UNIVERSIDADE FEDERAL DO ESPÍRITO SANTO
CENTRO DE CIÊNCIAS HUMANAS E NATURAIS
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

TETRAPODS OF SAMBAQUIS:

BIODIVERSITY, CULTURE, AND CONSERVATION ZOOARCHAEOLOGY

Augusto Barros Mendes

Vitória, ES
Dezembro, 2022

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Orientadora: Taissa Rodrigues Marques da Silva

Tese submetida ao Programa de Pós-Graduação em Ciências Biológicas (Biologia Animal) da Universidade Federal do Espírito Santo como requisito parcial para obtenção do grau de Doutor em Biologia Animal

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ATA DE DEFESA DE TESE DO CURSO DE DOUTORADO EM BIOLOGIA ANIMAL DO PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS DO CENTRO DE CIÊNCIAS HUMANAS E NATURAIS DA UNIVERSIDADE FEDERAL DO ESPÍRITO SANTO - ATA Nº 65 – 23/12/2022.

Em sessão pública ocorrida no dia 23 de dezembro de 2022, através de webconferência, conforme previsto na Portaria Normativa nº 08, da Pró-Reitoria de Pesquisa e Pós-Graduação/UFES de 01 de julho de 2021, procedeu-se a avaliação da tese do aluno **Augusto Barros Mendes**. Às quatorze horas, a Profa. Dra. Taissa Rodrigues Marques da Silva, Presidente da Comissão Examinadora de Defesa de Tese, deu início aos trabalhos, convidando a tomar assento à mesa os examinadores externos, Prof. Dr. Alberico Nogueira de Queiroz (UFS), Profa. Dra. Dione da Rocha Bandeira (UNIVILLE), Profa. Dra. Mírian Liza Alves Forancelli Pacheco (UFSCAR) e Profa. Dra. Michelle Rezende Duarte (UFF). A seguir, a presidente solicitou ao doutorando que fizesse uma explanação de seu trabalho intitulado **"TETRAPODS OF SAMBAQUIS: BIODIVERSITY, CULTURE, AND CONSERVATION ZOOARCHAEOLOGY".** Finda a apresentação, a presidente passou a palavra aos examinadores, que procederam a arguição do candidato. Ao final, a Comissão, em sessão reservada, deliberou pela **APROVAÇÃO** da referida tese nos termos do Regimento Interno do Programa de Pós-Graduação em Ciências Biológicas e alertou que o aprovado somente terá direito ao título de Doutor após entrega da versão final de sua tese, em papel e meio digital, à Secretaria do Programa. Encerrada a sessão, eu, Profa. Dra. Taissa Rodrigues Marques da Silva, presidente da Comissão Examinadora, lavrei a presente ata que vai com as devidas assinaturas (De acordo com a Portaria citada acima, membros de banca externos à UFES que não atuam como docentes permanentes ou colaboradores nos Programas de Pós-Graduação da UFES estão dispensados da obrigatoriedade de assinatura digital da ata. Caso o membro externo não assine a ata e, sendo o Coordenador o responsável final pela realização da banca, a assinatura do Coordenador via Lepisma assegura a legitimidade necessária do documento).

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A parte mais durável de mim
são os ossos
e a mais dura também

[...]

têm, creio eu,
algo de transparente
e dócil
tendem a solver-se
a esvanecer-se
para deixar no pó da terra

o osso
o fóssil
futura
peça de museu

o osso
este osso
(a parte de mim
mais dura
e a que mais dura)
é a que menos sou eu?

Reflexões sobre o osso da minha perna, de Ferreira Gullar

“— Acha que estou perdendo tempo? Me divertindo? E isso o aborrece? Mas não é bem assim. Uma vez segui profissionalmente uma expedição arqueológica e aprendi muito. Durante uma escavação, quando se descobre uma peça, primeiro limpa-se cuidadosamente em volta. Retira-se a terra, raspam-se certos lugares com uma faca, até finalmente chegar-se ao objeto. Só então é exibida e fotografada a peça, livre de impurezas e imperfeições. É o que estou tentando fazer [...]”

Hercule Poirot em Morte no Nilo, de Agatha Christie

Graffiti sem título, de Marcelo Voodoo

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Eu acho o trabalho acadêmico tão paradoxal: ao mesmo tempo que me causa uma imensa sensação de solidão, eu sinto (e reconheço) toda a ajuda e parceria que tive no processo. Pessoas que, sem elas, certamente este trabalho não existiria.

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SUMÁRIO

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RESUMO

Sambaquis são *shell mounds* comuns nas regiões Sul e Sudeste do Brasil. Esses sítios arqueológicos foram construídos por pescadores-coletores-caçadores que possuíam uma extrema afinidade com ambientes marinhos costeiros, nos quais eles exploravam uma grande variedade de peixes e moluscos. Outros grupos de animais nesses sítios, como mamíferos, aves, répteis e anfíbios são relativamente menos estudados, e por isso os objetivos dessa pesquisa almejam preencher esta lacuna de informação: identificar e inventariar a fauna de tetrápodes nos sambaquis, compreender as interações humanos-tetrápodes (aspectos culturais como caça e captura, dieta e confecção de artefatos) e discutir como dados pré-históricos sobre a biodiversidade podem contribuir para a conservação e manejo das espécies. Vestígios de tetrápodes de dez sambaquis da região Sul do Brasil foram anatômica e taxonomicamente identificados e analisados quanto ao seu uso na alimentação e fabricação de artefatos. Os dados foram quantificados (NISP, MNI) e a ingestão de carne consumível (biomassa) dos táxons identificados foi estimada. Um total de 46 táxons foi identificado. Como esperado, a maioria dos vestígios eram de animais marinhos: Cetacea (NISP = 1.696), Mysticeti (NISP = 811, MNI = 8), e Otariidae (NISP = 53 e MNI = 9). A fauna marinha teve grande relevância como fonte de alimento (79,63% da biomassa) e como matéria-prima para a confecção de artefatos (65,35% dos artefatos foram feitos a partir dos seus ossos), indicando que os tetrápodes marinhos eram um recurso relevante para os construtores de sambaqui. Os dados dos sambaquis do sul do Brasil foram complementados por dados da literatura disponível sobre inventários da fauna de tetrápodes nos sambaquis das regiões Sudeste e Sul do país. O inventário foi analisado em termos de riqueza taxonômica absoluta e relativa e frequências de ocorrência absoluta e relativa. A lista contém dados sobre 89 sambaquis e um total de 188 táxons, 96 dos quais a nível de espécie (51,06%): 55 de Mammalia (57,29%), 33 de Aves (34,38%), 7 de Reptilia (7,29%) e um de Amphibia (1,04%). *Cuniculus paca* (Linnaeus, 1766) e *Tapirus terrestris* (Linnaeus, 1758) tiveram as mais altas frequências de ocorrência. O inventário é a mais completa lista de verificação abrangente da fauna de tetrápodes de sambaquis e pode ajudar na preservação e manejo de áreas naturais e espécies em uma perspectiva de longo prazo. Esta é a primeira tese sobre a fauna dos sambaquis focada nos tetrápodes e aqui apresentamos informações que contribuem para o conhecimento não apenas sobre a cultura dos construtores de sambaquis, mas também sobre a biodiversidade do passado.

Palavras-chave: arqueologia costeira; artefatos ósseos; fauna do Holoceno; indústria óssea; pescadores-caçadores-coletores; zooarqueologia

ABSTRACT

Sambaquis are shell mounds common in the South and Southeast regions of Brazil. These archaeological sites were built by fishermen-gatherer-hunters who had an extreme affinity with marine and coastal environments, where they explored a great variety of fish and molluscs. Other groups of animals from these sites such as mammals, birds, reptiles, and amphibians are relatively less studied; thus, the objectives of this research are to bridge this information gap by identifying and inventoring the tetrapod fauna in sambaquis, understanding human-tetrapod interactions (cultural aspects such as hunting and capture, diet, and artifact manufacturing), and discussing how prehistoric biodiversity data can contribute to species conservation and management. Tetrapod remains from ten sambaquis of the South region of Brazil were anatomically and taxonomically identified and analysed regarding their use in diet and artifact manufacturing. We quantified data using NISP and MNI and estimated the intake of consumable meat (biomass) of the identified taxa. A total of 46 taxa were identified. As expected, most of the remains were from marine animals: Cetacea (NISP = 1,696), Mysticeti (NISP = 811, MNI = 8), and Otariidae (NISP = 53 and MNI = 9). Marine fauna had great relevance as a food source (79.63% of biomass) and as a raw material for artifact manufacturing (65.35% of the artifacts were made from their bones), indicating that marine tetrapods were a relevant resource for sambaqui builders. Data from the sambaquis of southern Brazil were complemented by literature data available on tetrapod fauna inventories on the sambaquis of the Southeast and South regions of the country. The inventory was analysed in terms of absolute and relative taxonomic richness and absolute and relative frequencies of occurrence. The list contains data on 89 sambaquis and a total of 188 taxa, 96 of which are at species level (51.06%): 55 from Mammalia (57.29%), 33 from Aves (34.38%), 7 from Reptilia (7.29%), and one from Amphibia (1.04%). *Cuniculus paca* (Linnaeus, 1766) and *Tapirus terrestris* (Linnaeus, 1758) had the highest frequencies of occurrence. The inventory is the most complete comprehensive checklist of sambaquis' tetrapod fauna and may help with the preservation and management of natural areas and species in a long-term perspective. This is the first doctoral dissertation on sambaquis fauna focused on tetrapods, and here we present information that contributes to our knowledge not only about the culture of the sambaqui builders but also about past biodiversity.

Keywords: artefacts; bone industry; coastal archaeology; fishermen-gatherer-hunters; Holocene fauna; zooarchaeology

PRESENTATION

In the book “Cabo Frio Revisitado” (Sophia Editora, 2020), there is a chapter by MaDu Gaspar and Gina Bianchini entitled “No tempo dos sambaquis: vida e espaço dos primeiros habitantes da Região dos Lagos”. In it there is the following sentence: “*Although Brazilian history devotes more attention to occupations after contact with the Portuguese colonizers, it is possible to affirm that there is still much to explore about what happened thousands of years before that*” (free translation).

When I read this, I was automatically transported to 2002. I was in the fifth grade of elementary school, and we were studying prehistory. Mesopotamia. Mayan civilization. I don't remember any of these themes. But I remember it like it was yesterday: I felt a question. I really did. That feeling of unease that only a question can bring: “But what was happening here in Brazil during prehistory?”, I thought.

That question has been my partner ever since. For ten years, it has accompanied me on my academic journey studying sambaquis. And that question is also here in this doctoral dissertation. There are some answers here too, of course. But, above all, there is the question.

GENERAL INTRODUCTION

Shell mounds are archaeological sites found on virtually every continent, dating back up to 115,000 years BP (before present; by convention, prior to 1950) (Souza et al., 2004). These sites are characterized as deposits of food remains, presenting a large volume of shells. In this sense, these sites are records of successive settlements of human populations that exploited the marine environment, such as groups of mollusc collectors and fishermen (Gonzalez, 2005a; Luby et al., 2006; Melo Júnior et al., 2016). They generally exhibit a stratigraphic succession of different compositions: layers of shells, other faunal remains, charcoal, artifacts, mortuary remains, and sediments more or less thickly interspersed by large amounts of thin, dark layers rich in organic matter. Although they may have often been stirred and rearranged, the layers of a shell mound represent the numerous stages of construction of these archaeological sites (Bendazolli, 2007; DeBlasis et al., 2007; Broughton, 2009; Belem and DeBlasis, 2015, Silva et al., 2016).

In Brazil these sites are known as sambaquis, are dated between 8,000 and 1,000 years BP, and are present throughout the Brazilian coast, although more abundant in the south and southeast regions (Scheel-Ybert et al., 2009; Souza et al., 2010a). They have various shapes (semi-spherical, conical, elongated, and flattened) and a range of sizes, averaging two to three meters in height to reaching up to about 70 meters. The name "sambaqui" comes from the Tupi etymology: *tamba* (shell) and *ki* (mound), likely because of the large number of molluscs present in these sites (Lima, 2000; Souza et al., 2005) (Figure 1).

Figure 1. Sambaqui Ilha dos Espinheiros II, Joinville, Santa Catarina.

Besides molluscs, these sites present sediments, charcoal, lithic material, mortuary remains, plant remains, and other faunal vestiges (from echinoderms, crustaceans, fish, amphibians, reptiles, birds, and mammals) that were accumulated by pre-Columbian populations during the Holocene (Kneip et al., 1986; Gaspar, 1996; Rodrigues et al., 2016a). Thus, sambaquis are sites artificially built by human groups of fishermen-gatherers-hunters, or sambaqui builders. They explored the marine environment, and, for this reason, sambaquis are found mainly in estuarine areas, places with great abundance of resources (Lima et al., 2003; DeBlasis et al., 2007). While some sambaquis have been described as habitational sites (Kneip et al., 1991; Kneip, 1992; Barbosa et al., 1994), others have been as essentially funerary structures (Duarte, 1968; Fish et al., 2000; DeBlasis, 2005). However, regardless of their artificial nature and how they are described, it is certain that these sites hold precious information regarding Holocene anthropology, biology, geography, and oceanography (Souza et al., 2005).

The zooarchaeological remains found in the sambaquis have symbolic and cultural value, indicating the presence and absence of species according to their utility for the sambaquis populations, whether in relation to their use as ornaments or artifacts, ritualistic symbols, or diet (Kneip, 1994; Fish et al., 2000; Gaspar, 2000). Among these remains, there is a huge amount of molluscs and fish. According to Klokler et al. (2010),

for a long time the diet of the sambaquis populations was based only on molluscs, mainly bivalves. However, the authors hypothesize that their subsistence could have shifted posteriorly to the consumption of fish after the mollusc beds were supposedly depleted due to overexploitation. Accordingly, Figuti (1993) states that collecting molluscs was a low cost-benefit activity since these animals do not have a high energy value. The author, therefore, argues that the capture of fish was the basis of the diet of these pre-Columbian populations.

As a result of the large number of these animals in sambaquis, most research aimed at studying specific taxa of sambaqui faunal remains are dedicated to analyzing the malacological (e.g. Mello, 1987, 1998, 1999; Mello and Coelho, 1989; Souza et al., 2003; Souza and Silva, 2010; Souza et al., 2010a, 2010b; Gernet & Birckolz, 2011; Rodrigues et al., 2011; Faria et al., 2014; Souza et al., 2016; Beauclair et al., 2016; Macario et al., 2017; Arruda et al., 2019) and ichthyological (e.g. Vogel and Veríssimo, 1981; Perez et al., 1995; Gonzalez and Amenomori, 2003; Gonzalez, 2005a, 2005b, 2007; Hilbert, 2011; Machado et al., 2011; Costa et al., 2012; Barbosa-Guimarães, 2013; Fossile, 2013; Mendes et al., 2014; Sousa et al., 2014; Lopes et al., 2016; Aguilera et al., 2016, 2017; Mendes et al., 2018; Fossile et al., 2019; Wagner et al., 2020) records. Comprehensive studies, such as those that analyzed the entire fauna or all vertebrates of a given sambaqui, sometimes approached tetrapods using taxonomic groups that are too inclusive (classes, for example) or even treated the zooarchaeological remains by common names (e.g. Mello & Mendonça de Souza, 1977; Gazzaneo et al., 1989; Franco and Gaspar, 1992; Perota and Assis, 1993; Kneip, 1995; Gaspar, 2003; Uchôa, 2009). Thus, this doctoral dissertation aimed to put three spotlights (biodiversity, culture, and conservation zooarchaeology) on tetrapods, a group understudied in the sambaquis' records.

A biodiversity and conservation approach is feasible because even though the tetrapod remains have a bias towards selectivity and cultural significance (such as use in diet, ornaments, artefacts, and symbolism), the sambaquis populations could only have exploited species available in the environments at the time, and therefore records of mammals, birds, reptiles, and amphibians can also provide data regarding Holocene biodiversity, such as species composition, abundance, distribution, and richness (Souza et al., 2010a, 2010b, 2016; Faria et al., 2014; Mendes et al., 2014; Beauclair et al., 2016; Rodrigues et al., 2016a, 2016b, 2018; Silva et al. 2016, 2017; Mendes et al., 2018, 2020). Therefore, although the sambaquis are sites built by pre-Columbian populations and are therefore configured as artificial accumulations, the presence or absence of species found

at these sites provides sufficient information for the preparation of a taxonomic inventory that can be a useful tool for the definition of a prehistoric record of biodiversity (Stahl, 2008). Such a record enables the study of biodiversity in a long-term framework, recognizing trends in the species composition of a community by indicating, for example, which were common or rare in a historical perspective (Willis and Birks, 2006; Raffaelli and White, 2013). A temporal approach allows us to understand the life history of certain species, especially population extinctions (Willis et al., 2007), being a useful tool for conservation and management of species, especially endangered ones, as is the case of many tetrapods of the Brazilian coast.

This doctoral dissertation is divided into three chapters (written and edited in article form), and in each chapter we focus on one of the three aforementioned spotlights. The first chapter presents primary data on the diversity of tetrapods recorded in ten sambaquis from southern Brazil. The second discusses cultural aspects (diet, artefacts) of the same vestiges studied in chapter one. Finally, the third chapter presents the most complete checklist of tetrapods from sambaquis of the South and Southeast regions, adding literature records to the primary data of this research. In that chapter, we discuss how this taxonomic inventory can be useful for the conservation of the species. The data were partially presented in four scientific events: XXVI and XXVII Congresso Brasileiro de Paleontologia, 10th Meeting of Bird Working Group of the International Council for Archaeozoology, and 4th Meeting of Neotropical Zooarchaeology Working Group of the International Council for Archaeozoology (Appendix).

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OBJECTIVES

The main objective was to analyse the contribution of tetrapod fauna to sambaquis. For that, the specific objectives were:

• to characterize the biodiversity of mammals, birds, reptiles, and amphibians recorded in sambaquis from the southern coast of Brazil;

• to discuss, from these zooarchaeological remains, cultural aspects of the sambaquis builders such as hunting and capture strategies, diet and manufacturing of artefacts;

• to use the tetrapod fauna from sambaquis of the Brazilian South and Southeast regions for establishing more complete and accurate baselines for species conservation and management of species.

CHAPTER ONE

Tetrapod biodiversity in sambaquis from southern Brazil

Augusto Barros Mendes, Taissa Rodrigues

Abstract
Fishermen-hunter-gatherers of sambaquis (Brazilian shell mounds) had an intimate affinity with marine-coastal environments, where they exploited a great variety of fish and molluscs that comprise the best documented fauna from sambaquis. However, other groups of animals as mammals, birds, reptiles, and amphibians are also present in these sites, but are relatively less studied. This paper is the first one focused exclusively on the Tetrapoda fauna of sambaquis and aimed to identify tetrapods of ten sites from southern Brazil. We present a faunal inventory and data regarding animal capture and environmental exploitation. We identified the specimens anatomically and taxonomically, analysed them concerning fragmentation, and quantified the data (NISP, MNI). Despite the high degree of fragmentation of remains, we identified 46 taxa. As expected, most were from marine animals: cetaceans (total NISP = 2,568 and MNI = 27), otariids (total NISP = 248 and MNI = 32), and seabirds (total NISP = 65 and MNI = 23), indicating great relevance of marine tetrapod fauna as a resource for sambaqui builders (79.39% of NISP). We thus document the close bond between fishermen-hunter-gatherers of sambaquis and the marine tetrapods in southern Brazil.

Keywords: Brazilian Atlantic Forest; coastal archaeology; faunal record; fishermen-hunter-gatherers; Holocene fauna; human-animal interactions; inventory; late Holocene; shell mounds; zooarchaeology

INTRODUCTION

Archaeological sites dating from 8,000 to 1,000 years BP (before present), sambaquis are shell mounds built by pre-Columbian populations that inhabited the Atlantic Forest on the Brazilian coast (Lima, 1999–2000), mainly in the south and southeast regions (Souza et al., 2010; Villagran, 2013). The name “sambaqui” comes from the Tupi etymology: *tamba* (shell) and *ki* (mound), as those sites present a large number of molluscs, but they also have sediments, charcoal, lithic material, mortuary and plant remains, and other faunal remnants of echinoderms, crustaceans, fish and tetrapods that fishermen-hunter-gatherers accumulated during the Holocene (Figuti, 1993; Wagner et al., 2011; Mendes et al., 2014).

Zooarchaeological remains found in the sambaquis have symbolic and cultural value, i.e. the presence and absence of species mainly indicate their usefulness in everyday practices for sambaqui builders (as ornaments, artefacts, ritualistic symbols or as part of their diet) (Gaspar, 1998; Bigarella, 2011). Despite this selectivity, fishermen-hunter-gatherers could only have exploited species available in the environments at the time. Therefore, the sambaquis' faunal records can provide data on the biodiversity at the time they were built (Souza et al., 2016; Silva et al., 2017; Rodrigues et al., 2018; Mendes et al., 2018, 2020; Lopes et al., 2022). Moreover, with zooarchaeological data it is possible to infer which environments were exploited by sambaqui builders for capturing resources and also possible techniques and technologies that were used to catch the fauna (Fossile et al., 2018).

Most studies aimed at researching specific groups of animals in sambaquis have been dedicated to analysing mainly malacological (e.g. Mello and Coelho, 1989; Souza et al., 2010; Gernet and Birckolz, 2011; Faria et al., 2014; Beauclair et al., 2016; Arruda et al., 2019; Cardoso et al., 2020) and ichthyological (e.g. Gonzalez and Amenomori, 2003; Costa et al., 2012; Barbosa-Guimarães, 2013; Mendes et al., 2014, 2018; Lopes et al., 2016; Ferreira et al., 2019; Wagner et al., 2020) records due to the abundance of those taxa in the archaeological sites. Rather, we focused our research on tetrapod fauna, a less studied group of animals in sambaquis (Fossile et al., 2020). Our study set out to investigate the tetrapod record in sambaquis from the southern coast of Brazil, aiming to contribute to a greater understanding of the array of mammals, birds, reptiles and amphibians that were exploited by pre-Columbian populations.

