonald and Steadman, 2022), New Zealand (Worthy et al., 2010) Australia (De Vis, 1905; Miller, 1963; Archer and Wade, 1976; Rich et al., 1987; Baird and Vickers-Rich, 1998; Fitzgerald, 2004; Worthy and Yates, 2018) Thailand (Cheneval et al., 1991) and probably Antarctica (Acosta Hospitaleche et al., 2019). Therefore, identifying ROT/environment patterns may have applications on larger geographical scales than those currently observed.

4.3. Environmental associations

Quantitative research correlates flamingo behavior with factors as age, individual physiological state, group size, intraflock hierarchy, habitat type, salinity, weather, season, breeding cycle and food availability (e.g., Espino-Barros and Baldassarre, 1989a, 1989b; Schmitz and Baldassarre, 1992a, 1992b; Bildstein, et al, 1993; Jaslow et al. 1997 Derlindati et al. 2014 Yohannes et al. 2014). Some of these factors are the primary determinants of time allocation for various activities, including foraging and feeding (Arengo and Baldassarre, 1995; Brereton and Rose, 2019); therefore, knowledge of the most conducive environmental types and parameters for stamping is essential to assess the accuracy of the resulting biogenic structures in interpreting the paleoenvironment. Some studies exemplified the influence of habitat type on the feeding style employed by flamingos. For instance, Arengo and Baldassarre (1998) at Ría Lagartos (Mexico) found that the daily percentage of stamping by American Flamingos in low-salinity ponds and in saline lagoon was significantly higher compared to high-salinity ponds. Hurlbert (1982) noted that stamping was used only in some Andean "lagunas" and never recorded in others. Not only between habitat variations was noted, but also within habitats. Liang (2014) showed that, for *Phoenicopterus roseus* in intertidal flats of Heuningnes Estuary, South Africa, ROTs distribution may vary according to landscape settings. In this site, Greater

Flamingos restricted their foraging to the upper mid and to the high shore at the intertidal region, avoiding the lower shoreline; also, they prefer to feed in flatter rather than in steeper shorelines. The size and abundance of the ROTs, however, did not varied according the two exploited shore position.

Stamping can also indicate productivity in paleoenvironments, as some studies relates the stamping to food quality, density and distribution. Stamping was the most employed feeding mechanism by American Flamingo in 75% of the feeding events as estimated by Arengo and Baldassarre (1995) in a four-month study in Ría Lagartos, where the time invested in feeding increased as food availability (measured as prey abundance) decreased. Derlindati et al. (2014) found that Andean Flamingos spent more time feeding in a high-altitude lake in the Andes during the breeding season than in another lake located in the lowlands of central Argentina where flamingos migrate during the winter (non-breeding season). The authors attributed this difference to the greater productivity of the lowland lake, allowing flamingos to invest in other activities such as courtship; the greater time dedicated to feeding in the high Andes could also be related to the increased energy demand due to the rearing of young. Interestingly, stamping was used more than walking-feeding in the lake with higher productivity and where feeding time was shorter, a result similar to that found for American Flamingos by Arengo and Baldassarre (1995). The exclusivity of stamping in some “lagunas” observed by Hurlbert (1982) suggests that stamping is used in specific conditions of patchy bottom carpets of the aquatic monocot *Ruppia*, which holds rewarding preys. Similarly, Gihwala et al. (2019) found that the stamping use by Greater Flamingos increased as benthic microalgae concentrations also increased. The two latter studies suggest that stamping may be associated with patchily, aggregated distributed prey biomass. This would imply that the pattern of ROTs distribution through the bed plane could reflect the pattern of targeted prey distribution in the environment – feeding structures dispersed across the topography indicate low productivity, while densely packed ROTs would indicate aggregated food resources.

The predominance of three depositional systems (lagoonal, lacustrine and tidal) corresponds to the preferred environments occupied by extant flamingos. However, there were certain species-specific preferences that could hamper the generalization of stamping-environment associations for the flamingo clade as a hole. The apparent higher plasticity of the Greater Flamingo – expressed as the number of habitat types where the species engaged in stamping – probably reflects the greater number of studies dealing with this species. Palustrine environments were found to be moderately used only by the Greater Flamingo, while tidal settings predominate for the American Flamingo, reflecting the predominantly coastal and insular distribution of the latter species, which seldom is found further inland (Del Hoyo, 1992). The exclusivity of the lacustrine environment for the Andean and Lesser Flamingos is also a result of its more lake-bound habitat selection by these two species (Del Hoyo, 1992).

Compared to other environmental scales, detecting a pattern in the third-order classification is more challenging due to the multiple habitat types occupied by flamingos. However, the significant relationship between habitat type and stamping described by some studies imply that this association could only be noted at local scale and not perceived in global-span investigations such our study.

The predominance of coastal (marginal-marine) environments in the stamping occurrence contrast with the predominance of continental, mainly lacustrine settings harboring the bulk of trace fossils of the flamingo lineage (Supplementary Data 3). One possible explanation is that ancestral flamingos evolved in a continental context, and only colonized the coastal environment around the divergence of the existing flamingo genera.

Muddy substrates were the most frequent substrate type where stamping was performed. Previous studies have suggested a relationship between grain size and the distribution and abundance of different infaunal types (suspension feeders x detritus feeders, Gall, 1983). However, subsequent studies have shown that grain size alone is not the primary parameter affecting the distribution of benthic bioturbating organisms (Snelgrove and Butman, 1994). Other factors, such as food supply and ecological interactions, could more accurately explain patterns of distribution and abundance of invertebrate bioturbators as well as the density and the preservation of their traces. The fact that flamingos preferentially stamp on the more plastic, muddy substrates, implies that their activity may distort the original feature of the ichnoassemblage on these substrates, possibly resulting in an impoverished ichnodiversity. On the other hand, the record of structures in fine sediments is a favorable factor for preservation, especially in conditions of subsequent subaerial exposure and desiccation, as occurs in tidal or evaporite environments. The most common substrates where stamping occurs indicate that the lithology most likely to encounter these structures are mudstones, followed by sandstones, evaporites and carbonates.