MATERIAL AND METHODS

Study area

The southern Brazilian region comprises the states of Paraná (PR), Santa Catarina (SC) and Rio Grande do Sul (RS) and is located at the Paulista zoogeographical province, presenting high diversity in coastal morphology: several sandy beaches, dunes with rocky coastlines, coastal lagoons, mangroves and mountains that border the coast (Palacio, 1982). The coastal vegetation consists predominantly of restingas, tropical forests (Atlantic Forest) and grasslands (Veloso, 1962).

The southern coast thus presents a plurality of environments where, not coincidentally, the sambaquis communities have settled, since they are areas of transition

between the marine and freshwater habitats, showing great biological productivity and diversity of resources (DeBlasis et al., 2007). The southern region is the most well-studied area of Brazil in terms of archaeology and presents several technological and cultural sets that are defined with a general chronological framework starting about 12,000 years BP (Noelli, 1999–2000). In this study, we analysed tetrapods from sambaquis located in the three states of the southern region (Figure 2). Table 1 summarises data on the studied sambaquis available in the literature.

Table 1. Sambaquis' location, excavation, preservation status of the sites at the moment of excavation, and dating data. UTM = Universal Transverse Mercator (22J zone, datum SAD-69).

Sambaqui	Code	Location		Excavation Date	Preservation Status	Conventional Radiocarbon Age (^{14}C yr BP) and material dated	References
		City, State	UTM				
Toral 51	T51	Paranaguá, PR	7.177.570 737.529	1962	Preserved	Undated, probably older than GUA and GUB	Menezes, 1968; Parellada and Neto, 1993
Guaraguaçu A	GUA	Pontal do Paraná, PR	7.166.735 754.944	1957–1960	Partially destroyed	4,220 ± 200 (Gsy-79), charcoal	Menezes, 1968; Parellada and Neto 1993
Guaraguaçu B	GUB	Pontal do Paraná, PR	7.166.547 754.107	1960–1962	Partially destroyed	4,128 ± 134 (Gsy-79), charcoal	Laming-Emperaire, 1968; Andreatta and Menezes, 1975; Parellada and Neto, 1993
Ilha dos Espinheiros II	IE2	Joinville, SC	7.090.076 721.825	1980–1989	Partially destroyed	1,170 ± 200 (Gif-6166), charcoal 2,730 ± 80 (Gif-6167), charcoal 3,000 ± 95 (St-8413), charcoal 3,015 ± 130 (St-8414), charcoal	Oliveira, 2000; Farias and Kneip, 2010
Caieira	CAI	Laguna, SC	6.848.627 717.962	1966	Partially destroyed	2,770 ± 100 (I-2628S), shell 3,230 ± 155 (I-1618C), charcoal	Hurt, 1974; Farias and Kneip, 2010
Congonhas I	CO1	Tubarão, SC	6.843.010 694.930	1967	Very destroyed	3,165 ± 55 (Az-10650), charcoal 3,350 ± 85 (Az-10650), charcoal	Beck, 1969; Fish et al., 2000; Farias and Kneip, 2010
Itapeva	ITA	Torres, RS	6.748.814 620.357	1982 / 1996	Preserved	3,130 ± 40 (Beta-248226), charcoal	Wagner, 2009; Wagner, 2012
Recreio	REC	Torres, RS	6.745.799 617.757	2007 / 2010	Partially destroyed	3,350 ± 50 (Beta-232731), charcoal 3,540 ± 50 (Beta-283771), charcoal	Wagner, 2009; Hilbert, 2011; Wagner, 2012
Figueira II	FI2	Arroio do Sal, RS	6.738.441 612.305	2010	Partially destroyed	3,660 ± 40 (Beta-263432), charcoal	Rogge and Schmitz, 2010; Wagner, 2012
Sereia do Mar	SER	Arroio do Sal, RS	6.727.518 605.650	2011	Partially destroyed	2,360 ± 60 (Beta-304479), charcoal	Wagner, 2012

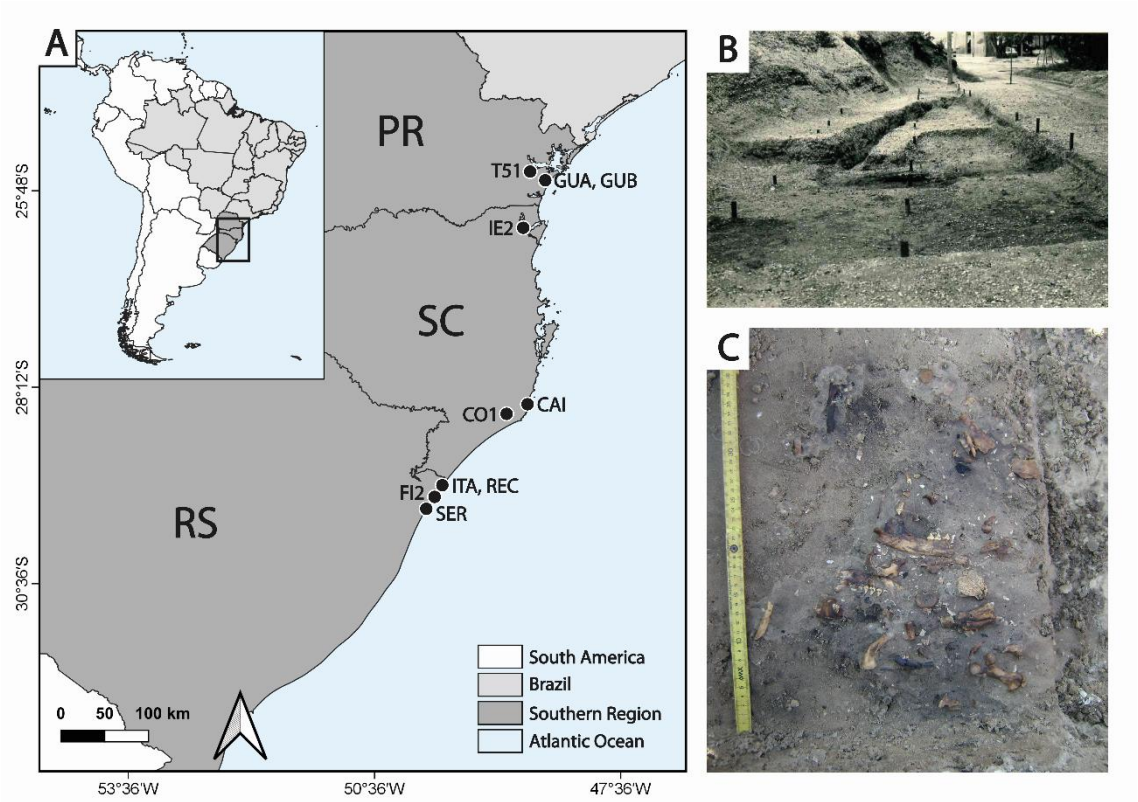

Figure 2. A: Map of the southern region of Brazil with the sambaquis' locations. **B:** IE2 excavation (Source: Museu Arqueológico de Sambaqui de Joinville); **C:** *In situ* otariid remains in FI2 (Source: Laboratório de Pesquisas Arqueológicas of Museu de Ciências e Tecnologia of Pontifícia Universidade Católica do Rio Grande do Sul).

Material

The analysed material is deposited at the Museu de Arqueologia e Etnologia of Universidade Federal do Paraná (T51, GUA, and GUB; Curitiba, Brazil – see Table 1 for abbreviations), Museu Arqueológico de Sambaqui de Joinville (IE2; Joinville, Brazil), Museu de Arqueologia e Etnologia of Universidade Federal de Santa Catarina (CAI and CO1; Florianópolis, Brazil), and Laboratório de Pesquisas Arqueológicas of Museu de Ciências e Tecnologia of Pontifícia Universidade Católica do Rio Grande do Sul (ITA, REC, FI2, and SER; Porto Alegre, Brazil).

We opted to work with sambaquis that had the most accurate information (excavation and dating methodology) available in the literature or field reports, with preference to the ones with remains of vertebrates previously sorted and washed. Moreover, no examined material had previously been submitted to zooarchaeological identification analysis. Almost all sites do not have published data on tetrapod fauna, except for ITA, which has published results concerning material excavated in the 1980s

(Jacobus and Gil, 1987; Gazzeano et al., 1989; Rosa, 1996). Here, we only analysed the artefacts from this excavation that had no prior taxonomic analyses and the material from excavations done in the 1990s. We analysed material from all the stratigraphic layers of the sites, including those from burials, in the case of CAI. Most of the material was stored in bags labelled "animal bones", thus we processed it to exclude fish and modern animals as cattle and domestic pigs, and even human remains.

Vestiges analysis

We made the anatomical and taxonomic identification of tetrapods by comparison to modern specimens deposited in the mammalogy, ornithology and herpetology collections of Departamento de Vertebrados of Museu Nacional of Universidade Federal do Rio de Janeiro (Rio de Janeiro, Brazil); the mammal collection of Laboratório de Mamíferos Aquáticos of Universidade Federal de Santa Catarina (Florianópolis, Brazil); the reference collection of Museu Arqueológico de Sambaqui de Joinville (Joinville, Brazil); the collection of birds and mammals of Museu de Ciências e Tecnologia of Pontifícia Universidade Católica do Rio Grande do Sul (Porto Alegre, Brazil); and the mammal collection of Universidade Federal do Espírito Santo (Vitória, Brazil). We also consulted reference literature and online databases to aid identification (Supplementary Table 1). One of us (ABM) took measurements with a digital caliper.

We analysed the specimens concerning the degree of fragmentation and, in case of marine mammals, also regarding ontogeny. We classified the fragmentation state according to Huisman et al. (2009), who categorized bones as (1) strong and complete; (2) fragile but complete; (3) disintegrated, fragmented; and (4) completely decayed (here referred as heavily, instead of completely, decayed). We estimated the ontogenetic age of fur seals following Borella et al. (2013), who defined five categories (pup, juvenile, subadult, adult, and older adult) based on macroscopic analyses of the fusion degree of epiphyses. For whales, we considered characteristics such as size and spongy texture of the tympanic bullae for the ontogenetic age estimation (Tsai and Chang, 2019).

Data quantification and richness analysis

We used traditional indices in zooarchaeological research to quantify the material: weight, number of identified specimens (NISP), minimum number of individuals (MNI), and minimum number of elements (MNE). The recording of the weight of remains was

done using a 0.001 g precision scale and was used as a proxy of the relative importance of a taxon in the sites (Peres, 2010). NISP is the number of identifiable skeletal elements and fragments of the taxon they represent (Lyman, 2008). It is an observational unit that does not take into account the various parts that may belong to the same individual or the same bone. For a better measurement of abundance, MNI and MNE can be used (Banning, 2000). MNI is the minimum number of individual animals needed to account for specimens of a taxon and was calculated by pairing the most representative and symmetrical elements of the body (primarily long bones) or single parts considering laterality, size, and age, and its final value was the highest number achieved for that element (Reitz and Wing, 2008). MNE is defined as the smallest number of skeletal elements necessary to account for a skeletal part and was calculated from the pairing of bone fragments taking into account laterality, size, age, and region of bone (Lyman, 1994). Finally, we analysed the faunal list similarly to Mendes et al. (2018), using taxonomic richness (number of taxa present in a site) and frequency of occurrence (number of sambaquis in which a given taxon occurs).

RESULTS

We studied ten sambaquis located in seven cities of the three southern states of Brazil, reflecting occupation in the region during the late Holocene, approximately from 4,220 ± 200 to 1,170 ± 200 ^{14}C years BP. We analysed 3,682 skeletal elements, of which 3,326 were mammals (90.33%), 243 birds (6.60%), 51 reptiles (1.38%) and 1 amphibian (0.03%). CAI was the sambaqui that presented the highest taxonomic richness, with 22 taxa. Conversely, SER recorded the lowest richness, with only one taxon (Table 2).

Table 2. NISP by Class and taxonomic richness (TR) of analysed material per sambaqui.

Sambaqui	NISP						TR
	Mammalia	Aves	Reptilia	Lissamphibia	Not id.	Total	
T51	51	20	0	0	9	80	10
GUA	2,053	0	8	0	3	2,064	8
GUB	421	13	39	0	14	487	16
IE2	57	3	1	0	4	65	15
CAI	328	24	3	1	19	375	22
CO1	30	110	0	0	1	141	19
ITA	125	0	0	0	0	125	5
REC	20	1	0	0	0	21	4
FI2	219	72	0	0	0	11	10
SER	22	0	0	0	0	22	1
Total	**3,326**	**243**	**51**	**1**	**61**	**3,682**	

We identified a total of 46 taxa, 44 of them at a level more inclusive than Class. Only 61 remains (1.66%) could not be identified in any taxon other than Tetrapoda (Table 3 and Supplementary Table 2). The number of elements of unidentified taxa and the taxonomic identification at more inclusive levels than families (e.g. Mammalia, Aves and Cetacea) can be explained by their high degree of fragmentation (91.66% of the remains were fragmented, 3.29% heavily decayed, 2.93% strong and complete bones, and 2.12% fragile but complete bones) and a large amount of non-diagnostic anatomical elements. For instance, only 16 out of 2,556 cetacean remains could be identified at the species level.

Table 3. NISP, MNI, frequency of occurrence (F), and material weight of identified taxa. See Table 1 for sambaquis' codes. See Supplementary Table 2 for NISP and MNI data of each sambaqui.

	Taxon Common name	NISP		MNI		F	Sambaquis	Weight (g)
		n	%	n	%			
Mammalia	Mammalia Linnaeus, 1758 indet. Mammals	333	9.08	—	—	9	T51, GUA, GUB, IE2, CAI, CO1, ITA, REC, FI2	2,801.058
	Didelphis sp. Linnaeus, 1758 Opossums	5	0.14	3	2.05	2	IE2, CAI	12.642
	Dasypodidae Gray, 1821 indet. Armadillos	2	0.05	2	1.37	2	GUB, IE2	7.172
	Alouatta sp. Lacépède, 1799 Howler monkeys	3	0.08	1	0.68	1	IE2	8.154
	Rodentia Bowdich, 1821 indet. Rodents	1	0.03	1	0.68	1	FI2	0.092
	Hydrochoerus hydrochaeris Linnaeus, 1766 Capybaras	4	0.11	3	2.05	3	GUB, IE2, CO1	48.977
	Cuniculus paca (Linnaeus, 1766) Lowland pacas	11	0.30	7	4.79	3	T51, GUB, IE2	52.222
	Otariidae Gray, 1825 indet. Eared seals	53	1.44	9	6.16	4	CAI, CO1, ITA, FI2	256.096
	Otaria flavescens (Shaw, 1800) South American sea lions	2	0.05	1	0.68	1	CAI	6.040
	Arctocephalus sp. Geoffroy Saint-Hilaire and Cuvier, 1826 Fur seals	193	5.24	22	15.09	6	T51, GUA, IE2, CAI, ITA, FI2	1,605.242
	Nasua nasua Linnaeus, 1766 South American coatis	1	0.03	1	0.68	1	CAI	10.602
	Felidae G. Fischer de Waldheim, 1817 indet. Felids	2	0.05	1	0.68	1	IE2	0.892
	Tapirus terrestris Linnaeus, 1758 South American tapirs	81	2.20	5	3.42	5	T51, GUB, IE2, CO1, ITA	530.348
	Tayassuidae Palmer, 1897 indet. Peccaries	36	0.98	9	6.16	5	T51, GUB, CAI, CO1, REC	297.123
	Tayassu pecari (Link, 1795)	11	0.30	6	4.11	3	GUB, CAI, CO1	71.398

	White-lipped peccaries							
	Dicotyles tajacu (Linnaeus, 1758) Collared peccaries	8	0.22	5	3.42	3	T51, CAI, CO1	55.396
	Cervidae Goldfuss, 1820 indet. Deers	7	0.19	4	2.74	4	GUB, IE2, CAI, FI2	43.440
	Mazama sp. Rafinesque, 1817 Brocket deers	2	0.05	1	0.68	1	CAI	23.694
	Ozotoceros bezoarticus Linnaeus, 1758 Pampas deers	3	0.08	1	0.68	1	CO1	21.714
	Cetacea Brisson, 1762 indet. Cetaceans	1,696	46.07	—	—	5	GUA, GUB, IE2, CAI, FI2	8,805.283
	Odontoceti Flower, 1867 indet. Toothed whales	41	1.11	5	3.42	5	GUA, GUB, IE2, CAI, FI2	506.780
	Delphinidae Gray, 1821 indet. Oceanic dolphins	4	0.11	3	2.05	2	GUA, CAI	60.246
	Tursiops truncatus (Montagu, 1821) Common bottlenose dolphins	5	0.14	2	1.37	2	IE2, CAI	123.056
	Mysticeti Cope, 1891 indet. Baleen whales	811	22.03	8	5.48	6	GUA, GUB, CAI, ITA, REC, SER	2,7702.159
	Eubalaena australis (Desmoulins, 1822) Southern right whales	11	0.30	9	6.16	3	GUA, GUB, ITA	2,062.000
Aves	Aves Linnaeus, 1758 indet. Birds	161	4.37	—	—	7	T51, GUB, IE2, CAI, CO1, REC, FI2	146.258
	Procellariidae Leach, 1820 indet. Procellariids	2	0.05	1	0.68	1	CAI	9.788
	Puffinus sp. Brisson, 1760 Shearwaters	4	0.11	1	0.68	1	CO1	2.120
	Thalassarche sp. Reichenbach, 1853 Albatrosses	3	0.08	2	1.37	1	FI2	5.488
	Laridae Rafinesque, 1815 indet. Larids	1	0.03	1	0.68	1	CO1	2.768
	Larus dominicanus (Lichtenstein, 1823) Kelp gulls	4	0.11	2	1.37	2	CAI, CO1	6.352
	Rynchops niger Linnaeus, 1758	2	0.05	1	0.68	1	CO1	0.942

	Black skimmers							
	Charadriidae Vigors, 1825 indet. Charadriids	2	0.05	1	0.68	1	CO1	1.468
	Sula leucogaster (Boddaert, 1783) Brown boobies	2	0.05	1	0.68	1	CO1	1.704
	Nannopterum brasilianus Gmelin, 1789 Neotropical cormorants	1	0.03	1	0.68	1	CO1	0.980
	Ardea sp. Linnaeus, 1758 Herons	10	0.27	2	1.37	1	CO1	14.272
	Spheniscus magellanicus Forster, 1781 Magellanic penguins	34	0.92	10	6.85	3	GUB, CAI, FI2	121.370
	Aramides sp. Pucheran, 1845 Wood rails	4	0.11	2	1.37	1	CO1	3.833
	Penelope sp. Merrem, 1786 Guans	1	0.03	1	0.68	1	CO1	1.328
	Amazona sp. Lesson, 1830 Amazon parrots	2	0.05	1	0.68	1	T51	0.968
	Accipitridae Vieillot, 1816 indet. Accipitrids	2	0.05	2	1.37	2	T51, GUB	2.380
	Cathartidae Lafresnaye, 1839 indet. Cathartids	8	0.22	2	1.37	2	CO1, FI2	20.220
Reptilia	Cheloniidae Linnaeus, 1758 indet. Sea turtles	41	1.11	2	1.37	2	GUB, CAI	155.724
	Chelonia mydas (Linnaeus, 1758) Green sea turtles	1	0.03	1	0.68	1	IE2	13.228
	Caiman latirostris Daudin, 1802 Broad-snouted caimans	9	0.24	2	1.37	2	GUA, GUB	44.896
Lissamphibia	Anura Merrem, 1820 indet. Anurans	1	0.03	1	0.68	1	CAI	1.352
Not id.		61	1.66	—	—			276.616
Total		**3,682**	**100**	**146**	**100**			**45,945.881**

DISCUSSION

The values of taxonomic richness of each sambaqui are not comparable due to different excavation, collection, and processing methodologies. GUB, for example, was extensively excavated by several surveys for five years, resulting in 470 m² of excavated area and the maximum depth of 12.35 m (Andreatta & Menezes, 1975). In CO1 the excavation had a mitigation aspect and lasted 23 days (Beck, 1969). In SER 18 m² were excavated in a survey with an average depth of the archaeological layer of 0.75 m, during 3 samplings that were conducted in 47 days of work (Wagner, 2012). All these differences in the methodologies used in each sambaqui provide a different volume of material for taxonomic identification.

The identification of zooarchaeological remains depends on many factors such as the researcher's analytical skill level, completeness of modern comparative osteological collections, and fragmentation level of the archaeological material (Peres, 2010), besides the presence of diagnostic parts. According to Davis (1995) and Beisaw (2013), post-cranial axial elements such as vertebrae and ribs are poorly diagnostic, often only allowing the identification of Classes. In our study, they comprise a significant part of the sample (Table 4 and Supplementary Table 3). Regardless, Lima (1989) points out that bones identified at the Class level should not be disregarded, since taxonomic ranks, even when broad, are informative for the understanding of cultural aspects of pre-Columbian populations.

Table 4. NISP and MNE of identified anatomical elements grouped by axial cranial, axial post-cranial, shoulder girdle, pelvic girdle, stylopodia, zeugopodia, and autopodia zones. See Supplementary Table 3 for a list of bones, NISP, and MNE data from each sambaqui.

Skeletal zones		Mammalia		Aves		Reptilia		Lissamphibia		Total	
		NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
Axial	Cranial	311	223	0	0	8	4	0	0	319	227
	Post-cranial	275	158	20	20	38	3	0	0	333	181
Appendicular	Shoulder girdle	24	14	7	7	1	1	0	0	32	22
	Pelvic girdle	8	7	2	2	0	0	0	0	10	9
	Stylopodia	83	78	78	67	3	3	0	0	164	148
	Zeugopodia	58	51	75	59	1	1	1	1	135	112
	Autopodia	162	141	27	25	0	0	0	0	189	166
Total		**921**	**672**	**209**	**180**	**51**	**12**	**1**	**1**	**1,182**	**865**

The presence of cetaceans in the sambaquis we studied is remarkable (Table 3 and Figures 3 and 4). Their zooarchaeological remains are strongly processed or modified for making objects (Tiburtius et al., 1949) but are relatively fragile due to their low mineral content, making them very fragmentary and difficult to be taxonomically identified (Buckley et al., 2014). Two examples of works on sambaquis from Santa Catarina illustrate how complex the identification of cetaceans at species or genus level is: Bryan (1993) classified the cetacean bones of Sambaqui Marechal Luz only as “whales” (NISP = 112) and “dolphins” (NISP = 5), and Pavei et al. (2015) identified 6.86% (53 out of 772) of the cetacean elements of Sambaqui do Papagaio at the genus level (*Delphinus* sp.).

The southern right whale (*Eubalaena australis*) was the only whale species identified, owing to the analysis of tympanic bullae, which are diagnostic at the species level in Mysticeti (Ekdale et al., 2011) and, unlike other bones, are relatively well preserved in the archaeological record due to their high compactness, density, and mineral content (De Buffrénil et al., 2004). Castilho (2008) also identified this species in two sambaquis of Santa Catarina (Pântano do Sul and Armação do Sul) by tympanic bullae, which displayed excellent preservation. In our study, the identifiable characters in those bones that allow us to recognize *Eubalaena* were the same used by Tsai and Chang (2019): relatively large size (average anteroposterior length of preserved elements = 11.58 cm), rectangular outline in medial view, short anterior lobe, rounded and dorsally elevated outer lip, squared anterior margin in anterior view, squared Eustachian outlet, salient transverse creases on the involucrum, bullae transversely compressed in anterior view, and parallel involucral and main ridges (Figure 3).

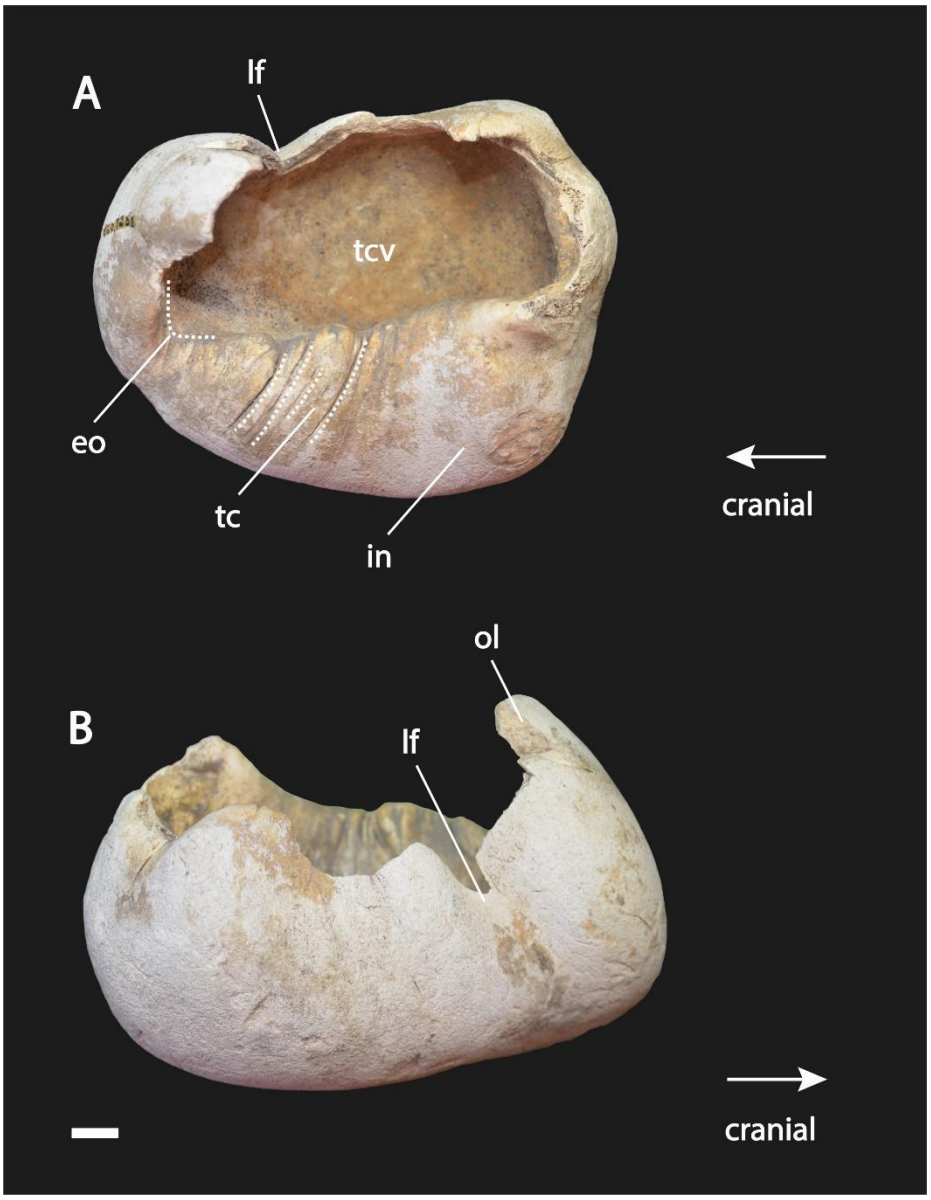

Figure 3. Right tympanic bulla of *Eubalaena australis* (GUA) in dorsal (**A**) and lateral (**B**) views. Abbreviations: **eo**, Eustachian outlet; **in**, involucrum; **lf**, lateral furrow; **ol**, outer lip; **tc**, transverse creases; **tcv**, tympanic cavity. Scale bar: 1 cm.

E. australis and the other seven species of baleen whales that currently occur in Brazil [humpback, *Megaptera novaeangliae* (Borowoski, 1781); blue, *Balaenoptera musculus* (Linnaeus, 1758); fin, *B. physalus* (Linnaeus, 1758), dwarf minke, *B. acutorostrata* Lacépède, 1804; antarctic minke, *B. bonaerensis* Burmeister, 1867; sei, *B. borealis* Lesson, 1828; and Bryde, *B. edeni* Anderson, 1878] (Monteiro-Filho et al., 2013) have migratory behaviour (Lockyer, 1984). The southern right and humpback whales, for example, spend the summer and early autumn in polar waters and migrate to tropical coastal waters during winter and spring for mating, breeding, and calving (Andriolo et

al., 2010; Danilewicz et al., 2016), while Bryde whales perform a local and shorter migration, from coastal areas where they feed to deeper oceanic areas where they breed (Gonçalves et al., 2016). Therefore, it is likely that the Mysticeti was a seasonal resource for fisherman-hunter-gatherers.

In the analysed sambaquis' records, five individuals were small cetaceans (Delphinidae and *Tursiops truncatus*) and all individuals of *Eubalaena australis* were young. As sambaqui builders lived mainly in environments close to the sea and had advanced technology and strategy for fishing, possessing braided fibre nets, weights, stakes, hooks, harpoons/spears, and boats (Calippo, 2011; Barbosa-Guimarães, 2013; Ferreira et al., 2018, 2019; Wagner et al., 2020), they had the necessary toolkit to actively hunt smaller-sized cetaceans. However, these animals may also have been bycatch, which is more significant on small cetaceans such as dolphins and whale juveniles or calves, which are more likely to become entangled in nets than larger animals (Knowlton et al., 2012; Brownell Jr. et al., 2019). Besides, whales may also have been collected in an opportunistic gather, during strandings. Greig et al. (2001) registered 25 such events of southern right whales at the south coast of Brazil between the 1970s and 1990s and, according to Castilho (2008), in ancient times cetacean populations were more consistent, thus stochastic strandings were probably more common.

Other marine mammals such as otariids were also very representative, amounting to at least 30 individuals (Figure 4). Fur seals, mainly *Arctocephalus australis*, and sea lions (*Otaria flavescens*) are frequent in archaeological sites on the South American coast. Borella (2014), for example, has compiled information on 56 sites on the Patagonian Atlantic coast with pinniped remains, many of them identified as Otariidae indet., *O. flavescens*, and *Arctocephalus*.

There are currently three species of *Arctocephalus* in Brazil: *A. australis*, *A. tropicalis* and *A. gazella* (Monteiro-Filho et al., 2013). As in some previous studies on the fauna of southern Brazilian sambaquis (e.g. Bandeira, 1992; Rosa, 2006; Teixeira, 2006), here we were unable to identify them at the species level. The sambaquis' remains only contained isolated post-canine teeth, and it was difficult to determine if they were maxillary or mandibular because the analysed material did not preserve key characters for the identification: tricuspid upper post-canine teeth for *A. australis*, unicuspid with remarkable diastema between the fifth and sixth post-canine for *A. tropicalis*, and unicuspid with flat fifth and sixth post-canines for *A. gazella* (Repenning et al., 1971; Pinedo et al., 1992). Thus unicuspid teeth could be from either *A. tropicalis* or *A. gazella*.

Moreover, post-canines of *A. australis* can present small anterior and posterior accessory cusps (Brunner, 2004). According to Repenning et al. (1971), in some cases the post-canines can consist almost entirely of a single main cusp with only a suggestion of accessory cusps. Therefore, it is challenging to separate species of *Arctocephalus* by anatomical analysis of isolated post-canines. In addition, hybridization cases between *A. tropicalis* and *A. gazella* have been reported (Kerley, 1983; Lancaster et al., 2006).

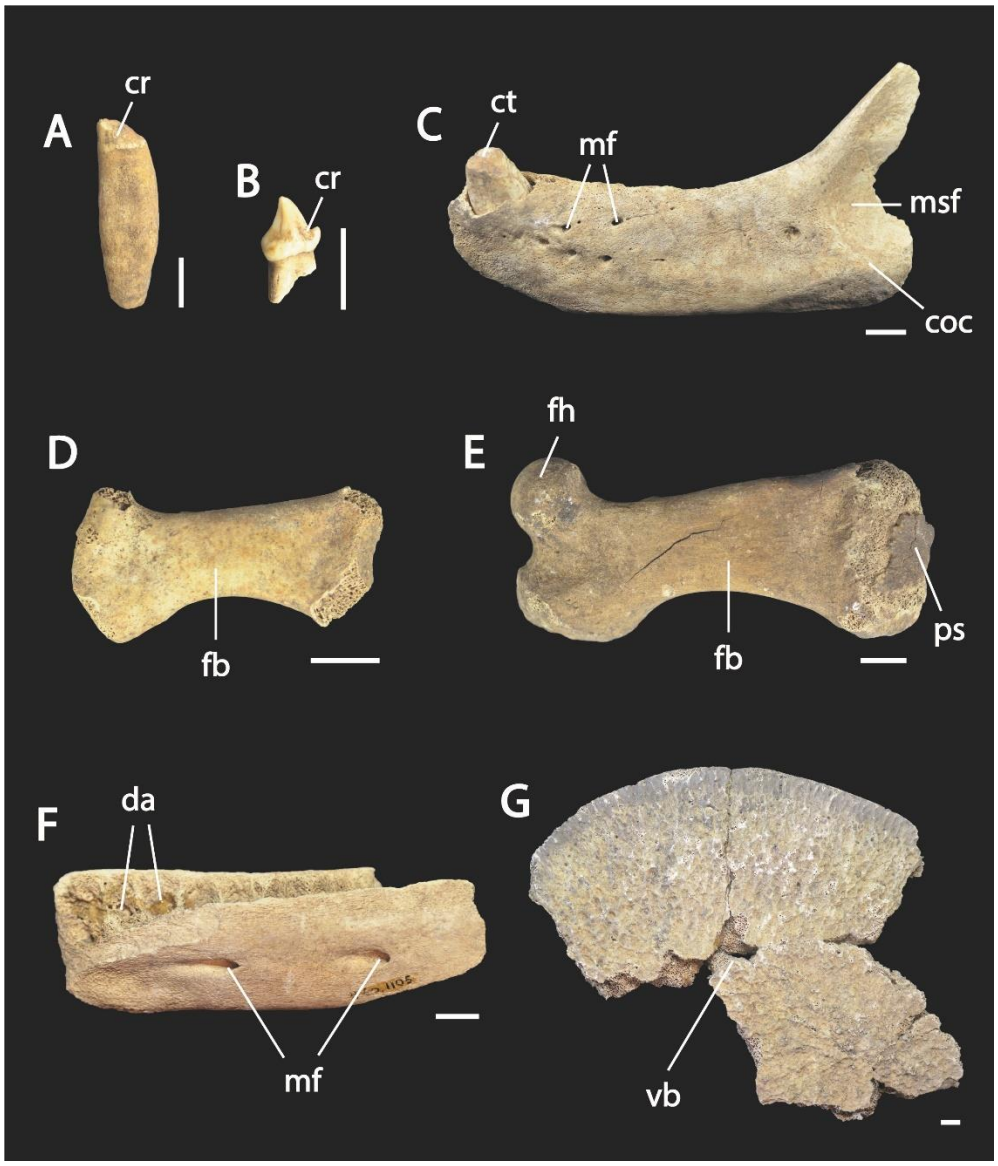

Figure 4. Remains of marine mammals. **A**: upper incisor tooth of *Otaria flavescens* (CAI) in labial view; **B**: postcanine tooth of *Arctocephalus* sp. (FI2) in lingual view; **C**: left mandible of *Arctocephalus* sp. (CAI) in lateral view; **D**: right femur of juvenile *Arctocephalus* sp. (CAI) in anterior view; **E**: right femur of adult *Arctocephalus* sp. (CAI) in anterior view; **F**: distal portion of left mandible of Delphinidae indet. (GUA) in lateral view; **G**: vertebral disc of Mysticeti (GUA) in anterior view. Abbreviations: **coc**, coronoid crest; **cr**, crown; **ct**, canine tooth; **da**, dental alveoli; **fb**, femoral body; **fh**, femoral head;

mf, mental foramen; **msf**, masseteric fossa; **ps**, patellar surface; **vb**, vertebral body. Scale bars: 1 cm.

The large number of individuals of *Arctocephalus* registered in the sambaquis studied here demonstrates that, like the southern right whale, fur seals were exploited by the sambaqui builders in south Brazil, and probably also in a seasonal manner. In the present day, fur seals usually reach the Brazilian coast between winter and spring months, from June to December (Simões-Lopes et al., 1995). These animals come from reproductive colonies in Argentina and Uruguay and are favoured in their post-reproductive movements mainly by the cold Malvinas current (Milmann et al., 2019). Many identified individuals (15 of 22, 68.18%) were juveniles, a similar pattern to that found by Ferrasso et al. (2021), who studied pinniped fauna of five sambaquis from the coast of Rio Grande do Sul. These authors observed that 71.43% of the individuals were juveniles and pointed out that, as today, many of the fur seals and sea lions that arrive in Brazil are young who would be making their first marine incursions and ended up debilitated, without being able to feed themselves. This scenario could be the same in the past and would facilitate the capture of these animals by the fishermen-hunter-gatherers of sambaquis. Furthermore, these animals could also have been collected stranded or resting on the beaches (Castilho and Simões-Lopes, 2001).

The Magellanic penguins, the most abundant penguin on the Brazilian coast, were a very representative species and could also have also been a seasonal resource, since they occur in Brazil primarily during the winter migration between March and September, coming mainly from Patagonian colonies (Brandão et al., 2011). The exploitation of Magellanic penguins as a seasonal resource has also been proposed by Cardoso et al. (2014) in their study on Galheta IV, a Jê-ceramic site historically and geographically involved with sambaqui culture in Santa Catarina. The high MNI of Magellanic penguins compared to other seabirds suggests that they were actively collected, while procelariids, albatrosses, and kelp gulls may have been collected as a bycatch (Figure 5), as they are in fishery activities nowadays (Žydelis et al., 2013).

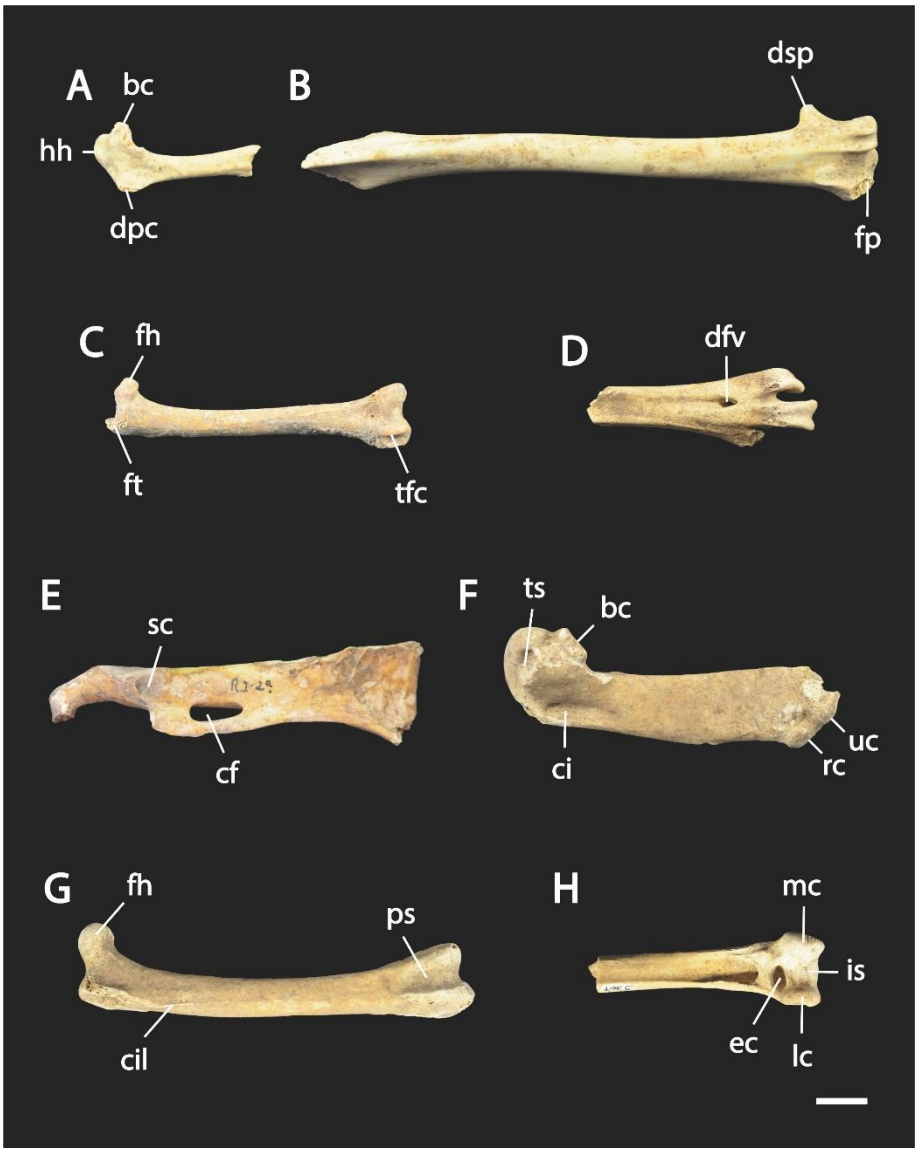

Figure 5. Seabird remains. **A**: proximal and middle portions of right humerus of *Puffinus* sp. (CO1) in anterior view; **B**: middle and distal portions of left humerus of *Larus dominicanus* (CO1) in posterior view; **C**: right femur of *L. dominicanus* (CO1) in posterior view, **D**: distal portion of left tarsometatarsus of *Thalassarche* sp. (FI2) in anterior view; **E**: right coracoid of *Spheniscus magellanicus* (GUB) in ventral view; **F**: right humerus of *S. magellanicus* (CAI) in lateral view; **G**: right femur of *S. magellanicus* (CAI) in posterior view; **H**: distal portion of tibiotarsus of *S. magellanicus* (FI2) in anterior view. Abbreviations: **bc**, bicipital crest; **cf**, coracoidal fenestra; **ci**, coracobrachial impression; **cil**, cranial intermuscular line; **dpc**, deltopectoral crest; **dsp**, dorsal supracondylar process; **dvf**, distal vascular foramen; **ec**, extensor canal; **fh**, femoral head; **fp**, flexor process; **ft**, femoral trochanter; **hh**, humeral head; **is**, intercondylar sulcus; **lc**, lateral condyle; **mc**, medial condyle; **ps**, patellar sulcus; **rc**, radial condyle; **sc**, scapular cotyle; **tfc**, tibiofibular crest; **ts**, transverse sulcus; **uc**, ulnar condyle. Scale bar: 1 cm.

The fishermen-hunter-gatherers also exploited terrestrial environments. The hunting of *Tayassu pecari* and *Dicotyles tajacu*, here identified by dental

characteristics—*D. tajacu* has slenderer, more elongate, and more hypsodont lower canine teeth (Woodburne, 1968; Figure 6)—seems to have been important owing to the high number of individuals (MNI = 20) of Tayassuidae. Based on the same premise as Teixeira (2006), who stated that the presence of land mammals suggests that the groups of sambaqui builders also exploited inland resources, the identified terrestrial fauna demonstrates that the fishermen-hunter-gatherers of the sambaquis studied here also exploited resources in interior Atlantic forest environments as grasslands and highlands. Similarly, the presence of animals such as broad-snouted caimans (Figure 7) suggests that environments such as swamps and wetlands were also exploited.