Flamingos typically forage at water column depths between 10 and 60 cm, avoiding waters deeper than 1 m (Hurlbert, 1982; Mascitti and Castañera, 2006; Boukhriss et al., 2007; Yohannes, 2014). Although information exclusively on stamping is scarce, the values reported in the literature do not differ from the generality of foraging behavior. Allen (1956) states that flamingos cannot stamp in water high than 60 cm. McFarlane (1975) observed Chilean flamingos engaging in walk-feeding in water deep to the flamingo's belly while stamping mainly occurred in shallower water. Overall, our data agree with a narrow depth range for the stamping in the flamingo clade, with the mean value for the ensemble of flamingo species around 22 cm deep, thus corroborating previous claims that stamping is a technique used most often in very shallow waters. The dataset also shows some species-specific variation: while American and Greater Flamingo tended to stamp in depths around 20 cm, Chilean Flamingo stamped in shallower water around 7 cm deep. If this pattern varies intra- and interspecifically in response to selected environmental parameters is currently unknown, and such relationship could be further explored in future studies. Also, biomechanics reasons could be involved in the stamping performance, as this highly energy-demanding and complex movement could face increasing restrictions as the water depth gets higher. In summary, ROTs are indicators of water depth accurate to the level of a few tens of centimeters.

Flamingos have physiological and anatomical adaptations to live in salt water, such as the large nasal salt gland accommodated in the *fossa supraorbitalis* (Feduccia, 1977; Reshag et al., 2016), perhaps indicating a long evolutionary history of adaptation to these environments. This do not prevent the flamingos to use freshwater habitats, either for drinking, bathing or even foraging (Gromme, 1930; Brown *et al.*, 1982). Despite overestimated claims for an almost strict tiering to high salinity (brine) environments, especially in the paleontological literature (e.g., Jehl, 1988; McDonald and Steadman, 2023), flamingos in fact occupy a broad range of physicochemical water conditions (Yohannes et al., 2014), and our data points to the predominant exploration of brackish and moderate saline waters, at least regarding the stamping behavior. Our observations agree with the study of Arengo and Baldassarre (1998), who attributed the differential prevalence of stamping to the differential distribution of prey items, which was more abundant in the substrate than in the water column of the low-salinity and saline settings. Thus, at hypersaline conditions, food concentrated in water column could elicit alternative feeding methods to stamping, such as sweeping and walk-feeding, thus influencing the type of biogenic structures left by flamingos according salinity conditions.

Alkaline water predominates in the stamping performance for all flamingo species sampled, with some species-specific singularities. Deep-keeled flamingos stamped exclusively on high alkaline environments (pH >9), while the shallow-keeled species showed a wider pH range with mean around pH >7<8, even including sporadic records in acidic pH. Although many studies relate flamingo abundance and food exploitation to higher pH values (*e.g*, Caziani and Derlindati, 2000; Kaggwa et al., 2013; Krienitz et al., 2016), in fact these birds exploit waters of a broader ionic concentration of hydrogen (*e.g*, Caziani et al., 2007; Esté et al., 2012). Our data suggest that stamping is a feeding technique used more frequently in environments with moderate alkalinity values. Nonetheless, some of our pH data were based on generic values from literature outside the context of stamping recorded in a given locality, so could not represent the predominant values at the very moment and location where stamping was performed.

Stamping behavior was recorded more frequently in inland areas (non-tidal) and in areas of low tidal amplitude (microtidal), suggesting an avoidance of regions where the tide develops amplitudes higher than 2 m; also, there was no record of stamping in macrotidal zones. The foraging pattern of flamingos in tidal environments preferentially occurs at shallow depths, and the birds apparently avoid foraging on subaerially exposed substrates during low tide (Boukhriss et al., 2007; Yohannes, 2014; Lee and Mayorga-Dussarrat, 2016). Such selection not only for stamping but apparently for feeding patterns in general could be associated to the energy of the raising and ebbing waters as well as to the greater depth that water reach in mesotidal and macrotidal zones. Tidal cycles influence benthic invertebrate density, distribution, and activity pattern, impacting the density of coastal birds and their tracks (Yates et al., 1993; Ribeiro et al., 2004; Melnick et al., 2022) – so flamingos used to track these changes by adapting their foraging techniques (Gihwala et al., 2017, 2019). Greater use of stamping in low-energy tidal zones means better chances of preserving ROT structures.

The main climates zones under stamping performance are characteristic of the temperate and subtropical latitudes, many of them with remarkable alternation between dry and wet seasons. Despite this, no clear seasonal pattern was detected, implying that stamping is a year-round foraging method. Alternatively, our sampling method could not be ideal to track local variations in flamingo behavior, what means that additional studies at local scale should be done in order to clarify seasonal patterns in stamping.