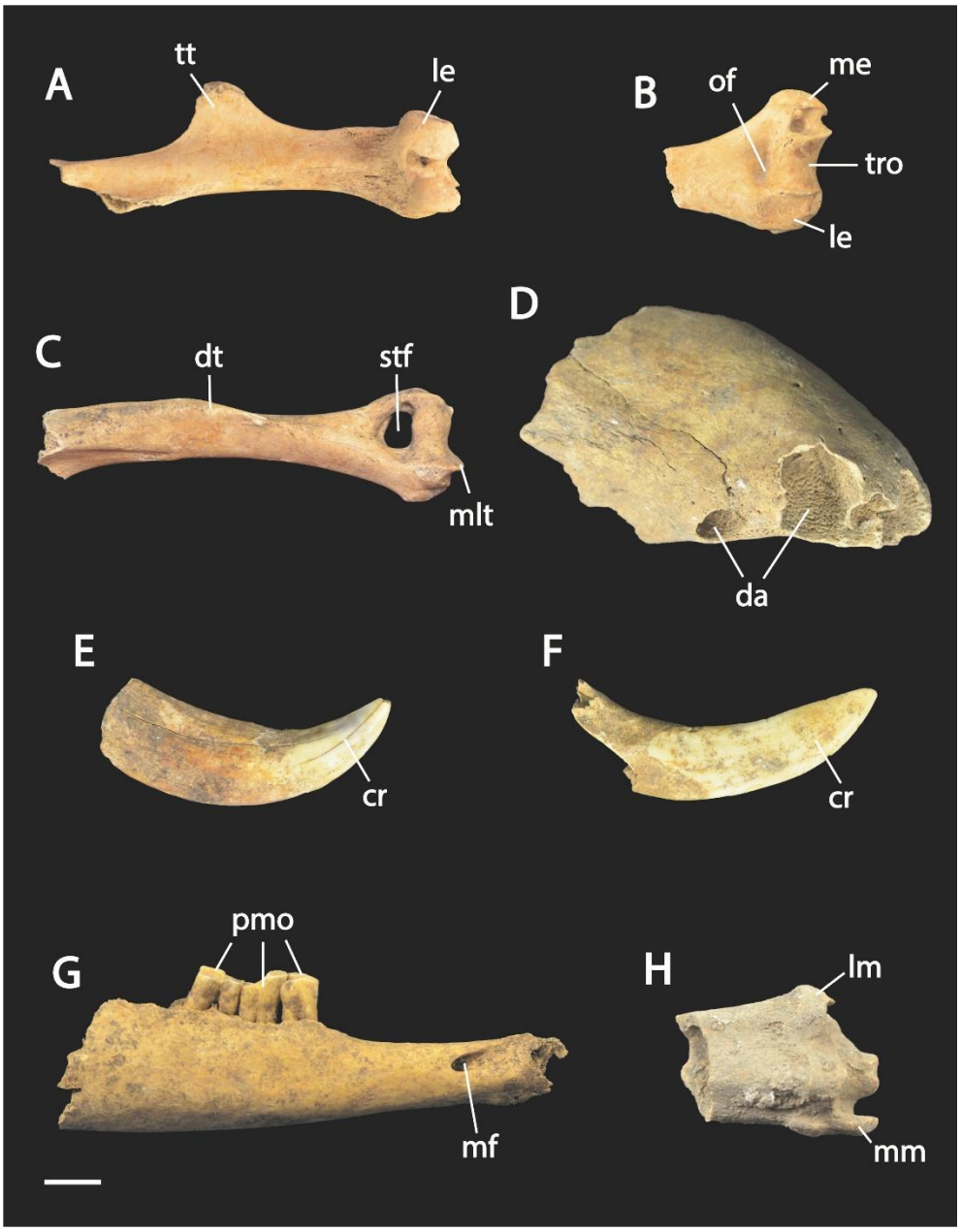

Figure 6. Remains of terrestrial mammals. **A**: middle and distal portions of right femur of Dasypodidae indet. (IE2) in anterior view; **B**: distal portion of left humerus of *Alouatta* sp. (IE2) in posterior view; **C**: middle and distal portions of left humerus of *Cuniculus paca* (GUB) in anterior view; **D**: distal portion of right maxilla of *Tapirus terrestris* (CO1) in lateral view; **E**: right lower canine tooth of *Tayassu pecari* (CAI) in labial view; **F**: right lower canine tooth of *Dicotyles tajacu* (CAI) in labial view; **G**: distal portion of right mandible of *Mazama* sp. (CAI) in lateral view; **H**: distal portion of left tibia of *Ozotoceros bezoarticus* (CO1) in posterior view. Abbreviations: **cr**, crown; **da**, dental alveoli; **dt**, deltoid tuberosity; **le**, lateral epicondyle; **lm**, lateral malleolus; **me**, medial epicondyle; **mf**, mental foramen; **ml**t, medial lip of the trochlea**; mm**, medial malleolus; **of**, olecranon fossa; **pmo**, premolar tooth; **stf**, supratrochlear foramen; **tro**, trochlea; **tt**, third trochanter. Scale bar: 1 cm.

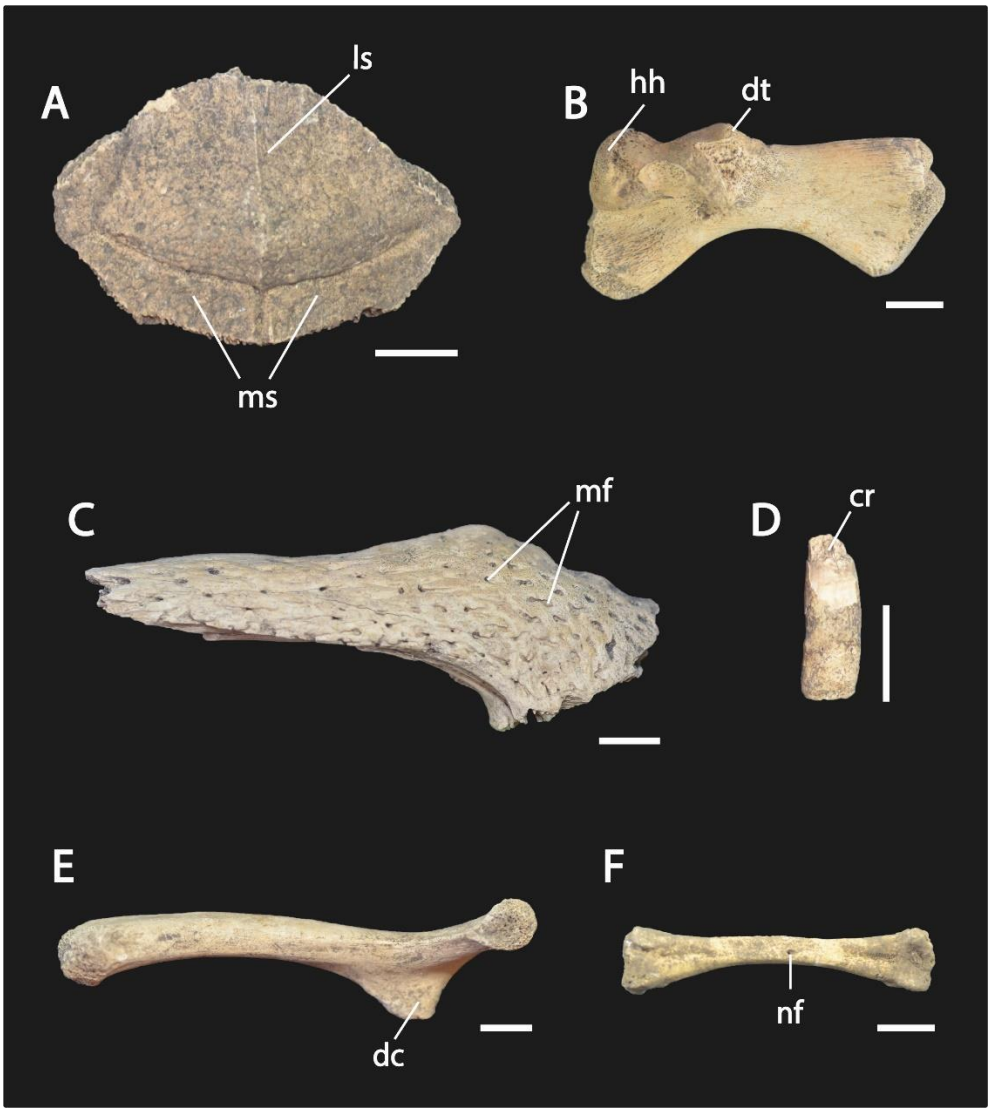

Figure 7. Remains of herpetofauna. **A**: distal portion of carapace of Cheloniidae indet. (GUB) in dorsal view; **B**: left humerus of *Chelonia mydas* (IE2) in ventral view; **C**: distal portion of right mandible of *Caiman latirostris* (GUA) in ventral view; **D**: lower tooth of *C. latirostris* (GUA) in labial view; **E**: left humerus of *C. latirostris* (GUB) in medial view; **F**: left tibiofibula of Anura indet. (CAI) in anterior view. Abbreviations: **cr**, crown; **dc**, deltoid crest; **dt**, deltoid tuberosity; **hh**, humeral head; **ls**, lateral scute; **mf**, mental foramen; **ms**, marginal scute; **nf**, nutrient foramen. Scale bars: 1 cm.

Five currently threatened species according to Brazilian Red List of Threatened Species (ICMBio, 2018) are present in our inventory: *Tapirus terrestris*, *Tayassu pecari*, *Ozotoceros bezoarticus*, *Eubalaena australis*, and *Chelonia mydas*. Records of pampas deer populations in coastal or near-coastal cities in SC are mostly historical, from the 1980s (Cherem et al., 2004), and prehistorical from sambaquis (Bandeira, 1992; Rosa, 2006; this study), indicating that this species was more common in coastal areas in

southern Brazil in the past, as suggested previously by Fossile et al. (2018) based on records of a sambaqui in Babitonga Bay, SC. Santos et al. (2018) discusses that the fishermen-hunter-gatherers of the sambaqui Lagoa dos Freitas in SC exploited land resources, mainly Tayassuidae, as in the site Içara 06, located further south in the state and studied by Rosa (2006) and Teixeira (2006). These studies indicate a high consumption of peccaries by sambaquis' builders. *T. terrestris* was also registered in other sambaquis in the Brazilian south region (e.g. Bandeira, 1992; Bryan, 1993; Pavei et al., 2015; Santos et al., 2018), as well *E. australis* (Castilho, 2008) and *C. mydas* (Ramos Junior, 2014). These records help to understand how these species have been exploited for thousands of years, contributing to a long-term framework on biodiversity and human-fauna interactions.

CONCLUSIONS

We present an inventory of 46 tetrapod taxa, 10 of which were identified at genus level and 17 at species level, that were exploited during the late Holocene by sambaqui fishermen-hunter-gatherers. Most remains were from marine animals, mainly cetaceans and baleen whales, and the species with the highest number of individuals were Magellanic penguins and southern right whales. The significant amount of juvenile fur seals and southern right whales recorded suggests both opportunistic and selective hunting for these animals, as young fur seals reach the south coast after migration and smaller cetaceans are more vulnerable to bycatch. Therefore, sambaqui builders heavily exploited seasonal resources: whales, fur seals, and penguins.

Terrestrial aniamals was also exploited, especially peccaries, but we also recorded lowland pacas, south american tapirs, deers, and broad-snouted caimans. The diversity of the fauna identified here is probably a reflection of the variety of instruments and techniques for fishing, gathering and hunting, and also the array of coastal and interior environments exploited by sambaqui builders. The zooarchaeological remains of the tetrapod species here identified indicate their usefulness to sambaqui builders, so the fauna recorded at these sites have sociocultural value, mainly in diet.

The information presented here refers to materials of sambaquis never studied before in a taxonomic approach and, focusing on tetrapod fauna—a relatively less studied group of animals in these archaeological sites—, contributes to a greater understanding of the Holocene biodiversity, sambaqui culture, and builders-animals' interactions.

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CHAPTER TWO

Food and tool from the sea: the relevance of marine tetrapod fauna in cultural practices of sambaqui builders

Augusto Barros Mendes, Gabriela Sartori Mingatos, Klaus Hilbert, Taissa Rodrigues

Abstract
Anthropic modification in bone remains, such as cut marks, burning and artefacts, are pieces of evidence to understand key aspects of cultural practices (fishing, hunting, artefact production, carcass manipulation, funeral rituals, and feasts) of ancient societies. However, for sambaquis, coastal archaeological sites common on the south and southeast coasts of Brazil, data on these marks are infrequent or incomplete and lack taxonomic and anatomical identification, especially for tetrapods – a less studied group in sambaquis. Thus, here we performed a multi-approach analysis (anatomical and taxonomic identification, identification of cutting, burning and modification marks for artefact confection, biomass estimation, and representation of skeletal parts) and present the most complete data on human modification in tetrapod bones from sambaquis done so far. As results, most of the identified bones are from marine fauna (Mysticeti indet., Cetacea indet, Otariidae indet. *Arctocephalus australis*, *Spheniscus magellanicus*) and cut marks are registered mainly in these animals. The biomass calculation revealed that, among tetrapods, marine fauna had the greater participation in the diet of the sambaqui builders, as expected. In some of them, like otariids, carcass processing aimed at selecting meaty parts, while fins were probably discarded due to their low yield of consumable protein. Most artefacts were made from cetacean bones, although terrestrial fauna was also used as raw material for tool manufacturing, including previously unknown items for sambaquis: composite hooks and a bony, instead of dental, perforated object. In summary, our research shows the importance of marine tetrapod fauna for the builders, being a substantial contribution to the understanding of the sambaqui culture.

Keywords: artefacts; bone industry; diet; fishermen-gatherer-hunters; human-animal interactions; shell mounds; taphonomy; zooarchaeology

INTRODUCTION

Studies on vertebrates recovered in archaeological sites provide information not only on the fauna and environment of the past, but also on the cultural aspects of ancient societies (Ritz and Wing, 2008; Russel, 2012). Human alterations on bones may reflect different cultural activities, such as those related to hunting, fishing, carcass-processing behaviours, mortuary practices, and technology, and result in the production of a series

of perimortem or postmortem modifications, such as cut marks and thermal alteration (Mazza et al., 2018).

Cut marks identified in faunal assemblages of archaeological sites are an important source of evidence of prehistoric butchery strategies (Egeland, 2003; Otárolla-Castillo, 2010) and their frequency in a sample depends on factors such as animal/carcass size and amount of meat (Castamagno et al., 2019), since the number of cut marks is determined by the different investment in meat or tissue removal (Binford, 1988). Vestiges of thermal alteration usually provide direct evidence of the use of the fauna by humans as food (Nicholson, 1993), even though burning could have occurred for other reasons (e.g., bone exposed to flames during offerings, resulting from an accident, or trash disposal) (Reitz and Wing, 2008). The bone toolkit present in an archaeological site can also indicate how the animals were captured (Kneip, 1994).

For sambaquis—shell mounds constructed by pre-Columbian human groups, especially at the southeast and south coasts of Brazil, dating back 8,000 to 1,000 years before the present (Schmitz, 1987; Gaspar, 1998; Lima, 1999-2000)—, until the end of the 2010s studies presenting taphonomic analyses of cut marks and burning marks on faunal remains were rather scarce (Rosa, 2008). An exception is the work of Castilho and Simões-Lopes (2008), who aimed to understand the interaction between prehistoric occupants of the Brazilian coast and the fauna by analysing bone modifications. In recent years, research on sambaquis set out to identify these features systematically (e.g., Santos et al., 2018; Klokler, 2020; Ferrasso et al. 2021), but it is not yet a frequent approach in the literature. In contrast, studies on bone artefacts from these sites were common, although only until the 1990s (e.g. Tiburtius et al., 1946, 1949; Tiburtius and Bigarella, 1953; Tiburtius, 1960; Beck et al., 1970; Beck, 1972, 1974; Rohr, 1977; Fossari, 1985; Kneip, 1987, 1994). While numerous, they rarely provide quantitative and anatomical information (Castilho and Simões-Lopes, 2008). To fill this gap, our study aims to analyse human modifications made in the bones of tetrapods from sambaquis in southern Brazil, as a tool to understand cultural aspects of the sambaqui builders and their relationships to the medium- and large-sized fauna.

MATERIAL AND METHODS

Study area and material

We analysed the material of ten sambaquis (Toral 51, T51; Guaraguaçu A, GUA; Guaraguaçu B, GUB; Ilha dos Espinheiros II, IE2; Caieira, CAI; Congonhas I, CO1; Itapeva, ITA; Recreio, REC; Figueira II, FI2; and Sereia do Mar, SER) located in the three states of the southern region of Brazil: Paraná (PR), Santa Catarina (SC), and Rio Grande do Sul (RS) (Figure 8, see Chapter 1 for detailed information on each sambaqui).

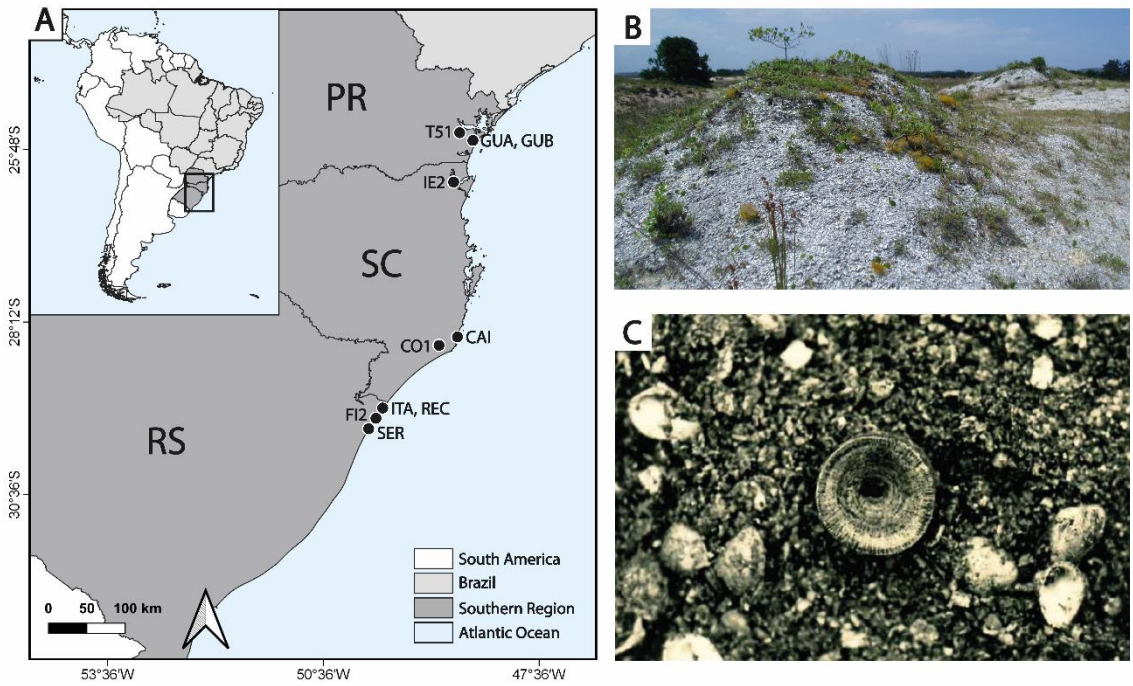

Figure 8. A: Map of the southern region of Brazil with the sambaquis' locations. **B**: REC panoramic view (Source: Laboratório de Pesquisas Arqueológicas of the Museu de Ciências e Tecnologia of the Pontifícia Universidade Católica do Rio Grande do Sul). **C:** In situ bone artefact (perforated object made on a fish vertebra) in IE2 (Source: Museu Arqueológico de Sambaqui de Joinville).

The material is currently deposited at the Museu de Arqueologia e Etnologia of the Universidade Federal do Paraná (T51, GUA, and GUB; Curitiba, Brazil), Museu Arqueológico de Sambaqui de Joinville (IE2; Joinville, Brazil), Museu de Arqueologia e Etnologia of the Universidade Federal de Santa Catarina (CAI and CO1; Florianópolis, Brazil), and Laboratório de Pesquisas Arqueológicas of the Museu de Ciências e Tecnologia of the Pontifícia Universidade Católica do Rio Grande do Sul (ITA, REC, FI2, and SER; Porto Alegre, Brazil).

Vestiges analysis

We made the anatomical and taxonomic identification of the tetrapod remains by comparison to modern specimens deposited in the collections of mammalogy, ornithology and herpetology of several institutions in Brazil (see Chapter 1).

We estimated the degree of burning after Shipman et al.'s (1984) five heating stages based on bone colouration: (category 1) neutral white, pale yellow, and yellow: 20–285ºC; (category 2) reddish-brown, neutral dark-grey, reddish-yellow: 285–525ºC; (category 3) neutral black with some reddish yellow: 525–645ºC; (category 4) neutral white with some light grey: 645–940ºC; (category 5) neutral white with some medium grey: 940+ºC.

Cut marks made from skinning, defleshing, and disarticulation activities were identified following the manuals of Lyman (1994), Serjeantson (2009), Fernández-Jalvo and Andrews (2016), and Castamagno et al. (2019). We also quantified the amount of bones that had cut marks.

Finally, we classified artefacts based on a typological analysis of the shapes of objects, the manufacturing techniques, and raw materials used (Sidéra, 1994). Our classification did not follow the nomenclatures already known in the Brazilian archaeological literature (Rohr, 1977), since many names assume functions that cannot be determined without adequate microscopic and experimental analysis. Therefore, we classified the artefacts adapting some models already present in Brazilian Archeology (e.g. Beck, 1972, 1974; Fossari, 1985; Gaspar, 1991, 2003) and others present in the international literature (Sidéra, 1994). The artefacts were thus classified as bevelled, piercing, and perforated objects, double point and grooved double point hooks, symmetric and asymmetric composite hooks, sphere, and zoomorphic item.Among the piercing objects category, it was possible to include previous nomenclatures (points, double points, etc). We opted for the nomenclature "piercing objects" to avoid the use of "point", which could assume the use of the artifact as a projectile point, as well as needles, which assume a specific use linked to sewing. Among the bevelled objects category, the often-used terms spatulas and gouges were included and, though frequently characterized by a rounded, rectilinear or even slightly tapered apex, they primarily have a bevel-shaped apical zone. In the perforated objects category are not only adornments, but also tools. Hooks were classified as such due to the similar shape to presently existing ones that are used for the same purpose in multiple cultural contexts (e.g. Tiburtius and Bigarella, 1953; Walters, 1988; Calippo, 2011; Pertulla and Walters, 2016; Nabais and Soares,

2017; O'Connor et al., 2017). Spheres and zoomorphic items were classified according to their similarity to those described in the literature regarding sambaquis (Tiburtius et al., 1949; Tiburtius, 1960, 1966; Chmyz et al., 2003; Ferreira et al., 2018).

Data quantification and analysis

As in Chapter 1, we quantified material based on their weight, number of identified specimens (NISP), minimum number of individuals (MNI), and minimum number of elements (MNE). We also weighted fish remains for IE2, CAI, and CO1 sambaquis, as the collections already had their fish material separated from other vertebrate remains.