4.4. Paleoenvironmental implications

Flamingos or birds with similar size and foot morphology are reputed as the producers of *Phoenicopterichnum* (Aramayo and Manera de Bianco, 1987), *Culcitapeda* (Sarjeant and Reynolds, 2001), and, less probably, *Presbyorniformipes* and *Uhangrichnus* (Yang et al., 1995) ichnogenera. While the relationship between *Phoenicopterichnum* and producers of the flamingo lineage seems well established, this is less certain with respect to the ichnogenera *Culcitapeda* and *Presbyorniformipes*, which may represent extramorphological variations of the footprints of the same type of producer of *Phoenicopterichnum* (Melchor et al., 2012; Camens and Worthy, 2019). However, *Uhangrichnus* is a Late Cretaceous ichnogenus, and thus predates the emergence of the Mirandornithes (the lineage encompassing flamingos and grebes), which is now generally accepted to have occurred in the Paleogene (Mayr, 2014). Most of these flamingo-like tracks occurs in facies indicative of saline and/or alkaline water chemistry for a number of fossil deposits worldwide (Alonso, 1987, 1992; Leonardi, 1994; Zavala and Freije, 2001; Abbassi and Shakeri, 2005; Aramayo, 2007; Thrasher, 2007; Scott et al., 2007, 2008, 2009; Melchor et al., 2012) (Table 7). One exception is the highly diverse ichnoassemblage of Pehuen-Có (Buenos Aires Province, Argentina), where the ichnospecies *Phoenicopterichnum rector* is preserved in beds with no clear evidence for saline/alkaline conditions (Aramayo and Manera de Bianco, 1987). Other tracks assigned to waterfowls (tentatively detailed as swans, ducks and geese) could prove to be registered by ancient flamingos (Melchor et al., 2012), expanding the range of habitat types and depositional environments that could be associated to flamingo evolution.

We assembled a dataset showing that potential fossil ROTs could be preserved in a range of aquatic paleoenvironments, from continental to transitional and from low to high elevations. Arguably, lacustrine environments show greater preservation potential for biogenic structures compared to other environmental settings, due to the predominance of typically low-energy depositional processes as the bellow-wavebase underflow currents in lacustrine bottom and the rapid non-erosive input of sand by sudden floods or strong winds on lake margin (Buatois and Mángano, 2004). These taphonomic processes could explain the predominance of traces attributed to flamingo and to other waterbirds in lacustrine settings. By its turn, coastal systems are regarded as depositional environments with moderate potential for trace registration and preservation (Abdel-Fattah, 2019), especially in those habitat types subjected to the alternating influence of fine sediments input (which promotes burial) and aerial exposure (which promotes desiccation and substrate firmness) by tide cycle (Currie et al., 1991; Dashtgard, 2011; Tomaselli et al., 2021). However, this same alternation in tidal environments also could lead to less stable substrate conditions, forcing the meiofauna to adapt quickly and thus generating intense sediment reworking and dismantling of any previous structures. Such effects could account for the least representation of flamingo traces in coastal environments, despite such settings arose as the most frequent in the practice of stamping. Only at exceptional conditions of favorable taphonomic window such structures could be preserved, as exemplified by Barcelos-Silveira et al. (2023) in the seaward side of shallow lagoonal bottom edges tidally exposed and adjacent to dune fields. Thus, if preserved, ROTs could indicate specific energy conditions for ancient tidal zones.

Melchor et al. (2012) proposed that the trace-fossil assemblages dominated by flamingo-like tracks in post Oligocene successions would be identified as *Phoenicopterichnum* ichnosubfacies within the “shorebird ichnofacies”. Diagnostic ichnogenera are *Phoenicopterichnum*, *Culcitapeda* and other similar unnamed tracks. Its occurrence is proposed as an indicator of saline and/or alkaline shallow waters, mostly in lacustrine settings. This relationship is inferred from the specialized filter-feeding mechanism of Late Oligocene to Recent flamingos and their common flocking behavior. Some limitations for the recognition of *Phoenicopterichnum* can be noted. Although the “shorebird ichnofacies” has received some acceptance in subsequent works (e.g., Doyle et al., 2000; Melchor et al., 2012; Díaz-Martinez et al. 2015; Camens and Worthy, 2019), this proposed tetrapod ichnofacies still lacks a formal description and a naming after a representative ichnogenus (Melchor et al., 2012). Furthermore, a strict association with alkaline, saline and shallow water of lacustrine settings could be hampered because extant flamingos explore a large range of environments and environmental conditions, as previous authors and our own study showed, mainly regarding the widespread occurrence in non-lacustrine settings as coastal lagoons and tidal settings. Despite this, in overall the frequency of ROTs by environmental descriptors broadly agree with the conditions proposed to be represented by the *Phoenicopterichnum* tracks. In this way, flamingo ROTs could be inserted either in the *Phoenicopterichnum* subichnofacies or as a suite (*sensu* Buatois and Mángano 2011) in the various invertebrate ichnofacies from continental and coastal aquatic settings (e.g., *Psilonichnus*, *Skolithos*, *Skoyenia* Ichnofacies), excluding perhaps the *Mermia* Ichnofacies, which represents deeper waters where flamingos do not forage (Buatois and Mángano, 1995, 2020).

Tracks and trackways are not always recorded on the same surface as ROTs, so the preservation of the latter adds to the body of evidence for detection of flamingos in fossil record. In modern environments, some authors reported the ROT preservation as the only local evidence of flamingo activity (Abdulali, 1964). Thus, ROTs could signal the presence of ancestral flamingos in facies where trackways or isolated footprints of these birds may not have been preserved. However, this assumption would require field studies addressing the presence or absence of both footprints and ROTs in modern settings, along with a detailed investigation of sediment attributes (*e.g.*, grain size, texture, saturation, among others) and taphonomic processes controlling the preservation of these traces in each environment. Despite being abundant and with good preservation potential, flamingo feeding mounds have not yet been reported in the fossil record, possibly due to unknown diagenetic aspects or underestimation of these structures in the field by the possibility of being confused with other traces in similar environments, such as the nidification/feeding bowls of *Piscichnus*.

5. Conclusions

Flamingos showed a tendency to stamping more frequently in coastal, lagoonal environments with brackish and very shallow environments. However, this result is biased toward the predominance of records from the Greater Flamingo, thus more data is needed for the other flamingo taxa in order to verify if this is an overall tendency for the clade. Our data reveals that stamping are a versatile technique not tied to a single environmental parameter other than water level >25 cm. This result implies that stamping may be more controlled at local scale, while widespread at the metapopulation/species level. The broad range of environmental conditions were stamping occurs amplify the span of paleoenvironments where hypothetical fossil ROTs could be found. The higher frequency of ROTs in shallow and slightly alkaline waters places them as additional elements for the recognition of the *Phoenicopterichnum* ichnosubfacies, whether it is recognized as a tetrapod subichnofacies, or as a suite within the classic vertebrate ichnofacies, although the strict interpretation of *Phoenicopterichnum*-bearing deposits as highly saline and highly alkaline lacustrine conditions must be based in additional sources of evidence. Finally, comparison with structures with similar appearance, as the nidification/feeding bowls of *Piscichnus*, will be welcomed, even for strata prior to the flamingo origin, as those from Late Cretaceous, where *Uhangrichnus* could imply in convergent flamingo-life style for some cretaceous birds.

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CRediT author contributions

André Barcelos-Silveira: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. Henrique Cardoso Delfino: Methodology, Formal analysis, Data curation. Cesar Leandro Schultz: Writing - review & editing, Supervision, Funding acquisition. Heitor Francischini: Investigation, Writing - review & editing, Supervision, Visualization. Paula Dentzien-Dias: Investigation, Writing - review & editing, Funding acquisition.

Declaration of competing interest

We declare no competing interests.

Data availability

The raw datasets data used in this article are presented in Supplementary Data 1, 2 and 3.

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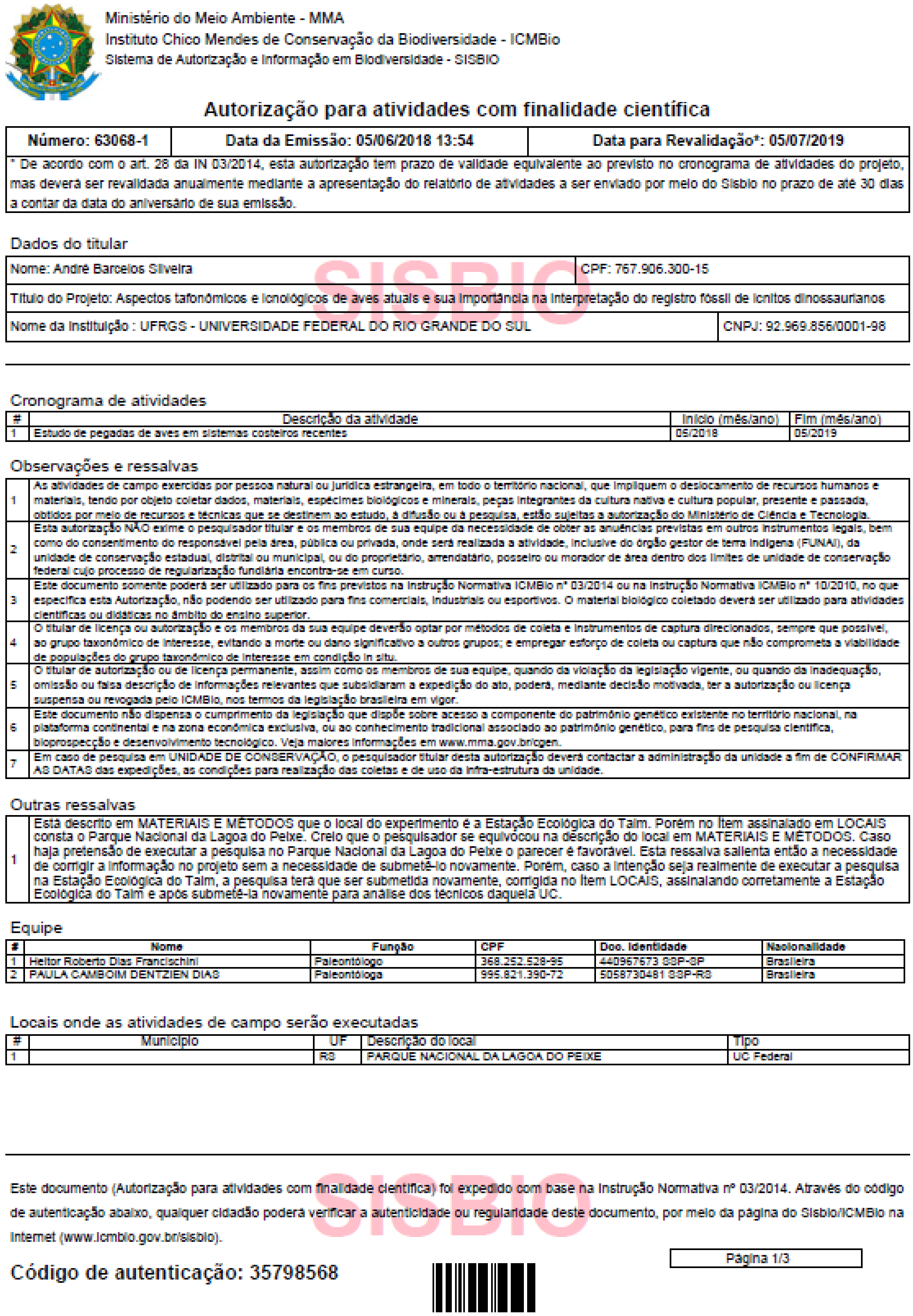
10. ANEXOS