We calculated the percentage of representation of skeletal parts (PR) and biomass (Binford, 1991; Vigne, 1991; Reitz and Wing, 2008; Borges, 2015), both dependent on MNI. PR determines the proportion of each bone or tooth for a given taxon and was calculated following Borges (2015): PR = (FO × 100) / (FT × MNI), where FO is the number of each skeletal element in a sample and FT is the frequency of that element in a complete skeleton. This method allows to analyse if there was selectivity for parts of carcasses (Borges, 2015). We calculated PR for otariids [grouping Otariidae Gray, 1825 indet., *Otaria flavescens* (Shaw, 1800), and *Arctocephalus* sp. Geoffroy Saint-Hilaire and Cuvier, 1826], Magellanic penguins (*Spheniscus magellanicus* Forster, 1781), and sea turtles [grouping Cheloniidae Linnaeus, 1758 indet. and *Chelonia mydas* Linnaeus, 1758] as they were the groups with the highest number of individuals for mammals, birds and reptiles, respectively.

We estimated biomass (Vigne, 1991; Reitz and Wing, 1999; Borges, 2015) by multiplying the weight of consumable meat (a percentage of an average body weight) (White, 1953) per individual by the MNI of each species and genera, except whales, due to the bias caused by the enormous weight of a single individual (Borges, 2015; Cardoso, 2018). The average weight of individuals of each species and genera were calculated based on data available in the literature and databases [Paglia et al. (2012) for mammals; Schreiber and Burger (2002) and WikiAves (2021) for birds; and Pritchard (1979) and Verdade (1995) for reptiles], and the percentage of the consumable weight of different taxa followed White (1953), Smith (2011), and Borges (2015). The latter author highlights some limitations of this analysis, such as underestimating the meat consumption of animals because it is based on MNI and generally disregards age and sex

variations in the average weight of some animals, but stresses that it is still a useful estimate to, for example, infer the contribution of different species in hunting.

RESULTS

In total, we analysed 3,682 remains and identified 46 taxa, 25 of which mammals, 17 birds, three non-avian reptiles and one amphibian. Most identified taxa were marine fauna (e.g. Cetacea Brisson, 1762 indet., NISP = 1,696; Mysticeti Cope, 1891 indet., NISP = 811; Otariidae indet., NISP = 53; *Arctocephalus* sp., NISP = 193; *Spheniscus magellanicus*, NISP = 34; and Cheloniidae indet., NISP = 41; see Chapter 1 for detailed anatomic and taxonomic data). The estimated biomass showed greater contribution of marine animals (79.63%) in hunting than terrestrial ones (see Supplementary Table 4 for biomass calculated for each taxon).

The weight of fish material from IE2, CAI, and CO1 were 2.954 kg, 10.802 kg, and 16.249 kg respectively; and the weight of tetrapod remains were 0.762 kg, 6.984 kg, and 0.362 kg, respectively.

We identified cut marks in the material (Table 5). Most were in marine fauna (in 15 otariid bones, 8 cetacean bones, and 8 Magellanic penguins bones) and show patterns consistent with a skinning process (47.27%). Marks were mainly identified on long bones such as the humeri, radia, ulnae, femora, tibiae, and phalanges (63.64%), which were made primarily on the diaphyses (64.71%, see Supplementary Table 5 for complete data on remains with these marks).

The identified burning marks are mostly included in category 2, and category 3 burning marks were observed only on mammalian bones (Table 5).

Table 5. Number of bones with human-made modifications.

Modifications	Mammalia	Aves	Reptilia	Not id.	Total
Cut marks	40	11	1	3	55
Skinning	21	4	0	1	26
Defleshing	10	1	1	2	14
Disarticulation	9	6	0	0	15
Burning marks	1598	12	35	10	1655
Category 2	1507	12	35	10	1564
Category 3	91	0	0	0	91
Artefact manufacturing	127	0	0	0	127
Absent	1573	220	15	58	1857

In otariids, Magellanic penguins, and sea turtles, bones such as femur, radius, and humerus were recorded and in some cases with high representativeness (Figure 9). On the other hand, autopod bones had low representation in relation to the other bones in otariids.

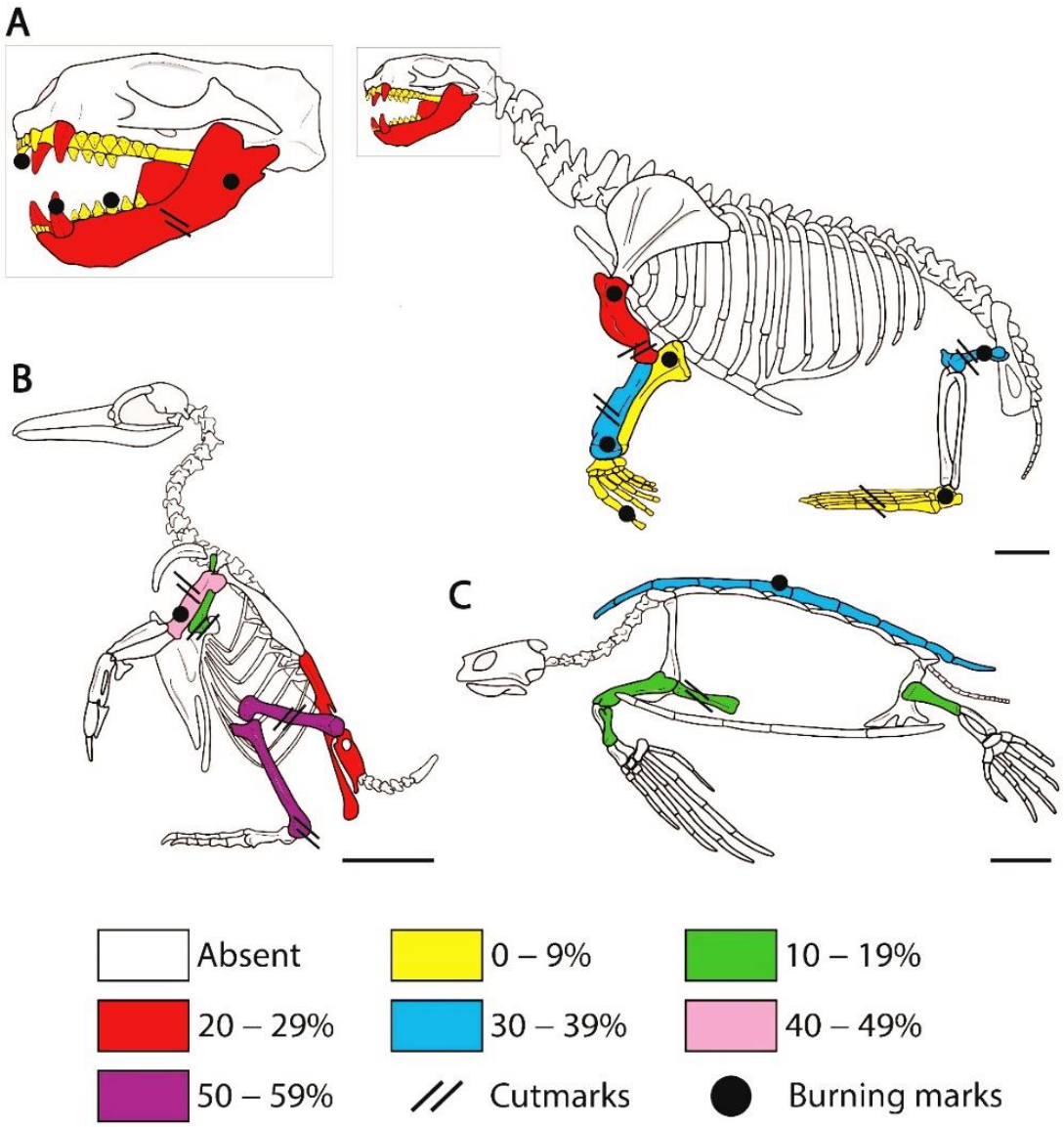

Figure 9. Percentage of representation of skeletal parts and anthropic modification marks in otariids (**A**), Magellanic penguins (**B**), and sea turtles (**C**). Scale bars: 10 cm. Skeletal illustrations by R. Buchmann and adapted from Berta et al. (2006) for the otariid, Chávez Hoffmeister (2012) for the Magellanic penguin, and CoMBINe (2017) for the sea turtle.

Regarding artefacts, we recorded 127 pieces (bone modified for artefact manufacture) distributed in T51, GUA, GUB, CAI, and ITA sambaquis, manufactured

from the bones of Mammalia Linnaeus, 1758 indet. (33.07%), Cetacea indet. (10.24%), Mysticeti indet. (46.46%), *Eubalaena australis* (Desmoulins, 1822) (7.87%), Tayassuidae Palmer, 1897 indet. (1.57%), and *Tapirus terrestris* Linnaeus, 1758 (0.79%) (Table 6).

Table 6. Number of artefacts registered for each identified taxon. See Supplementary Table 6 for detailed data on each sambaqui.

Artefact	Taxon						Total
	Mammalia indet.	**Cetacea indet.**	**Mysticeti indet.**	***Eubalaena australis***	**Tayassuidae indet.**	***Tapirus terrestris***	
Bevelled object	0	11	51	10	0	0	72
Piercing object	12	2	1	0	2	0	17
Perforated object	0	0	6	0	0	1	7
Double point hook	12	0	0	0	0	0	12
Grooved double point hook	1	0	0	0	0	0	1
Symmetric composite hook	5	0	0	0	0	0	5
Asymmetric composite hook (stem)	5	0	0	0	0	0	5
Asymmetric composite hook (point)	6	0	0	0	0	0	6
Sphere	0	0	1	0	0	0	1
Zoomorphic item	0	1	0	0	0	0	1
Total	**41**	**14**	**59**	**10**	**2**	**1**	**127**

DISCUSSION

Diet

Fishermen-gatherer-hunters of sambaquis, groups with a consolidated exploitation system of the coastal environment, had a diet based mainly on molluscs and fishes (Figuti, 1993; Klokler and Gaspar, 2019). According to Klokler et al. (2010), until the mid-1990s many studies defined the sambaqui builders as groups of simply organised nomads who explored the Brazilian coast capturing molluscs but, after their supposed depletion due to overexploitation, developed fishing as a subsistence activity. However,

Figuti (1993), after comparing the amount of meat from bones and shells, concluded that collecting molluscs was a low cost-benefit activity, since these animals do not have high energy value. The author thus suggested fish consumption as the basis of the subsistence of the sambaqui builders. Today, isotopic analyses allowed to establish that fish were in fact the most important food resource and molluscs were a supplement to the diet (De Masi, 2009; Klokler, 2014; Oppitz et al., 2018). Nowadays, the sambaqui builders are considered complex and stable groups that settled in places with rich resources and easy access to the sea, lagoons, mangroves, and forest, which allowed the practice of fishing, hunting and gathering (Klokler et al. 2010).

The weight of the material from IE2, CAI, and CO1 agrees with the relevance of fish in the diet of the sambaqui builders. All these sambaquis had a much higher weight of fish than that of tetrapods, even where the presence of large mammals with heavy bones, such as cetaceans, was recorded. Furthermore, NISP of fish remains is much higher than tetrapods in the same sambaqui. Benz (2000), in his preliminary fauna study of IE2, recorded 8,846 fish remains, while here we recorded only 65 tetrapod specimens. For REC, Hilbert (2011) documented 1,128 fish elements, while we recorded only 21 of tetrapods.

Considering only the tetrapods, the diet of fishermen-gatherer-hunters of the sambaquis we analysed was mainly based on marine animals. The MNI and biomass values we obtained are similar to those of Cardoso (2018), who recorded 58.34% of MNI and 90.67% of biomass for marine mammals in the Galheta IV site (a Jê-ceramic site involved with sambaqui culture in SC). However, Borges (2015) recovered different results for Mar Casado, a sambaqui in São Paulo state: 16.76% of MNI and 34.31% of biomass for marine mammals. Both authors also excluded Mysticeti from the meat weight calculation, as we did. These results suggest that the importance of marine tetrapods in the diet of southern sambaqui builders might have been greater than in lower latitudes of Brazil. If this was indeed the case, those findings could be explained by two hypotheses: (i) distinct selectivity and dietary taboos between groups of sambaqui builders, and/or (ii) different regional availability of these resources. According to Castilho and Simões-Lopes (2001), the Brazilian southern region is located on the migratory routes and breeding areas of cetaceans, an especially diverse group in this region due to the subtropical convergence between the Malvinas and Brazilian currents. This, added to the proximity with reproductive colonies of otariids, may have increased the relevance of these animals for the sambaqui fishermen-hunter-gatherers of southern Brazil. Those

authors also state that in historical times, southern Brazil had fur seals colonies which were latter completely decimated by European colonizers. Thus, in prehistoric times these animals could have been common in the southern region and could have been a more important resource than for sambaqui builders further north. However, data from more sambaquis is still needed to test these hypotheses.

Fishermen-hunter-gatherers of sambaquis manipulated otariid carcasses and selected parts that would be consumed more frequently. The low representativity of autopod bones indicates that pinniped flippers were discarded, an expected result since they contain few edible soft parts (muscle and fatty tissue) and thus present low meat/food utility value (Lyman et al., 1992). Borges (2015) inferred that the sambaqui builders of Mar Casado might also have discarded otariid and dolphin flippers. Processing and selecting parts of the carcasses could have been done at the site of capture or collection of the marine animals, taking only selected parts to the sambaqui area (Castilho, 2008).

Anthropic cut marks in zooarchaeological vestiges are mostly associated with carcass butchering processes that leave traces of cutting and chopping activities (Binford, 1981). We identified 55 bones with butchery cut marks (skinning, defleshing, disarticulation; Table 5, Figure 10), the majority on marine fauna: otariids, cetaceans, and Magellanic penguins. Previous works have already shown that this fauna was extensively exploited and processed by ancient coastal Amerindians in southern Brazil: Ferrasso et al. (2021) identified cut marks on 25 of 130 otariid bones in the sambaqui Xangri-Lá in RS and recorded a predominance of cut marks on long bones; Castilho (2008) recorded cut marks in 24 of 931 dolphins and whales when analysing the cetacean fauna from six sambaquis in SC; and Cardoso et al. (2014) identified cut marks on 178 of the 444 bones of Magellanic penguins in Galheta IV, mostly on long bones. Thus the builders of the sambaquis manipulated the carcass of the hunted animal to select parts of greater interest, usually long bones that hold more meat and fat. Indeed, in GUB, CO1, and SER, lithic artefacts used to do these activities, such as choppers, hammers, cutters, axes, and scrapers, have already been recorded (Beck, 1969; Andreatta and Menezes, 1975; Wagner, 2012).

Regarding burning marks, all bones with thermal alteration vestiges were allocated in categories 2 and 3. Their colour indicates that they more often were probably exposed to temperatures of 285–525ºC (42.48%, category 2), and more rarely 525–645ºC (2.47%, category 3, Figure 10). Non-uniform colour in some bones demonstrates that they were not completely fleshed and still had soft parts when exposed to fire (Buikstra and

Swegle, 1989). We rule out the possibility that the blackish colour in bones was caused by manganese impregnation, since dark stainings did not present a dendritic pattern (Tomassini et al., 2010; Fernández-Jalvo and Andrews, 2016).

Thermal alteration in bones do not necessarily mean that the animal remains were intentionally burned for dietary purposes (Reitz and Wing, 2008), for instance buried bones may suffer thermal action if there is a fire on them, so if deposited in layers close to the bonfires they may have been accidentally burned (Stiner and Kuhn, 1995). However, in the CAI and FI2 sambaquis more than half (51.35% in CAI and 89.85% in FI2) of the bones allocated in categories 2 and 3 of thermal alteration were found in layers that had large bonfires, charcoal, ashes, and even ovens (source: Diário de Campo de Anamaria Beck, jazida SC.LL.29 – Sambaqui da Caieira, available at MArquE-UFSC; and Relatório IPHAN Arqueologia do Litoral Norte, available at LPA-MCT-PUCRS), suggesting that they were probably exposed to fire intentionally, agreeing with Menezes (1968) and Hurt (1974), who pointed out the importance of bonfires in the feeding of sambaqui builders for GUA and CAI, respectively. Pinto (2013) also observed in the sambaqui Amourins in Rio de Janeiro that the layers that presented more faunal elements with burning marks were the same that had several bonfires.

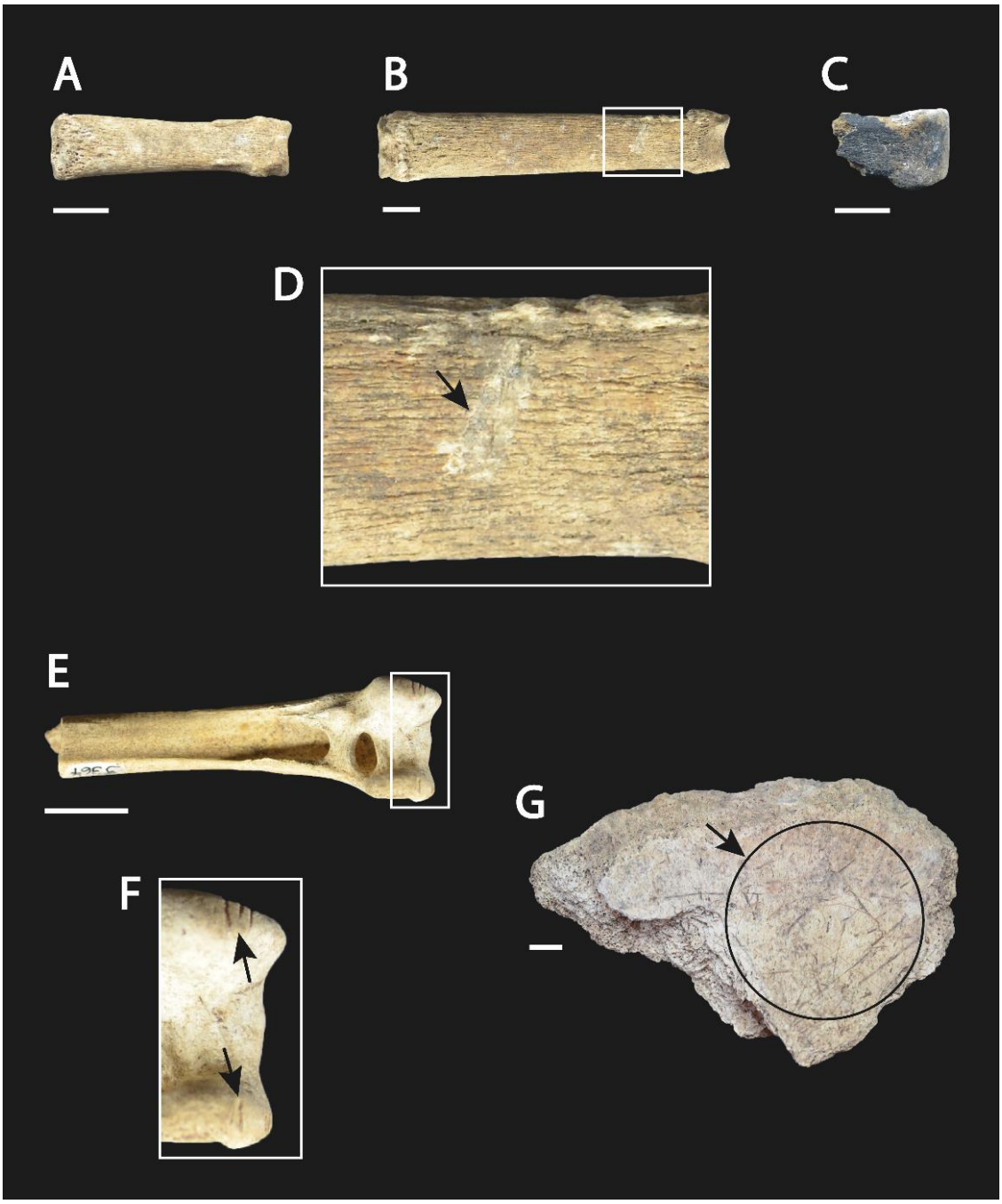

Figure 10. Vestiges with cut marks and burning marks. Phalanges of Otariidae in ventral view allocated in categories 1 (**A**), 2 (**B**), and 3 (**C**) of thermal alteration; the arrow in **D** (detail of B) indicates a skinning cut mark. Distal portion of tibiotarsus of *Spheniscus magellanicus* in anterior view (**E**); the arrows in **F** (detail of E) indicate disarticulation cut marks. Indetermined fragmented bone of Cetacea with an arrow indicating a group of defleshing pattern cut marks (**G**). Remains are from CAI (A and B), FI2 (C and E), and GUA (G). Scale bars: 1 cm.

Besides their role in the diet, some animals had symbolic funerary value for sambaqui builders (Klokler, 2016). Magellanic penguins, for example, were an important

food resource, probably because, among sea birds, they are the easiest to catch and have high meat yields (Cruz, 2006). But these sea birds also had other cultural functions: Cardoso et al. (2014) noted the presence of *Spheniscus magellanicus* bones near five of the eight burials of Galheta IV and hypothesised that they could represent food offerings, speculating that the figure of the bird could be linked to the journey of the dead or be a clan symbol. Avian elements are also found associated with burials in other sambaquis in Santa Catarina, such as Jabuticabeira II and Cabeçuda (Klokler, 2016). As we identified that 36.84% (7 of 19) of the remains of *S. magellanicus* from CAI were located near burials, we hypothesise that these animals probably also had a funerary value for the CAI builders.

Artefacts

Besides being used for food consumption and ritualistic feasts, animals were important sources of raw material for the manufacture of artefacts, although modified bones for making artefacts are not as abundant as lithic materials in most archaeological sites of Brazil (Mingatos and Okumura, 2020). Perhaps because they are infrequent in samples in relation to other types of tools, in the Brazilian Archaeology literature there is no manual for the identification of bone artefacts, as there is for lithic (Prous, 1986; Bueno and Isnardis, 2007; Martins and Kashimoto, 2014) and ceramic (La Silva and Brochado, 1989; Amorim, 2010; Kashimoto and Martins, 2019) ones. Studies that can contribute to the identification of sambaquis artefacts propose a classification based on morphology and raw material (e.g. Gaspar, 2003) and many terminologies denote the role of artefacts (eg. Beck, 1972; Rohr, 1977) without further analysis to confirm the function of the pieces to the sambaqui builders. Traceological and experimental analyses for tools, for example, are extremely recent for sambaquis (Simon and Lessa, 2021; Gilson et al., 2021). The absence of a bone toolkit that proposes an artefactual nomenclature based on a multi-analysis approach of the pieces limited a more in-depth classification of the pieces we registered, and performing traceological (Mansur et al., 2014) and experimental analyses (Gilson and Lessa, 2021) is well beyond the aims of the present research. We thus chose here to focus mainly on the anatomical and taxonomic identification of these remains and hypothesise on the function of objects based on their similarity to those described in the literature, which also used criteria such as shapes of objects, the manufacturing techniques, and raw materials for bone industry classification.