10.1. Anexo 1. Autorização para atividades com finalidade científica



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Autorização para atividades com finalidade científica

Número: 63068-1	**Data da Emissão: 05/06/2018 13:54**	**Data para Revalidação*: 05/07/2019**

* De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: André Barcelos Silveira	CPF: 767.906.300-15
Título do Projeto: Aspectos tafonômicos e icnológicos de aves atuais e sua importância na interpretação do registro fóssil de icnitos dinossaurianos	
Nome da Instituição : UFRGS - UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL	CNPJ: 92.969.856/0001-98

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
1	Estudo de pegadas de aves em sistemas costeiros recentes	05/2018	05/2019

Observações e ressalvas

1	As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia.
2	Esta autorização NÃO exime o pesquisador titular e os membros de sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, inclusive do órgão gestor de terra indígena (FUNAI), da unidade de conservação estadual, distrital ou municipal, ou do proprietário, arrendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso.
3	Este documento somente poderá ser utilizado para os fins previstos na Instrução Normativa ICMBio nº 03/2014 ou na Instrução Normativa ICMBio nº 10/2010, no que especifica esta Autorização, não podendo ser utilizado para fins comerciais, industriais ou esportivos. O material biológico coletado deverá ser utilizado para atividades científicas ou didáticas no âmbito do ensino superior.
4	O titular de licença ou autorização e os membros da sua equipe deverão optar por métodos de coleta e instrumentos de captura direcionados, sempre que possível, ao grupo taxonômico de interesse, evitando a morte ou dano significativo a outros grupos; e empregar esforço de coleta ou captura que não comprometa a viabilidade de populações do grupo taxonômico de interesse em condição in situ.
5	O titular de autorização ou de licença permanente, assim como os membros de sua equipe, quando da violação da legislação vigente, ou quando da inadequação, omissão ou falsa descrição de informações relevantes que subsidiaram a expedição do ato, poderá, mediante decisão motivada, ter a autorização ou licença suspensa ou revogada pelo ICMBio, nos termos da legislação brasileira em vigor.
6	Este documento não dispensa o cumprimento da legislação que dispõe sobre acesso a componente do patrimônio genético existente no território nacional, na plataforma continental e na zona econômica exclusiva, ou ao conhecimento tradicional associado ao patrimônio genético, para fins de pesquisa científica, bioprospecção e desenvolvimento tecnológico. Veja maiores informações em www.mma.gov.br/cgen.
7	Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infra-estrutura da unidade.

Outras ressalvas

1	Está descrito em MATERIAIS E MÉTODOS que o local do experimento é a Estação Ecológica do Taim. Porém no Ítem assinalado em LOCAIS consta o Parque Nacional da Lagoa do Peixe. Creio que o pesquisador se equivócou na déscrição do local em MATERIAIS E MÉTODOS. Caso haja pretensão de executar a pesquisa no Parque Nacional da Lagoa do Peixe o parecer é favorável. Esta ressalva salienta então a necessidade de corrigir a informação no projeto sem a necessidade de submetê-lo novamente. Porém, caso a intenção seja realmente de executar a pesquisa na Estação Ecológica do Taim, a pesquisa terá que ser submetida novamente, corrigida no Ítem LOCAIS, assinalando corretamente a Estação Ecológica do Taim e após submetê-la novamente para análise dos técnicos daquela UC.

Equipe

#	Nome	Função	CPF	Doc. Identidade	Nacionalidade
1	Heitor Roberto Dias Francischini	Paleontólogo	368.252.528-95	440967673 SSP-SP	Brasileira
2	PAULA CAMBOIM DENTZIEN DIAS	Paleontóloga	995.821.390-72	5058730481 SSP-RS	Brasileira

Locais onde as atividades de campo serão executadas

#	Município	UF	Descrição do local	Tipo
1		RS	PARQUE NACIONAL DA LAGOA DO PEIXE	UC Federal

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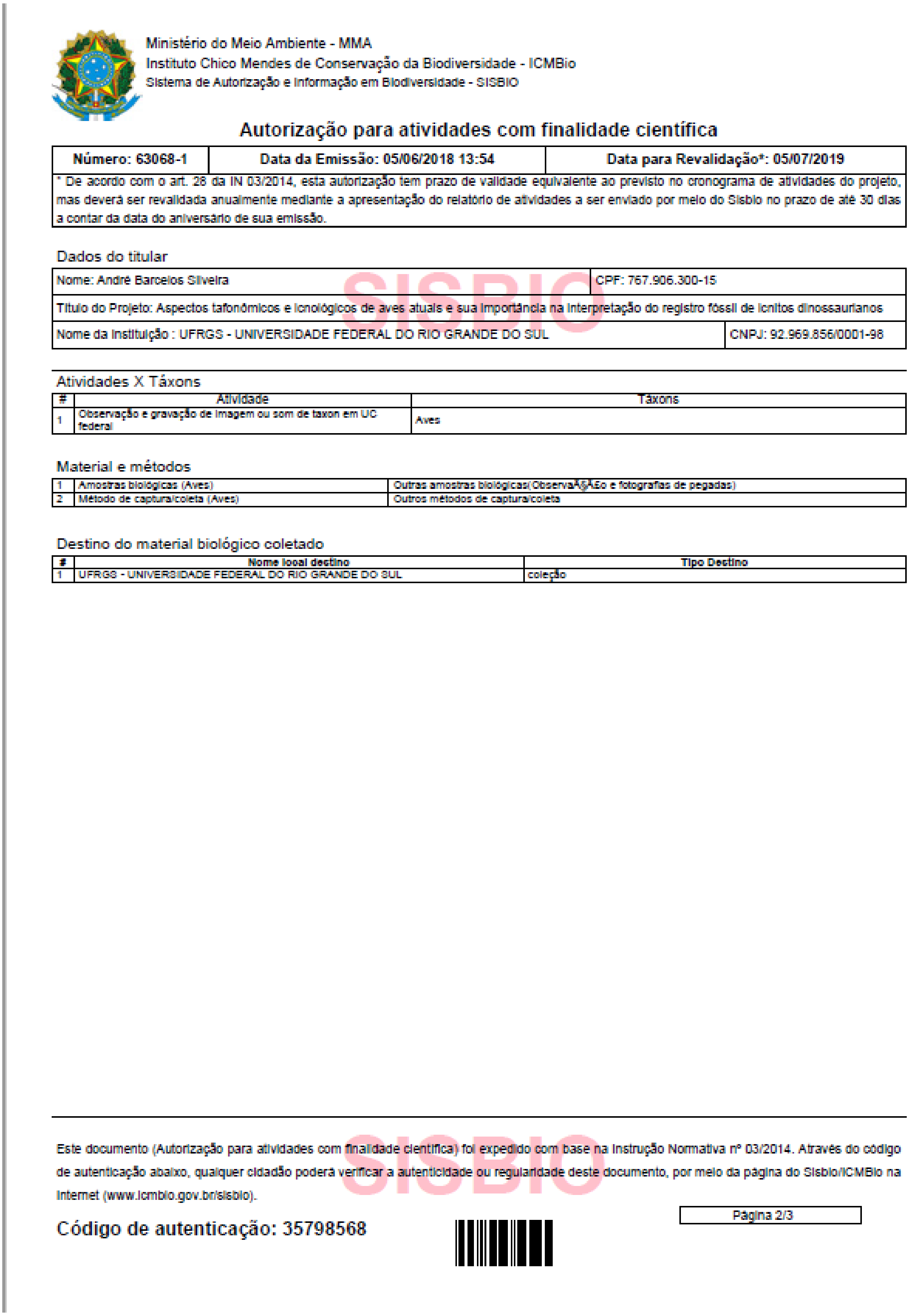

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Nome da Instituição : UFRGS - UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL	CNPJ: 92.969.856/0001-98

Atividades X Táxons

#	Atividade	Táxons
1	Observação e gravação de imagem ou som de taxon em UC federal	Aves

Material e métodos

1	Amostras biológicas (Aves)	Outras amostras biológicas(ObservaÃ§Ã£o e fotografias de pegadas)
2	Método de captura/coleta (Aves)	Outros métodos de captura/coleta

Destino do material biológico coletado

#	Nome local destino	Tipo Destino
1	UFRGS - UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL	coleção

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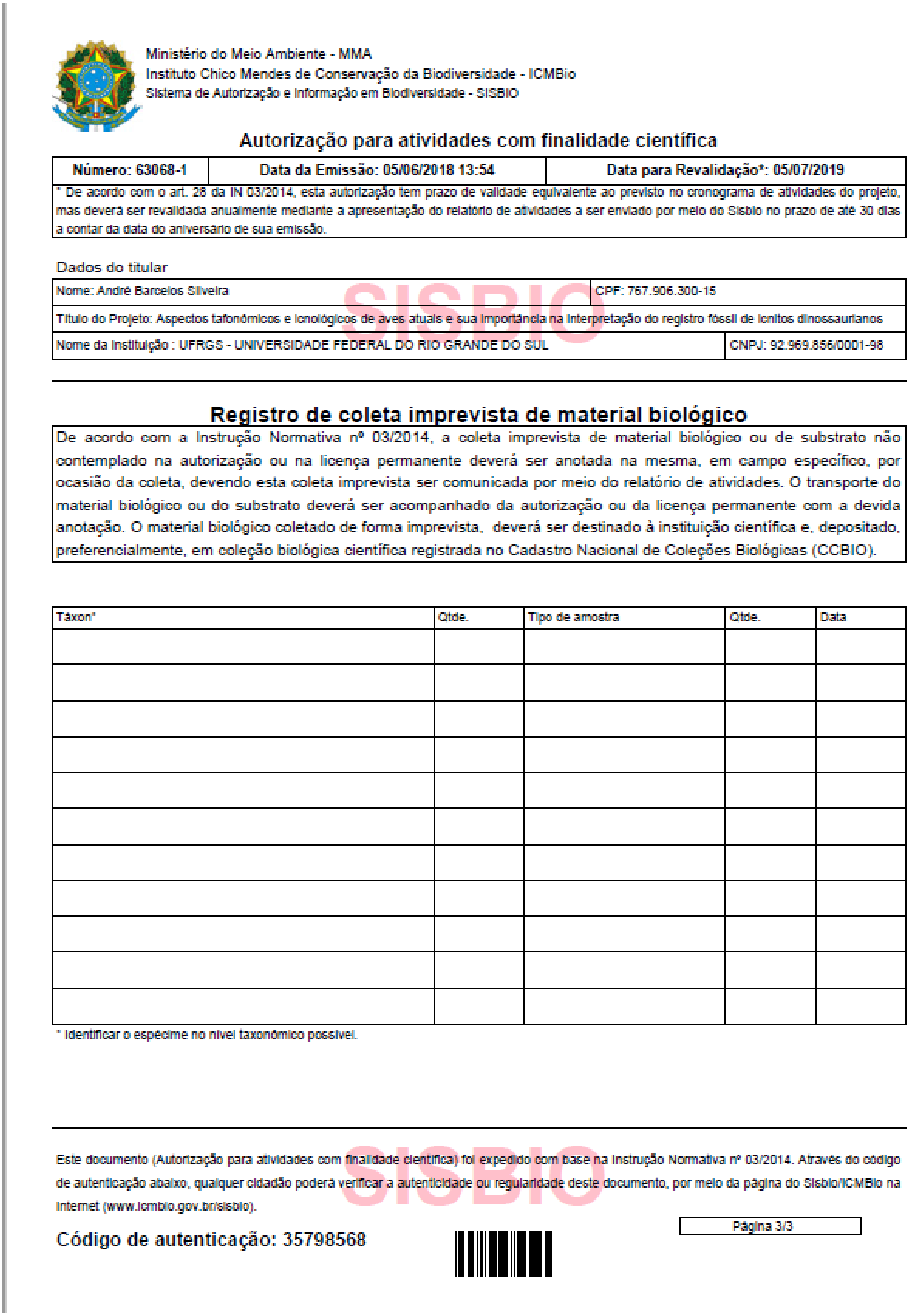