Previous studies have described some bone artefacts in the sambaquis GUB (Andreatta and Menezes, 1975) and ITA (Gazzeano et al., 1989; Thaddeu, 1995), but the animals used to make these tools were not identified. Most artefacts we identified were bevelled objects (72) made from ribs of baleen whales and indetermined cetaceans. There are not many records of these items made from cetaceans in southern sambaquis, but two examples include two and 14 spatulas in the Praia das Laranjeiras site in SC and ITA, respectively (Rohr, 1984; Gazzeano et al., 1989). Not having many mentions of this type of artefact in sambaquis does not mean that they were not present, but as cetacean axial bones are extremely fragile because of their low mineral content, they are easily fragmented (Murray, 2008; Buckley et al., 2014), rendering their identification difficult.

Cetacean bones modified by artefact manufacturing are very abundant in the sambaquis we studied, amounting to 64.57% of artefacts. Tiburtius et al. (1949) already pointed out that sambaqui fishermen-gatherer-hunters used cetacean skeletons extensively in the bone industry, mainly the large ribs and tympanic bullae. Ribs were probably the most used element to make bevelled and piercing objects (Figure 11) recorded in our study, due to their size, shape, and low relative density of bone tissue (Borella, 2004; Margaris, 2014), enabling easy polishing, and bevelled cutters made from whale ribs in sambaqui Macedo in PR have already been recorded (Hurt and Blasé, 1960). On the other hand, the tympanic bullae are more mineralized with ivory-like properties (Tiburtius et al., 1954), being easy to chip but difficult to polish, and were used to make bevelled and perforated objects, as well as spheres (Figure 11). Tiburtius et al. (1954) recorded ten objects made from tympanic bullae accompanying human burials in sambaqui Rio Pinheiros (SC), suggesting a probable use in feasts and funeral rituals as adornments or amulets. Chmyz et al. (2003) and Orssich (1977), when studying the sambaquis Matinhos and Araújo II, respectively, both in PR, also recorded perforated discs made of whale tympanic bullae associated with burials. Thus, although it is not possible to assert whether the artefacts registered in the sambaquis we studied were found in burial pits or not, it is possible that they were also used as funerary furniture.

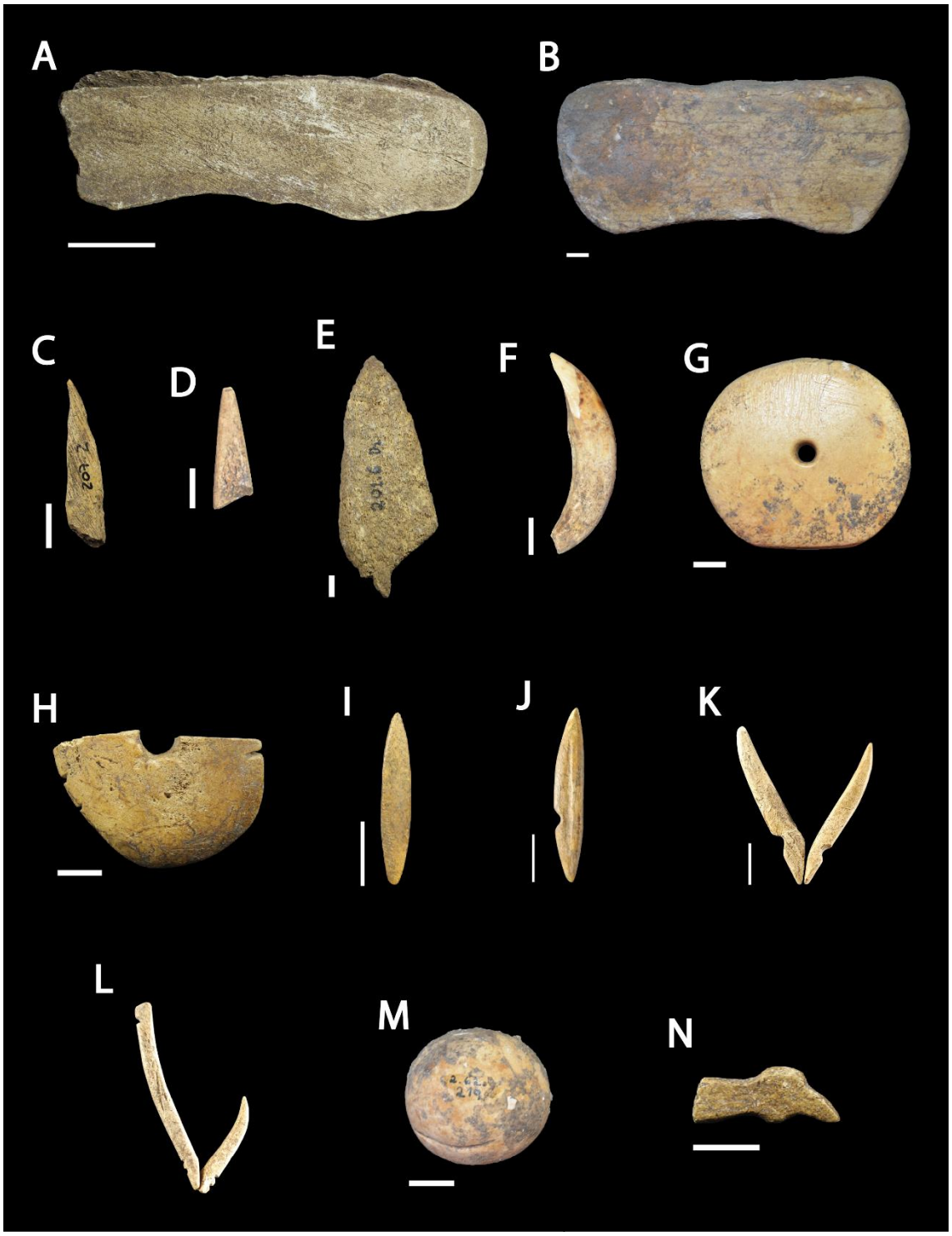

Figure 11. Bone artefacts registered in the sambaquis. **A** and **B**: bevelled objects made from Mysticeti indet. (ITA and GUB, respectively); **C** and **D**: piercing objects made from Mammalia indet. (ITA and T51, respectively); **E**: piercing object made from Cetacea indet. (ITA); **F**: piercing object made from canine tooth of Tayassuidae indet. (GUB); **G**: perforated object made from tympanic bulla of Mysticeti indet. (GUA); **H**: grooved perforated object made from tympanic bulla of Mysticeti indet. (ITA); **I**: double point hook made from Mammalia indet. (ITA); **J**: grooved double point hook made from Mammalia indet. (ITA); **K**: symmetric composite hook made from Mammalia indet. (ITA); **L**: asymmetric composite hook made from Mammalia indet. (ITA); **M**: sphere

made from tympanic bulla of Mysticeti indet. (GUB); **N**: aviform zoomorphic item made from Cetacea indet. (ITA). Scale bars: 1 cm.

Cetacean bones were also used to make a bird-like zoomorphic object registered in ITA (Figure 11). Aviform objects made from bones have been recorded before: a sculpture resembling an albatross made at the tip of a bone stick was found in the sambaqui Matinhos, PR (Chmyz et al., 2003), and another one, with a bird carved at the tip, in the sambaqui Conquista, in SC (Tiburtius, 1966). Prous (2018) recorded bone sculptures resembling birds in other sambaquis of Joinville (SC) and PR, also sculpted at the tip of bone sticks, and identified them as propellants. We hypothesise that the zoomorphic object found in ITA could correspond to an ornate hook of a spearthrower, which could have been used in everyday hunting practices or even as a mortuary offering and cerimonial symbol, since some similar artefacts were found associated with burials in sambaquis of Santa Catarina (Ferreira et al., 2018).

Bones of terrestrial mammals were raw material for making tools such as hooks, points, and burins. We recorded composite hooks probably made from long bones, a novel record in sambaquis. However, as with bevelled items, the absence of record in the literature does not mean that they did not exist; it is possible that researchers have not identified the loose parts, confusing them with piercing objects or even adornment pieces (Thaddeu, 1995). Hooks already recorded in other sites were made of a single piece and were curved (Tiburtius and Bigarella, 1953; Beck et al., 1970; Rohr, 1984; Bryan, 1993).

We categorized composite hooks in two types: symmetric and asymmetric (Figure 11), the latter has a larger piece (stem) and a smaller one (point). Both have grooves where the sambaqui builders could have tied the parts of the hook, probably with vegetal fibre, a plant element that has already been recorded in the sambaquis Cubatão I (Peixe et al., 2007; Bandeira et al., 2009) and Espinheiros II (Afonso and De Blasis, 1994) in SC, but is underdocumented because it is difficult to preserve (Bandeira, 1992).

Similar to the study by Beck et al. (1970) on the bone industry in sambaqui Enseada I in SC, here the modified mammalian teeth were few in number: only two lower canine teeth of Tayassuidae indet. were registered as a piercing object (Figure 11). According to Tiburtius et al. (1954), who recorded similar modified *Dicotyles tajacu* (Linnaeus, 1758) canine teeth in sambaqui Rio Pinheiros in SC, these artefacts could perform several functions such as cutting, smoothing, scratching, and drilling.

We recorded another terrestrial mammal artefact in ITA, a perforated object made from a metatarsal of a lowland tapir (*Tapirus terrestris*, Figure 12). This artifact had already been noted by Thaddeu (1995), but it was not identified taxonomically and anatomically then. It is distinctive because items similar to pendants are usually made with teeth and not bone (Tiburtius, 1960). Tapirs might have had symbolic value for the sambaqui culture, as Prous (2018) recorded a tapir-like zoolith in the Rio Vermelho sambaqui in SC.

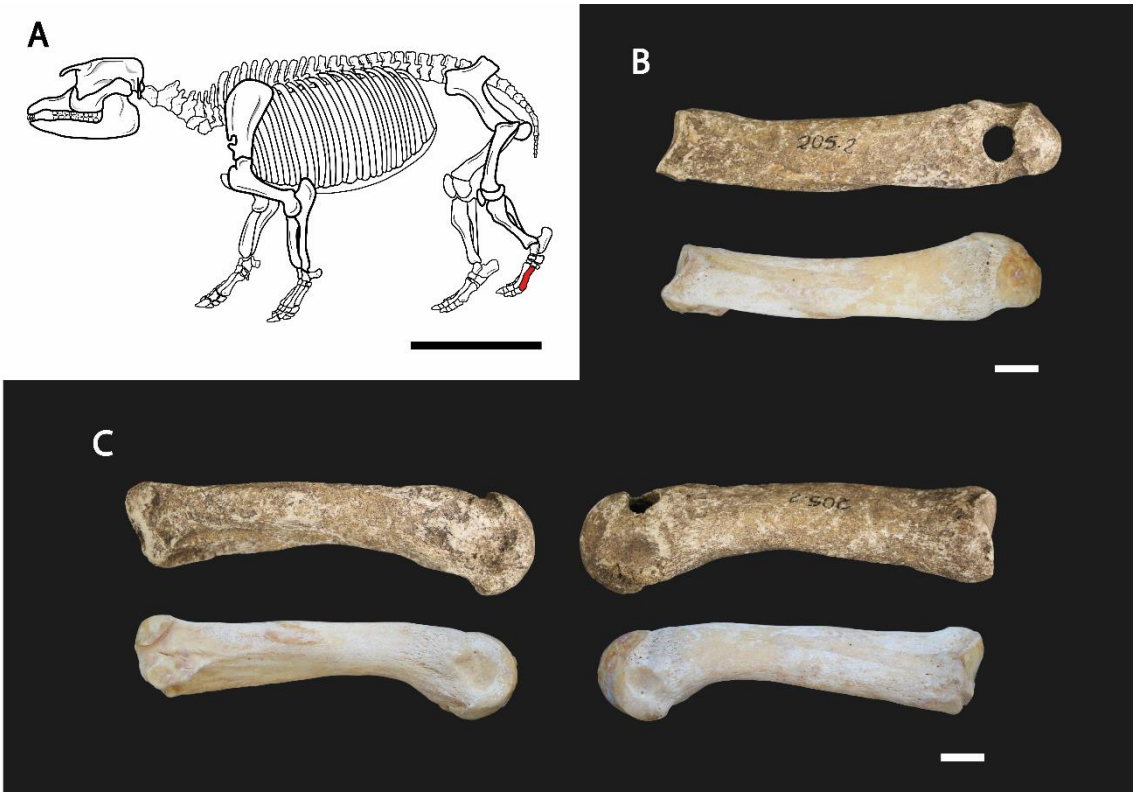

Figure 12. Perforated object made of *Tapirus terrestris* (ITA). Skeleton of tapir with IV left metatarsal in red (**A**). Comparison between the sambaqui artefact (top) and a IV left metatarsal of modern tapir deposited in the Mammalogy Collection of Universidade Federal do Espírito Santo, Brazil (bottom) in posterior (**B**) and right and left, respectively, lateral (**C**) views. Scale bars: 40 cm (A) and 1 cm (B and C). Skeletal illustration adapted from Haowen et al. (2002) by R. Buchmann.

CONCLUSIONS

Through a multi-approach analysis (anatomical and taxonomic identification, identification of cutting, burning and modification marks for artefacts confection, biomass estimation, and representation of skeletal parts), we documented the importance of marine tetrapod fauna in cultural practices of sambaqui builders. Marine animals were

a preferred source among tetrapods for diet and for artefact manufacturing in the sambaquis of southern Brazil, especially mammals.

We present here the most complete data on human modification in tetrapod bones from sambaquis. Most of the identified bones are from marine fauna, such as whales, dolphins, fur seals, and Magellanic penguins. The biomass calculation revealed that, as expected, marine tetrapods had a higher participation in the diet of the sambaqui builders compared to terrestrial animals. However, the weight calculation suggests that the participation of tetrapods in the diet of fishermen-hunter-gatherers is not as relevant as that of fish, their major source of protein.

Cut marks were identified mainly on bones of otariids, cetaceans, and penguins. In some animals, like otariids, the processing of the carcass aimed at selecting meaty parts, thus fins were probably discarded due to their low yield of consumable protein. The burning marks were more frequent in the layers where bonfires were found, strongly suggesting the use of fire for cooking.

Bevelled objects were the most frequent tool in the sample. Most artefacts were made from cetacean bones, but terrestrial fauna was also used as raw material for artefact manufacturing, including previously unknown items for sambaquis: composite hooks and a bony, instead of a dental, perforated object.

Building upon previous studies, we hypothesise that the animals described here were used in routine practices (fishing, hunting, gathering, feeding, production of artefacts) and ceremonies (funeral rituals, feasts). However, the paucity of studies on osteological artefacts precludes more precise identifications of their use among sambaqui builders. Further studies will need to address this issue by testing current hypotheses that have been presented for these objects.

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CHAPTER THREE

Old but gold: checklist of tetrapods from sambaquis for the conservation of Atlantic Forest and coastal-marine fauna

Augusto Barros Mendes, Taissa Rodrigues

Abstract
The Atlantic Forest is one of the most important hotspots for the conservation of the planet's biodiversity. However, this biome faces drastic reductions in tetrapod populations due to several anthropic impacts resulting in several species being threatened. For better conservation and management measures of these animals, baselines (reference inventories of biodiversity) should include not only modern data but also past information for the establishment of a long-term temporal perspective. Thus, this work presents the first complete inventory of tetrapod fauna of sambaquis (shell mounds) in Brazil, Holocene archaeological sites present within the boundaries of that biome. From an extensive bibliographic survey and primary data, we inventoried 188 taxa from 89 sambaquis, 96 of which identified at species level. This checklist is a comprehensive inventory of Holocene tetrapod fauna from the southeast and south regions of Brazil and may improve the understanding of natural areas and species in a long-term perspective, thus being useful not only for archaeological studies, but also for ecological, evolutionary, and biogeographic research on conservation and management of tetrapod species from the Atlantic Forest.

Keywords: baselines; conservation and management; conservation archaeology; conservation zooarchaeology; faunal records; fishermen-gatherers-hunters; inventory; shell mounds; zooarchaeology

INTRODUCTION

The Atlantic Forest is a coastal biome that extends from Rio Grande do Sul to Ceará states in Brazil, with a great heterogeneity of phytophysiognomies, climates, and landscapes (Tabarelli et al., 2005; Ribeiro et al., 2009). Closely associated with this biome are coastal and marine ecosystems, such as restingas, mangroves, estuaries, reefs, and islands, which present an expressive number of species and have a strong relationship with the land environments (MMA, 2011; SOS Mata Atlântica/INPE, 2018). More than 70% of the Brazilian population lives in this domain, about 145 million inhabitants (Pinto et al., 2006; SOS Mata Atlântica, 2021), a factor that contrasts with the overwhelming biodiversity present in the biome and that has resulted in several anthropogenic threats to species, especially to endemic taxa. The Atlantic Forest is one of the most important

hotspots for biodiversity conservation on the planet (Myers et al., 2000; Mittermeier et al., 2005) for three reasons: its high levels of endemism, high species richness, and increasing threats to this already highly fragmented biome (Martini et al., 2007). About 9% of its forest fragments are protected by the federal government, which represents only 1% of its original area (Ribeiro et al., 2009) and for coastal and marine environments, about 25% of the area is currently under protection (Rocha et al. 2020, SOS Mata Atlântica, 2021).

The biodiversity of the Atlantic Forest can be translated into expressive numbers regarding its tetrapod fauna: it is home to 719 species of amphibians, 517 of reptiles, 1,025 of birds and 384 of mammals (Figueiredo et al., 2021), many of which are endemic to the biome and endangered. According to the most recent data from the Red Book of Endangered Brazilian Fauna (ICMBio, 2018), among the country's biomes the Atlantic Forest is the one with the highest number of threatened continental mammal species, 53 (about 52% from a total of 102 endangered in the country), 31 of which are endemic. The biome has 51 species of marine mammals, eight of which are considered threatened (ICMBio, 2018). Regarding birds, in Brazil the biome with the largest number of threatened taxa is again the Atlantic Forest, which presents 120 taxa at some level of threat (about 51.3% of the threatened Brazilian birds) (ICMBio, 2018). The Atlantic Forest also figures as the biome with the largest number of threatened reptile and amphibian taxa, with, respectively, 39 (49% of the total threatened reptile species in Brazil) and 37 (90.2% of the total amphibian species threatened) species (ICMBio, 2018).

This disturbing pattern highlights the constant need for the establishment of baselines to support conservation projects. Baselines are reference inventories of biodiversity that directly assess the species composition of a given location at a given space and time. The data they generate are important in decision-making regarding the conservation and management of natural areas and, especially, their threatened species (Silveira et al., 2010; Mendes et al., 2018). In particular, the establishment of baselines is essential for the conservation of tetrapods in the Atlantic Forest, since a large number of their species is threatened by anthropic impacts such as deforestation, exploratory hunting, habitat fragmentation and loss, overfishing, pollution, and the introduction of exotic species (Costa et al., 2005; Tabarelli et al., 2005; Ribeiro et al., 2009; Graipel et al., 2017; Rossa-Feres et al., 2017).

In order to develop more complete inventories and management plans, a long-term temporal perspective should be adopted in data collection because it acknowledges

the fact that human changes in natural environments, including the Atlantic Forest, have been occurring for thousands of years, long before the emergence of historical records (Lyman, 2015; Roberts et al., 2017). Thus, the study of archaeological sites such as sambaquis (Brazilian shell mounds), extremely common in the south and southern coastal regions of Brazil, can provide valuable contributions to conservation debates in the Atlantic Forest by offering such a long-term temporal perspective, whose adoption comes as a response to an increasing demand for a multidisciplinary approach in conservation debates (Fossile et al., 2020; Mendes et al., 2020). Data on past species richness are important for establishing more complete and accurate baselines, and should thus include fossil and subfossil records, which should not be overlooked in ecological studies (Froyd and Willis, 2008; Fossile et al., 2020; Mendes et al., 2020). This research presents a conservation archaeology—here specifically referred to as conservation zooarchaeology—approach, playing a similar role to conservation palaeobiology, where palaeoecological data provide essential input for understanding recent extinctions, preventing future extinctions, and developing conservation strategies (Kosnik and Kowalewski, 2016; Tyler and Schneider, 2018). Therefore, we aimed to analyse zooarchaeological remains of sambaquis of the Brazilian coast to build an inventory of prehistoric fauna that can improve the accuracy and completeness of reference inventories and to establish a historical perspective of biodiversity, underpinning more appropriate and effective future management measures to mitigate the current threat to tetrapod populations.

METHODS

The inventory was constructed with primary and secondary data. Primary data was presented in Chapter 1 of this thesis. Secondary data was collected from an extensive bibliographical survey of the libraries of universities and institutions with archaeological collections from sites along the southeast and south coasts of Brazil and from online databases (e.g. Scientific Electronic Library Online-SciELO and Google Scholar; see Supplementary Table 7). Using the boolean operators “AND” and “OR” to further refine the results (Pizzani et al., 2012), we searched for the combination of the keywords “sambaqui”, “shell mound”, “shell midden”, and “zooarchaeology” with the terms “Brazil”, “fauna”, “tetrapod”, “mammal”, “bird”, “reptile”, and “amphibian”, in English and in Portuguese. We then only kept on the inventory data from (i) scientific articles and books, PhD and MSc dissertations, and technical reports (undergraduate dissertations and

abstracts published in proceedings of scientific events were not included because they generally present only a preliminary assessment of the fauna, often without confirming the identification); and (ii) faunal records using scientific names (records with only common names were excluded in order to focus on research that aimed to taxonomically identify zooarchaeological remains, thus avoiding misclassifications).