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Registro de coleta imprevista de material biológico

De acordo com a Instrução Normativa nº 03/2014, a coleta imprevista de material biológico ou de substrato não contemplado na autorização ou na licença permanente deverá ser anotada na mesma, em campo específico, por ocasião da coleta, devendo esta coleta imprevista ser comunicada por meio do relatório de atividades. O transporte do material biológico ou do substrato deverá ser acompanhado da autorização ou da licença permanente com a devida anotação. O material biológico coletado de forma imprevista, deverá ser destinado à instituição científica e, depositado, preferencialmente, em coleção biológica científica registrada no Cadastro Nacional de Coleções Biológicas (CCBIO).

Táxon*	Qtde.	Tipo de amostra	Qtde.	Data

* Identificar o espécime no nível taxonômico possível.

Este documento (Autorização para atividades com finalidade científica) foi expedido com base na Instrução Normativa nº 03/2014. Através do código de autenticação abaixo, qualquer cidadão poderá verificar a autenticidade ou regularidade deste documento, por meio da página do Sisbio/ICMBio na Internet (www.icmbio.gov.br/sisbio).

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10.2. Anexo 2. Bases de dados da Tese

Link do Google Drive para acessar o material suplementar (em planilhas Excel) utilizada no artigo 2: https://drive.google.com/drive/folders/1Z7CDPT80EfFgtrhDK1SxalwLIAkaGIum

10.3. Anexo 3. Outros artigos e projetos ao longo do doutoramento

10.3.1. Artigo publicado

Francischini, H., Sipp, G. S., Barcelos-Silveira, A., Schultz, C. L. & Dentzien-Dias, P. (2022). Revisiting the southernmost occurrence of *Brasilichnium elusivum* Leonardi, 1981 with comments on the tetrapod track record of eolian environments. *Revista Brasileira de Paleontologia*, 25(4): 249-254.

10.3.2. Artigo submetido

Deiques, D., Barcelos-Silveira, A., Dentzien-Dias, P.; Francischini, H. New dinosaur tracks from the Guará Formation (Upper Jurassic, Brazil), focusing on the first record of an original theropod track and the second record of Ankylosauria.

10.3.3. Capítulo de livro publicado

Barcelos-Silveira, A. & Francischini, H. 2020. Ninhos e sítios de nidificação de vertebrados. In: Sedorko, D. & Francischini, H. (Eds.). *Icnologia: interações entre organismos e substratos*. Curitiba, Editora CRV, p. 283-316. DOI:10.24824/978655578074.1.

ANEXO I

Título da Tese:

“NEOICNOLOGIA DOS FLAMINGOS (AVES, PHOENICOPTERIDAE): ESTRUTURAS BIOGÊNICAS, COMPORTAMENTO PRODUTOR, TAFONOMIA E IMPLICAÇÕES PALEOAMBIENTAIS”

Área de Concentração: Paleontologia

Autor: **André Barcelos Silveira**

Orientador: Prof. Dr. Cesar Leandro Schultz
Coorientador: Prof. Dr. Heitor Roberto Dias Francischini

Examinadora: Profa. Dra. Renata Guimarães Netto

Data: 04/12/2023

Conceito: A

PARECER:

A tese é muito interessante, pois traz luz a um conjunto de estruturas biogênicas produzidas por flamingos e que possuem bom potencial de preservação que ainda não são discutidas no registro geológico. O doutorando documenta com excelência essas estruturas, as descreve com detalhes suficientes para que possam ser caracterizadas dentro dos critérios que se utiliza para a caracterização de icnofósseis (icnotaxobases), e discute sua gênese, significado comportamental e potenciais tafonômicos. Para realizar o trabalho, o doutorando utilizou metodologia adequada, com manuseio de diferentes técnicas de análise. O texto é bem escrito, fácil de ler, e contempla uma gama de novos conhecimentos que serão de grande interesse para a icnologia como um todo. As ilustrações são excelentes e complementam o texto de forma exemplar. A literatura científica utilizada para suportar dados, descrições, interpretações e argumentos de discussão são pertinentes, apesar de alguns dos trabalhos citados estarem ausentes da lista de referências e outros da lista aparentemente não estarem citados no texto.

Não me ative a revisar o artigo 1, por já estar publicado e por ter me parecido um excelente trabalho (já o havia lido quando saiu publicado). O artigo 2 discute o comportamento e a distribuição das estruturas em contextos ambientais habitados por flamingos em todo o mundo, a fim de criar parâmetros para o entendimento e a interpretação de estruturas semelhantes no registro fóssil. É uma ótima contribuição para a icnologia e acredito que seja recomendado para publicação com alguns ajustes menores.

Por essas razões, considero que o doutorando cumpriu os requisitos mínimos para a obtenção do título de doutor e foi além, abrindo espaço para novos trabalhos dentro de linha de estudos a que se dedicou.