The resulting inventory was then refined by (i) updating the taxonomy with the aid of the *Integrated Taxonomic Information System* (ITIS, 2021); (ii) critically assessing the biogeographic distribution of species in the sampled area, using the *Encyclopedia of Life* (Parr et al., 2014)—impossibilities or low chances of occurrence were excluded from the inventory [e.g. *Nasua narica* (Linnaeus, 1766)]—; (iii) exclusion of invasive alien fauna [e.g. *Rattus norvegicus* (Berkenhout, 1769) and *Capra* sp. Linnaeus, 1758]; (iv) and constraining to genus level species whose exact identification was not made (e.g. *Hydromedusa* cf. *tectifera* was considered *Hydromedusa* sp. Wagler 1830). All these procedures were adopted to build a more reliable list of tetrapods from sambaquis.

The list of taxa was then analysed following Mendes et al. (2018). We calculated the absolute and relative taxonomic richness and absolute and relative frequencies of occurrence. Absolute taxonomic richness is the number of taxa present at a sampled sambaqui, while the relative taxonomic richness is the ratio between that number and the total number of taxa from all analysed sambaquis. Similarly, the absolute frequency of occurrence is the number of sites at which a specific taxon occurs, and the relative frequency is the ratio between that number and the total number of analysed sites.

Habitat data on each inventoried species were retrieved from the *Encyclopedia of Life* (Parr et al., 2014). Habitats were categorised into coastal (coastal plain, coastal, estuarine, lagoon), marine, freshwater (river, riverbank), forest, grassland, wetland (marsh, swamp), and highland (mountain) (Marques and Grelles, 2021). The conservation status of species was collected from the *Brazilian Red List of Threatened Species* (ICMBio, 2018) and the International Union for Conservation of Nature Red List *of Threatened Species* (IUCN, 2021). Vulnerable (VU), endangered (EN), and critically endangered (CR) species were considered as threatened.

RESULTS

The inventory contains information on 89 sambaquis from 38 cities along the three coastal states of the Southeast region of Brazil (Espírito Santo - ES, Rio de Janeiro - RJ, and São Paulo - SP) and the three states of the South region (Paraná - PR, Santa Catarina - SC, and Rio Grande do Sul - RS, Figure 13). RJ and SC were the two states with more sambaquis recorded (33; 37.08% and 23; 25.84%, respectively), while ES and PR had the lowest numbers of sites (6; 6.74% and 7; 7.86%, respectively) (Table 7). The city with the highest number of sambaquis (7 sites; 7.86%) was Saquarema in the state of RJ. From the 89 sambaquis, 73 had conventional radiocarbon age recorded (^{14}C years BP; before present, by convention prior to 1950) and most of them were built and occupied during the period defined by Cohen et al. (2013) as Meghalayan (Figure 14).

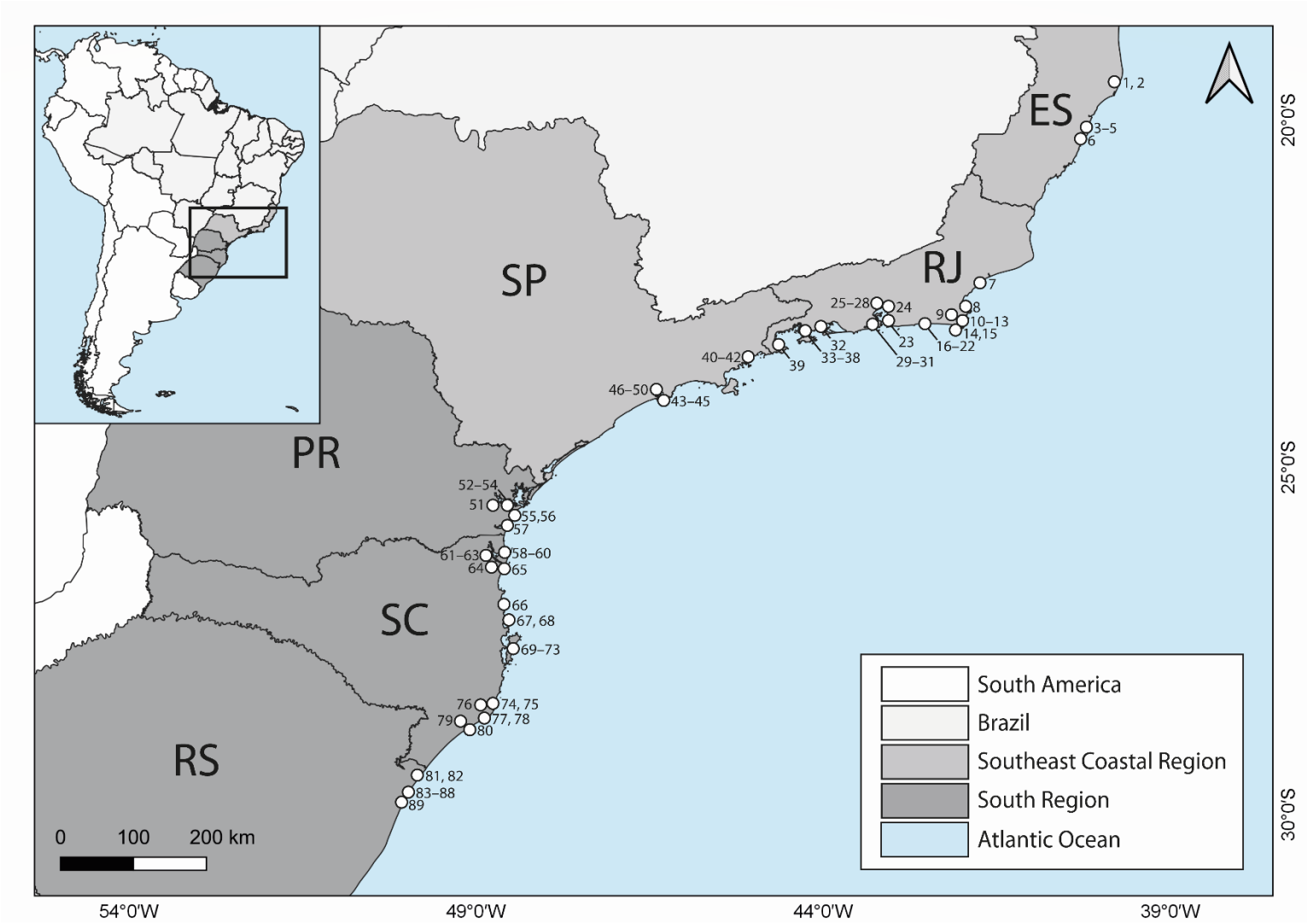

Figure 13. Map with locations of inventoried sambaquis. See Table 7 for sites' codes.

Table 7. Sambaquis inventoried with absolute (TR) and relative (Relative TR) taxonomic richness and their respective references from the literature.

Location (City, State)	Sambaqui	Code	TR	Relative TR	References
Linhares, ES	Lagoa Bonita 17	1	22	0.117	Costa, 2019
	Suruaca 20	2	21	0.112	Costa, 2019
Serra, ES	Jacuhy	3	9	0.048	Rhea Estudos e Projetos, 2008
	Morro	4	9	0.048	Rhea Estudos e Projetos, 2008
	Péricles II	5	7	0.037	Rhea Estudos e Projetos, 2009
Vitória, ES	Campus 2	6	4	0.021	Perota, 1972
Macaé, RJ	Ilha de Santana	7	16	0.085	Lima, 1991
Armação de Búzios, RJ	Geribá II	8	3	0.016	Gaspar 1991; Gaspar, 2003
São Pedro da Aldeia, RJ	Corondó	9	27	0.144	Carvalho, 1984; Gaspar, 1991; Azevedo et al., 1981–1982; Gaspar, 1995-1996; Gaspar, 2003
Cabo Frio, RJ	Boca da Barra	10	7	0.037	Gaspar, 1991; Barbosa, 1999
	Forte	11	9	0.048	Kneip, 1977; Gaspar 1991; Gaspar, 1995–1996; Gaspar, 2003
	Meio	12	4	0.021	Gaspar, 1991; Gaspar, 2003
	Salina Peroano	13	6	0.032	Gaspar, 1991; Gaspar, 2003
Arraial do Cabo, RJ	Brejo do Mato I	14	1	0.005	Gaspar 1991; Gaspar, 2003
	Ponta da Cabeça	15	5	0.027	Gaspar 1991; Gaspar, 2003
Saquarema, RJ	Beirada	16	30	0.160	Kneip et al., 1988; Kneip, 1994; Kneip et al., 1995; Magalhães et al., 2001
	Madressilva	17	11	0.059	Kneip, 1997; Magalhães et al., 2001
	Manitiba I	18	13	0.069	Magalhães et al., 2001
	Moa	19	28	0.149	Kneip, 1994; Kneip et al., 1995; Magalhães et al., 2001
	Pontinha	20	24	0.128	Kneip, 1994; Kneip et al., 1995; Magalhães et al., 2001
	Saco	21	2	0.011	Kneip, 1997; Magalhães et al., 2001
	Saquarema	22	13	0.069	Kneip, 1994; Magalhães et al., 2001
Niterói, RJ	Camboinhas	23	4	0.021	Souza Cunha et al., 1981; Souza Cunha et al., 1986
Guapimirim, RJ	Arapuan	24	6	0.032	Bezerra, 1995

Magé, RJ	Amourins	25	3	0.016	Pinto, 2013
	Rio das Pedrinhas	26	8	0.043	Mendonça de Souza and Mendonça de Souza, 1981–1982
	Saracuruna	27	3	0.016	Mello and Mendonça de Souza, 1977; Mendonça de Souza, 1981
	Sernambetiba	28	5	0.027	Beltrão et al., 1981–1982
Rio de Janeiro, RJ	Galeão	29	12	0.064	Lopes et al., 2022
	Embratel	30	5	0.027	Kneip et al., 1984a; Kneip et al., 1984b
	Zé Espinho	31	9	0.048	Kneip et al., 1986; Vogel, 1987
Mangaratiba, RJ	Guaíba	32	1	0.005	Heredia et al., 1984
Angra dos Reis, RJ	Algodão	33	20	0.106	Lima, 1991
	Bigode	34	7	0.037	Lima, 1991
	Caieira I	35	4	0.021	Lima, 1991
	Caieira II	36	14	0.074	Lima, 1991
	Major	37	6	0.032	Lima, 1991
	Peri	38	13	0.069	Lima, 1991
Paraty, RJ	Trindade III	39	3	0.016	Mendonça de Souza, 1981
Ubatuba, SP	Couves 1	40	4	0.021	Anenomori, 2005
	Mar Virado	41	15	0.080	Nishida, 2001; Anenomori, 2005
	Tenório	42	15	0.080	Garcia, 1972; Anenomori, 2005
Guarujá, SP	Buracão	43	46	0.245	Duarte, 1968; Borges, 2015
	Maratuá	44	36	0.191	Duarte, 1968; Borges, 2015
	Mar Casado	45	72	0.383	Duarte, 1968; Borges, 2015
Cubatão, SP	COSIPA 1	46	13	0.069	Figuti, 1993
	COSIPA 2	47	11	0.059	Figuti, 1993
	COSIPA 3	48	1	0.005	Figuti, 1989
	COSIPA 4	49	17	0.090	Figuti, 1993
	Piaçaguera	50	37	0.197	Garcia, 1972; Garcia and Uchôa, 1980; Borges, 2015
Morretes, PR	Ramal	51	1	0.005	Rauth, 1971
Paranaguá, PR	Ilha das Pedras	52	11	0.059	Ramos Júnior, 2014
	Macedo	53	1	0.005	Hurt and Blase, 1960
	Toral 51	54	10	0.053	This research

Pontal do Paraná, PR	Guaraguaçu A	55	8	0.043	This research
	Guaraguaçu B	56	16	0.085	This research
Matinhos, PR	Matinhos	57	1	0.005	Chmyz et al., 2003
São Francisco do Sul, SC	Bupeva II	58	7	0.037	Bandeira, 2004; Bandeira, 2015
	Enseada I	59	25	0.133	Bandeira, 1992
	Forte Marechal Luz	60	12	0.064	Bryan, 1993
Joinville, SC	Espinheiros II	61	3	0.016	Castilho, 2008
	Ilha dos Espinheiros II	62	15	0.080	This research
	Morro do Ouro	63	5	0.027	Beck, 1972; Castilho, 2008
Araquari, SC	Rio Pinheiros	64	7	0.037	Tiburtius et al., 1954
Balneário Barra do Sul, SC	Conquista	65	4	0.021	Tiburtius, 1966
Balneário Camboriú, SC	Laranjeiras I	66	14	0.074	Schmitz and Bitencourt, 1996a; Castilho, 2008
Bombinhas, SC	Papagaio	67	21	0.112	Pavei et al., 2015
	Rua 13	68	6	0.032	Ricken et al., 2010
Florianópolis, SC	Armação do Sul	69	17	0.090	Schmitz et al., 1992; Castilho, 2008
	Pântano do Sul	70	25	0.133	Schmitz and Bitencourt, 1996b; Castilho, 2008
	Porto do Rio Vermelho	71	13	0.069	Castilho and Simões-Lopes, 2001; Castilho, 2008
	Porto do Rio Vermelho II	72	1	0.005	Castilho and Simões-Lopes, 2005
	Rio Lessa	73	1	0.005	Beck, 1972
Laguna, SC	Caieira	74	17	0.090	This research
	Cabeçuda	75	1	0.005	Pinto, 2018
Tubarão, SC	Congonhas I	76	19	0.101	This research
Jaguaruna, SC	Encantada III	77	3	0.016	Kloker et al., 2010
	Jabuticabeira II	78	16	0.085	Kloker et al., 2010
Içara, SC	Içara 06	79	27	0.144	Rosa, 2006; Teixeira, 2006
Balneário Rincão, SC	Lagoa do Freitas	80	14	0.074	Santos et al., 2018; Pavei et al., 2019; Pavei, 2019
Torres, RS	Itapeva	81	21	0.112	Jacobus and Gil, 1987; Gazzeano et al., 1989; Rosa, 1996; This research
	Recreio	82	4	0.021	This research
Arroio do Sal, RS	Arroio Seco V	83	7	0.037	Ferrasso, 2018; Ferraso et al., 2010; Ferrasso et al., 2021
	Figueira II	84	12	0.064	Ferrasso, 2018; Ferrasso et al., 2021; This research

	Marambaia I	85	1	0.005	Ferrasso, 2018; Ferrasso et al., 2021
	Praia do Paraíso	86	7	0.037	Ricken et al., 2016
	Sereia do Mar	87	1	0.005	This research
	Serra Azul 2	88	1	0.005	Ferrasso, 2018; Ferrasso et al., 2021
Xangri-Lá, RS	Xangri-Lá	89	4	0.021	Ferrasso, 2018; Ferrasso et al., 2021

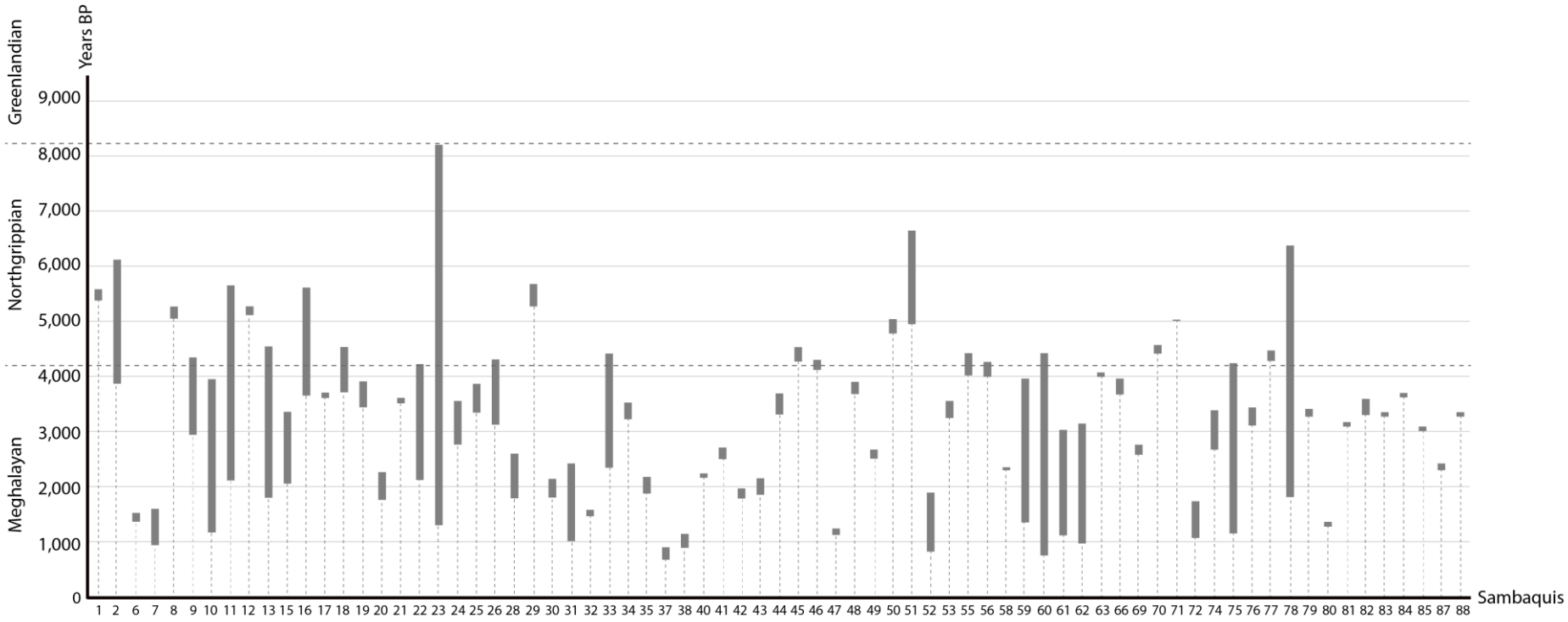

Figure 14. The conventional radiocarbon age (^{14}C years BP) of the 73 inventoried sambaquis from the Brazilian southeast and south regions. In the x axis are the sambaquis (codes defined at Table 7) and in the y axis are the ranges of ^{14}C radiocarbonic dating found in the literature. The different periods of the Holocene were defined by Cohen et al. (2013): Greenlandian (11,700–8,200 BP), Northgrippian (8,200–4,200 BP) and Meghalayan (4,200 BP–till present). See Supplementary Table 8 for datation of each sambaqui.

Initially, a total of 215 taxa were listed. After the refinement, 188 comprised the final inventory, 96 of which identified at the species level (51.06%): 55 mammals (57.29%), 33 birds (34.38%), 7 reptiles (7.29%), and one amphibian (1.04%) (Table 8). The sambaqui with the highest taxonomic richness was Mar Casado (Guarujá, SP), with 72 inventoried taxa and a relative taxonomic richness value of 0.383 (Table 7).

Cuniculus paca (Linnaeus, 1766) and *Tapirus terrestris* (Linnaeus, 1758) had the highest frequencies of occurrence, being found in 42 (relative frequency = 0.472) and 37 (relative frequency = 0.416) sambaquis, respectively (Table 8). The inventoried species occupy a wide range of habitats and most of them (53.12%) are currently at some level of concern regarding their conservation status (threatened, near threatened, and least concern with decreasing population; see Supplementary Table 9 for conservation status of each species according to IUCN and ICMBio) (Figure 15).

Table 8. Tetrapods from sambaquis in the southeast and south regions of Brazil with their absolute (F) and relative (Relative F) frequencies of occurrence and the archaeological sites in which they were recorded. The codes representing the sambaquis are defined in Table 7.