Assinatura: Data: 04/12/2023

Ciente do Orientador:

Ciente do Aluno:

ANEXO I

Título da Tese:

“NEOICNOLOGIA DOS FLAMINGOS (AVES, PHOENICOPTERIDAE): ESTRUTURAS BIOGÊNICAS, COMPORTAMENTO PRODUTOR, TAFONOMIA E IMPLICAÇÕES PALEOAMBIENTAIS”

Área de Concentração: Paleontologia

Autor: **André Barcelos Silveira**

Orientador: Prof. Dr. Cesar Leandro Schultz
Coorientador: Prof. Dr. Heitor Roberto Dias Francischini

Examinador: Prof. Dr. Caio José Carlos

Data: 04/12/2023

Conceito: A

PARECER:

A tese cujo título é mencionado acima inclui dois capítulos principais, ambos elaborados no formato de manuscritos. Importante mencionar que o primeiro desses capítulos já está formalmente publicado. Por um lado, isso é um pouco frustrante, porque, mesmo que este avaliador tenha críticas sobre o trabalho, do ponto de vista prático, essas serão de pouco (ou nenhum) uso; por outro lado, entendo perfeitamente as exigências atuais de produção cientifica atuais, quer seja para os PPGs, que seja para o próprio candidato, e dou os parabéns pela publicação. Concentrei-me, pois, em avaliar o capítulo 2, manuscrito ora em processo de revisão.

De modo geral, o trabalho tem uma sequência lógica clara e está bem escrito. Logo na seção introdutória, o autor se propõe a responder lista 3 perguntas – e isso é muito bom. No entanto, eu sugiro que, após a primeira revisão o autor faça um esforço para propor hipóteses para suas perguntas (e procure deduzir algumas predições dessas). Isso traria muito mais, vamos dizer, sofisticação científica ao trabalho. Tanto os métodos quanto as análises pareceram-me adequados. Os resultados estão organizados de forma satisfatória e dou os parabéns pela qualidade da apresentação desses. Mas aqui, retomo a sugestão das hipóteses, que inclusive, poderiam guiar mais bem a discussão.

Assim como as demais seções, a discussão tem uma sequência lógica. Chamou-me a atenção o cuidado que o autor teve de reconhecer as limitações de seus dados, procurando não fazer especulações; e, principalmente, sugerindo novos esforços de pesquisa – isso foi muito bem vindo e tem de ser enfatizado.

Se bem que o autor tenha tido todo esse cuidado, alguns pontos precisam ser revisados com cuidado, quais sejam: há alguns trechos da discussão (em alguns poucos casos parágrafos inteiros) em que o autor não fornece referências para suas afirmações/explicações. Como o cuidado do autor para com seu trabalho é nítido (comentei isso mais acima), assumo que essa falta de referenciamento pode ser resolvido por meio de uma revisão cuidadosa, logo que a primeira decisão editorial seja feita.

Por fim, gostaria fazer um pequeno alerta sobre o uso de alguns termos que não são condizentes com a teoria a qual se aplicam. Exemplos: “Táxon basal”, para se referir às linhagens que emergem de um clado mais inclusivo, ou “preferência”, que de forma alguma pode ser testada em campo. É claro que nada disso vai afetar o trabalho do autor, e é possível que nenhum dos revires do manuscrito os comente, porque alguns desses termos já têm estatuto de jargão na literatura. Contudo, não me furtei a oportunidade de comentar sobre isso aqui. A tese com anotações minhas foram encaminhadas ao autor e seu orientados, e espero que lhe sejam úteis dalguma forma.

Em resumo, penso que o trabalho avaliado contempla todos os pontos de uma tese de doutorado, quais sejam: exposição de um estudo científico de tema único e bem delimitado, que se constitui em contribuição real não somente para a Paleontologia. Por isso, e por todos outros pontos comentados acima, considero o candidato aprovado.

Assinatura: Data: 04/12/2023

Ciente do Orientador:

Ciente do Aluno:

ANEXO I

Título da Tese:

“NEOICNOLOGIA DOS FLAMINGOS (AVES, PHOENICOPTERIDAE): ESTRUTURAS BIOGÊNICAS, COMPORTAMENTO PRODUTOR, TAFONOMIA E IMPLICAÇÕES PALEOAMBIENTAIS”

Área de Concentração: Paleontologia

Autor: **André Barcelos Silveira**

Orientador: Prof. Dr. Cesar Leandro Schultz
Coorientador: Prof. Dr. Heitor Roberto Dias Francischini

Examinador: Prof. Dr. Ricardo Néstor Melchor

Data: 4 diciembre 2023

Conceito: A (Exelente)

PARECER:

Como he expressado em la defensa, entendo que es muy importante documentar la forma de preservación de las estructuras ROT em el registro fóssil. Recomendo, que futuros estúdios se enfoquen em este aspecto, essencial para que las ideas puedan ser aplicadas em paleoicnología. Se puede intentar hacer calicatas (excavaciones) em sectores altos de la Lagoa do Peixe, para intentar identificar las estructuras. Entiendo que la tesis demuestra la capacidade de llevar adelante uma investoigación y es um tema original. Um comentário pontual: la unidad estratigráfica que aflora em Pehuen Co (Buenos Aires) es la secuencia Aguas Blancas (no Formación Pehuen Co).

Assinatura: Data: 6 de diciembre de 2023

Ciente do Orientador:

Ciente do Aluno:

Instituto de Geociências
Programa de Pós-Graduação em Geociências

FORMULÁRIO DE CADASTRO DE PARTICIPANTE EXTERNO À UFRGS
REGISTRATION FORM FOR PARTICIPANTS EXTERNAL TO UFRGS

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