	Taxon	Common name / Brazilian common name	F	Relative F	Sambaquis
Mammals					
	Mammalia Linnaeus, 1758 indet.	Mammal / Mamífero	30	0.337	1, 2, 3, 4, 5, 10, 25, 43, 44, 50, 52, 54, 55, 56, 58, 62, 67, 68, 71, 74, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85
	Didelphidae Gray, 1821 indet.	Didelphid / Didelfídeo	7	0.079	3, 4, 13, 22, 29, 79, 80
	Chironectes minimus (Zimmermann, 1980)	Water opossum / Cuíca-d'água	1	0.011	45
	Didelphis sp. Linnaeus, 1758	Opossum / Gambá	20	0.225	1, 2, 9, 10, 28, 33, 34, 36, 37, 38, 42, 46, 47, 49, 50, 59, 62, 74, 79, 81
	Didelphis aurita Wied-Neuwied, 1826	Brazilian common opossum / Gambá-de-orelha-preta	4	0.045	6, 43, 45, 50
	Didelphis marsupialis Linnaeus, 1758	Common opossum / Gambá-comum	8	0.090	1, 16, 17, 18, 19, 20, 31, 41
	Lutreolina crassicaudata (Desmarest, 1804)	Little water opossum / Cuíca-da-cauda-grossa	1	0.011	79
	Marmosa sp. Gray, 1821	Mouse opossum / Cuíca	1	0.011	11
	Philander opossum (Linnaeus, 1758)	Gray four-eyed opossum / Cuíca-verdadeira	3	0.034	33, 43, 45
	Xenarthra Cope, 1889 indet.	Xenarthran / Xenartro	2	0.022	3, 86
	Dasypodidae Gray, 1821 indet.	Armadillo / Tatu	17	0.191	1, 2, 10, 13, 16, 19, 20, 40, 41, 46, 49, 56, 62, 66, 67, 75, 86
	Cabassous unicinctus (Linnaeus, 1758)	Southern naked-tailed armadillo / Tatu-de-rabo-mole	1	0.011	34
	Dasypus sp. Linnaeus, 1758	Armadillo / Tatu	10	0.112	9, 12, 31, 33, 35, 36, 37, 38, 69, 80
	Dasypus septemcinctus Linnaeus, 1758	Brazilian lesser long-nosed armadillo / Tatuí	1	0.011	1

Dasypus novemcinctus Linnaeus, 1758	Nine-banded armadillo / Tatu-galinha	9	0.101	42, 43, 44, 45, 50, 58, 59, 78, 79
Euphractus sexcinctus (Linnaeus, 1758)	Six-banded armadillo / Tatu-peba	2	0.022	78, 79
Tamandua tetradactyla (Linnaeus, 1758)	Southern tamandua / Tamanduá-mirim	3	0.034	35, 36, 59
Bradypus sp. Linnaeus, 1758	Three-toed sloths / Preguiça	2	0.022	41, 44
Primates Linnaeus, 1758 indet.	Primate / Primata	6	0.067	1, 4, 8, 9, 24, 67
Alouatta sp. Lacépède, 1799	Howler monkey / Bugio	14	0.157	1, 7, 9, 27, 42, 46, 47, 48, 49, 50, 62, 66, 78, 81
Alouatta guariba (Humboldt, 1812)	Southern brown howler monkey / Bugio-ruivo	12	0.135	11, 16, 19, 20, 33, 34, 36, 38, 43, 44, 45, 50
Brachyteles arachnoides (É. Geoffroy Saint-Hilaire, 1806)	Southern muriqui / Muriqui	1	0.011	33
Callithrix sp. Erxleben, 1777	Marmoset / Sagui	3	0.034	1, 2, 9
Sapajus sp. Kerr, 1792	Capuchin monkey / Macaco-prego	7	0.079	13, 17, 33, 34, 36, 43, 50
Lagomorpha Brandt, 1855 indet.	Lagomorph / Lagomorfo	1	0.011	9
Sylvilagus brasiliensis (Linnaeus, 1758)	Brazilian cottontail / Coelho-silvestre	5	0.056	16, 18, 19, 20, 22
Rodentia Bowdich, 1821 indet.	Rodent / Roedor	13	0.146	1, 2, 3, 4, 5, 25, 43, 44, 67, 68, 79, 80, 89
Caviidae Fischer de Waldheim, 1817 indet.	Caviid / Cavídeo	1	0.011	2
Cavia sp. Pallas, 1766	Guinea pig / Preá	11	0.124	1, 2, 7, 9, 16, 26, 38, 46, 47, 49, 59
Cavia aperea Erxleben, 1777	Brazilian Guinea pig / Preá	6	0.067	42, 43, 44, 45, 50, 65
Cavia fulgida Wagler, 1831	Shiny Guinea pig / Preá	6	0.067	16, 17, 18, 19, 20, 22
Hydrochoerus hydrochaeris (Linnaeus, 1766)	Capybara / Capivara	33	0.371	6, 9, 19, 26, 33, 38, 41, 43, 44, 45, 46, 47, 50, 52, 56, 57, 58, 59, 60, 62, 64, 65, 66, 67, 69, 70, 71, 72, 76, 78, 79, 80, 81
Cricetidae Fischer, 1817 indet.	Cricetid / Cricetídeo	8	0.090	33, 41, 43, 44, 45, 50, 59, 80

Sigmodontinae Wagner, 1843 indet.	Sigmodontines / Sigmodontes	1	0.011	29
Holochilus sp. Brandt, 1835	Marsh rat / Rato-d'água	1	0.011	80
Holochilus brasiliensis (Desmarest, 1819)	Brazilian marsh rat / Rato-d'água	1	0.011	30
Nectomys sp. Peters, 1861	Water rat / Rato-d'água	2	0.022	16, 20
Oligoryzomys sp. Bangs, 1900	Pygmy rice rat / Rato-da-árvore	1	0.011	2
Ctenomys sp. Blainville, 1826	Tuco-tuco / Tuco-tuco	1	0.011	79
Ctenomys minutus Nehring, 1887	Tiny tuco-tuco / Tuco-tuco	1	0.011	80
Cuniculus paca (Linnaeus, 1766)	Lowland paca / Paca	42	0.472	2, 6, 7, 8, 9, 14, 17, 18, 19, 20, 22, 24, 28, 29, 33, 34, 36, 37, 38, 41, 42, 43, 44, 45, 46, 47, 49, 50, 54, 56, 58, 59, 60, 62, 64, 65, 66, 67, 69, 70, 78, 79
Dasyprocta sp. Illiger, 1811	Agouti / Cutia	11	0.124	1, 2, 33, 34, 35, 36, 37, 38, 41, 64, 65
Dasyprocta azarae Lichtenstein, 1823	Azara's agouti / Cutia	4	0.045	59, 66, 70, 81
Dasyprocta leporina (Linnaeus, 1758)	Red-rumped agouti / Cutia	11	0.124	13, 26, 39, 41, 42, 43, 44, 45, 49, 50, 60
Myocastor coypus (Molina, 1782)	Coypu / Ratão-do-banhado	3	0.034	69, 78, 81
Phyllomys pattoni Emmons, Leite, Kock and Costa, 2002	Rusty-sided Atlantic tree-rat / Rato-da-árvore	1	0.011	2
Trinomys sp. Thomas, 1921	Atlantic spiny rat / Rato-de-espinho	2	0.022	1, 2
Erethizontidae Bonaparte, 1845 indet.	Erethizontid / Eretizontídeo	1	0.011	78
Coendou sp. Lacépède, 1799	Prehensile-tailed porcupine / Ouriço-cacheiro	1	0.011	43
Muridae Illiger, 1811 indet.	Murid / Murídeo	1	0.011	41
Carnivora Bowdich, 1821 indet.	Carnivoran / Carnívoro	5	0.056	3, 9, 43, 45, 67
Felidae Fischer de Waldheim, 1817 indet.	Felid / Felino	9	0.101	3, 4, 9, 11, 24, 26, 27, 49, 62
Leopardus pardalis (Linnaeus, 1758)	Ocelot / Jaguatirica	10	0.112	2, 33, 36, 44, 45, 59, 60, 64, 69, 70

Leopardus geoffroyi (d'Orbigny and Gervais, 1844)	Geoffroy's cat / Gato-do-mato-grande	1	0.011	70
Panthera onca (Linnaeus, 1758)	Jaguar / Onça-pintada	9	0.101	16, 18, 20, 21, 43, 44, 45, 50, 64
Puma concolor (Linnaeus, 1771)	Puma / Onça-parda	3	0.034	45, 60, 64
Puma yagouaroundi (É. Geoffroy Saint-Hilaire, 1803)	Jaguarundi / Jaguarundi	2	0.022	44, 45
Eira barbara (Linnaeus, 1758)	Tayra / Irara	1	0.011	33
Lontra longicaudis (Olfers, 1818)	Neotropical otter / Lontra	11	0.124	7, 33, 36, 43, 50, 66, 69, 70, 71, 79, 81
Otariidae Gray, 1825 indet.	Otariid / Otarídeo	15	0.169	10, 36, 45, 66, 67, 68, 74, 76, 79, 81, 83, 84, 85, 88, 89
Arctocephalus sp. Geoffroy Saint-Hilaire and Cuvier, 1826	Fur seal / Lobo-marinho	10	0.112	45, 54, 55, 59, 62, 74, 79, 81, 84, 89
Arctocephalus australis (Zimmermann, 1783)	South American fur seal / Lobo-marinho-sulamericano	4	0.045	69, 71, 84, 89
Arctocephalus tropicalis (J. E. Gray, 1872)	Subantarctic fur seal / Lobo-marinho-subantártico	1	0.011	71
Otaria flavescens (Shaw, 1800)	South American sea lion / Leão-marinho-do-sul	3	0.034	59, 74, 89
Procyonidae Gray, 1825 indet.	Procyonid / Procionídeo	1	0.011	67
Nasua nasua (Linnaeus, 1766)	South American coati / Quati	8	0.090	9, 33, 43, 44, 45, 50, 59, 74
Procyon cancrivorus (G. Cuvier, 1798)	South American raccoon / Mão-pelada	18	0.202	20, 24, 26, 29, 30, 31, 33, 38, 39, 42, 43, 44, 45, 49, 50, 60, 70, 79
Tapirus terrestris (Linnaeus, 1758)	Lowland tapir / Anta	37	0.416	1, 5, 6, 9, 11, 16, 18, 19, 20, 22, 28, 29, 30, 34, 37, 38, 43, 44, 45, 46, 49, 50, 52, 54, 56, 59, 60, 62, 67, 69, 70, 71, 76, 78, 79, 80, 81
Artiodactyla Owen, 1848 indet.	Artiodactyl / Artiodáctilo	2	0.022	67, 80
Cervidae Goldfuss, 1820 indet.	Cervid / Cervídeo	13	0.146	7, 9, 29, 56, 62, 66, 67, 69, 74, 79, 81, 84, 86

Blastocerus dichotomus (Illiger, 1815)	Marsh deer / Cervo-do-pantanal	2	0.022	70, 86
Mazama sp. Rafinesque, 1817	Brocket deer / Veado	14	0.157	1, 11, 12, 28, 42, 47, 49, 50, 52, 60, 74, 78, 79, 80
Mazama gouazoubira (G. Fischer [von Waldheim], 1814)	Gray brocket / Veado-catingueiro	8	0.090	16, 17, 18, 19, 20, 22, 44, 45
Mazama americana (Erxleben, 1777)	Red brocket / Veado-mateiro	12	0.135	16, 18, 19, 20, 33, 36, 38, 43, 44, 45, 50, 59
Ozotoceros bezoarticus (Linnaeus, 1758)	Pampas deer / Veado-campeiro	7	0.079	19, 20, 59, 70, 76, 79, 81
Tayassuidae Palmer, 1897 indet.	Peccary / Porco-do-mato	24	0.270	1, 9, 15, 41, 42, 43, 44, 45, 46, 47, 49, 50, 52, 54, 56, 58, 59, 67, 74, 76, 78, 80, 81, 82
Dicotyles tajacu (Linnaeus, 1758)	Collared peccary / Cateto	23	0.258	8, 13, 29, 31, 32, 33, 37, 38, 43, 44, 45, 50, 51, 53, 54, 59, 63, 64, 70, 73, 74, 76, 81
Tayassu pecari (Link, 1795)	White-lipped peccary / Queixada	22	0.247	7, 18, 19, 20, 26, 27, 36, 38, 39, 43, 44, 45, 50, 56, 59, 60, 66, 69, 70, 74, 76, 79
Cetacea Brisson, 1762 indet.	Cetacean / Cetáceo	12	0.135	28, 42, 55, 56, 58, 62, 67, 68, 74, 79, 81, 84
Mysticeti Flower, 1864 indet.	Baleen whale / Baleia	15	0.169	31, 44, 45, 55, 56, 61, 63, 66, 67, 70, 71, 74, 81, 82, 87
Eubalaena australis (Desmoulins, 1822)	Southern right whale / Baleia-franca-austral	7	0.079	23, 24, 55, 56, 69, 70, 81
Balaenopteridae Gray, 1864 indet.	Rorqual / Baleia	7	0.079	16, 17, 18, 19, 20, 22, 66
Balaenoptera sp. Lacépède, 1804	Rorqual / Baleia	6	0.067	40, 41, 61, 63, 70, 71
Megaptera novaeangliae (Borowski, 1781)	Humpback whale / Baleia-jubarte	2	0.022	23, 45
Odontoceti Flower, 1867 indet.	Toothed whale / Odontoceto	5	0.056	55, 56, 62, 74, 84
Delphinidae Gray, 1821 indet.	Oceanic dolphin / Golfinho	15	0.169	17, 30, 31, 45, 50, 52, 55, 59, 61, 63, 66, 69, 70, 74, 79
Delphinus delphis Linnaeus, 1758	Short-beaked common dolphin / Golfinho-comum-de-bico-curto	6	0.067	45, 59, 67, 69, 70, 71

	Globicephala macrorhynchus Gray, 1846	Short-finned pilot whale / Baleia-piloto-de-peitorais-curtas	1	0.011	44
	Globicephala melas (Traill, 1809)	Long-finned pilot whale / Baleia-piloto-de-peitorais-longas	1	0.011	7
	Orcinus orca (Linnaeus, 1758)	Killer whale / Orca	3	0.034	45, 50, 70
	Pseudorca crassidens (Owen, 1846)	False Killer Whale / Falsa-orca	1	0.011	70
	Sotalia sp. Gray, 1866	Dolphin / Boto	6	0.067	12, 15, 23, 31, 42, 50
	Sotalia fluviatilis (Gervais and Deville, 1853)	Tucuxi / Tucuxi	4	0.045	33, 44, 45, 50
	Sotalia guianensis (van Bénéden, 1864)	Guiana dolphin / Boto-cinza	8	0.090	16, 17, 18, 19, 20, 22, 40, 41
	Stenella sp. Gray, 1866	Dolphin / Golfinho	3	0.034	45, 69, 70
	Stenella frontalis (G. Cuvier, 1829)	Atlantic spotted dolphin / Boto-pintado-do-atlântico	3	0.034	69, 70, 71
	Steno bredanensis (G. Cuvier in Lesson, 1828)	Rough-toothed dolphin / Golfinho-de-dentes-rugosos	3	0.034	45, 70, 71
	Tursiops truncatus (Montagu, 1821)	Bottlenose dolphin / Golfinho-nariz-de-garrafa	8	0.090	45, 62, 63, 66, 69, 70, 71, 74
	Pontoporia blainvillei (Gervais and d'Orbigny, 1844)	La Plata dolphin / Toninha	12	0.135	33, 35, 36, 42, 43, 44, 45, 50, 66, 69, 70, 71
Birds	Aves Linnaeus, 1758 indet.	Bird / Ave	29	0.326	1, 2, 3, 4, 5, 10, 24, 25, 41, 42, 43, 44, 45, 50, 52, 54, 58, 62, 67, 68, 77, 78, 79, 80, 81, 82, 83, 84, 86
	Tinamidae Gray, 1840 indet.	Tinamid / Tinamídeo	5	0.056	2, 9, 43, 47, 50
	Tinamus solitarius (Vieillot, 1819)	Solitary tinamou / Macuco	1	0.011	45
	Anatidae Leach, 1820 indet.	Anatid / Anatídeo	6	0.067	43, 45, 46, 47, 49, 50
	Amazonetta brasiliensis (Gmelin, 1789)	Brazilian teal / Marreca-pé-vermelho	2	0.022	19, 20
	Cairina moschata (Linnaeus, 1758)	Muscovy duck / Pato-do-mato	4	0.045	20, 43, 44, 45
	Cracidae Rafinesque, 1815 indet.	Cracid / Cracídeo	2	0.022	43, 45
	Aburria jacutinga (Spix, 1825)	Black-fronted piping guan / Jacutinga	2	0.022	43, 45
	Crax sp. Linnaeus, 1758	Curassow / Mutum	3	0.034	43, 44, 45

Penelope sp. Merrem, 1786	Guan / Jacu	4	0.045	43, 44, 45, 76
Podicipedidae Bonaparte, 1831 indet.	Podicipedid / Podicipedídeo	1	0.011	9
Podilymbus podiceps (Linnaeus, 1758)	Pied-billed grebe / Mergulhão-caçador	2	0.022	16, 20
Spheniscidae Bonaparte, 1831 indet.	Penguin / Pinguim	3	0.034	13, 15, 78
Spheniscus magellanicus (Forster, 1781)	Magellanic penguin / Pinguim-de-magalhães	12	0.135	16, 19, 45, 52, 56, 59, 67, 70, 78, 80, 81, 84
Procellariiformes Fürbringer, 1888 indet.	Procellariform / Procellariforme	3	0.034	16, 67, 68
Diomedeidae Gray, 1840 indet.	Albatross / Albatroz	2	0.022	67, 83
Diomedea sp. Linnaeus, 1758	Albatross / Albatroz	2	0.022	44, 45
Thalassarche sp. L. Reichenbach, 1853	Albatross / Albatroz	5	0.056	16, 19, 45, 83, 84
Thalassarche melanophris (Temminck, 1828)	Black-browed albatross / Albatroz-de-sobrancelha	1	0.011	59
Procellariidae Leach, 1820 indet.	Procellariid / Procelarídeo	5	0.056	7, 9, 43, 45, 79
Calonectris borealis (Cory, 1881)	Cory's shearwater / Bobo-grande	1	0.011	45
Macronectes giganteus (Gmelin, 1789)	Southern giant petrel / Petrel-gigante	2	0.022	16, 19
Procellaria aequinoctialis Linnaeus, 1758	White-chinned petrel / Pardela-preta	3	0.034	16, 19, 45
Puffinus sp. *Brisson, 1760*	Shearwater / Pardela	2	0.022	76, 79
Puffinus gravis (O'Reilly, 1818)	Great shearwater / Pardela-de-barrete	1	0.011	19
Puffinus griseus (Gmelin, 1789)	Sooty shearwater / Pardela-escura	2	0.022	16, 45
Puffinus puffinus (Brunnich, 1764)	Manx shearwater / Pardela-sombria	1	0.011	16
Ciconia maguari (Gmelin, 1789)	Maguari stork / Maguari	2	0.022	16, 20
Jabiru mycteria (Lichtenstein, 1819)	Jabiru / Tuiuiú	1	0.011	19
Mycteria americana Linnaeus, 1758	Wood stork / Cabeça-seca	1	0.011	44
Fregata magnificens Mathews, 1914	Magnificent frigatebird / Tesourão	3	0.034	7, 15, 45
Sula sp. Brisson, 1760	Booby / Atobá	1	0.011	11
Sula leucogaster (Boddaert, 1783)	Brown booby / Atobá-pardo	3	0.034	7, 16, 76
Nannopterum brasilianus (Gmelin, 1789)	Neotropic cormorant / Biguá	2	0.022	16, 76

Anhinga anhinga (Linnaeus, 1766)	Anhinga / Biguatinga	1	0.011	20
Ardeidae Leach, 1820 indet.	Ardeid / Ardeídeo	5	0.056	1, 2, 46, 49, 78
Ardea sp. Linnaeus, 1758	Heron / Garça	1	0.011	76
Eudocimus ruber (Linnaeus, 1758)	Scarlet ibis / Guará	1	0.011	45
Cathartidae Lafresnaye, 1839 indet.	Cathartid / Catartídeo	2	0.022	76, 84
Cathartes aura (Linnaeus, 1758)	Turkey vulture / Urubu-de-cabeça-vermelha	1	0.011	16
Accipitridae Vigors, 1824 indet.	Accipitrid / Acipitrídeo	5	0.056	9, 45, 50, 54, 56
Buteogallus sp. Lesson, 1830	Hawk / Gavião	1	0.011	45
Buteogallus meridionalis (Latham, 1790)	Savanna hawk / Gavião-caboclo	1	0.011	16
Spizaetus sp. Vieillot, 1816	Hawk-eagle / Gavião	1	0.011	45
Urubitinga urubitinga (Gmelin, 1788)	Great black hawk / Gavião-preto	1	0.011	16
Rallidae Rafinesque, 1815 indet.	Rallid / Ralídeo	1	0.011	9
Aramides sp. Pucheran, 1845	Wood rail / Saracura	2	0.022	54, 76
Aramides cajaneus (Statius Muller, 1776)	Gray-necked wood rail / Saracura-de-três-potes	1	0.011	7
Aramides saracura (Spix, 1825)	Slaty-breasted wood rail / Saracura-do-mato	1	0.011	31
Rallus longirostris Boddaert, 1783	Mangrove rail / Saracura-matraca	1	0.011	50
Charadriidae Leach, 1820 indet.	Charadriid / Caradrídeo	2	0.022	76, 84
Jacana jacana (Linnaeus, 1766)	Wattled jacana / Jaçanã	1	0.011	45
Laridae Rafinesque, 1815 indet.	Larid / Larídeo	2	0.022	7, 76
Larus dominicanus Lichtenstein, 1823	Kelp gull / Gaivotão	1	0.011	76
Thalasseus sp. F. Boie, 1822	Tern / Trinta-réis	1	0.011	11
Thalasseus acuflavidus (Cabot, 1847)	Cabot’s tern / Trinta-réis-de-bando	1	0.011	19
Rynchops niger Linnaeus, 1758	Black skimmer / Talha-mar	1	0.011	76
Columbidae Leach, 1820 indet.	Columbid / Columbídeo	2	0.022	7, 9
Ramphastos sp. Linnaeus, 1758	Toucan / Tucano	1	0.011	50
Psittacidae Rafinesque, 1815 indet.	Psittacid / Psitacídeo	1	0.011	45

	Amazona sp. Lesson, 1830	Parrot / Papagaio	3	0.034	43, 45, 54
	Amazona aestiva (Linnaeus, 1758)	Turquoise-fronted parrot / Papagaio-verdadeiro	3	0.034	43, 44, 45
	Ara chloropterus Gray, 1859	Red-and-green macaw / Arara-vermelha	1	0.011	19
	Aratinga sp. Spix, 1824	Parakeet / Periquito	1	0.011	43
	Passeriformes Linnaeus, 1758 indet.	Passerine / Passeriforme	5	0.056	5, 7, 11, 30, 79
Reptiles	Reptilia Laurenti, 1768 indet.	Reptile / Réptil	5	0.056	3, 4, 24, 77, 78
	Testudines Batsch, 1788 indet.	Turtle / Tartaruga	8	0.090	3, 5, 9, 23, 52, 81, 83, 86
	Cheloniidae Oppel, 1811 indet.	Sea turtle / Tartaruga-marinha	27	0.303	1, 2, 7, 9, 10, 12, 15, 16, 18, 19, 20, 22, 26, 29, 40, 41, 42, 43, 44, 45, 46, 47, 49, 50, 56, 59, 60
	Caretta caretta (Linnaeus, 1758)	Loggerhead sea turtle / Tartaruga-marinha-comum	2	0.022	44, 45
	Chelonia mydas (Linnaeus, 1758)	Green sea turtle / Tartaruga-verde	5	0.056	31, 43, 45, 52, 62
	Eretmochelys imbricata (Linnaeus, 1766)	Hawksbill sea turtle / Tartaruga-de-pente	1	0.011	45
	Dermochelys coriacea (Vandelli, 1761)	Leatherback sea turtle / Tartaruga-de-couro	1	0.011	45
	Chelonoidis sp. Fitzinger, 1835	Tortoise / Jabuti	3	0.034	43, 44, 45
	Chelidae Gray, 1825 indet.	Austro-South American side-neck turtles / Cágado	5	0.056	9, 43, 45, 50, 78
	Hydromedusa sp. Wagler 1830	South American snake-necked turtle / Tartaruga-pescoço-de-cobra	7	0.079	1, 2, 42, 43, 44, 45, 60
	Phrynops sp. Wagler 1830	Toadhead turtle / Cágado	5	0.056	16, 17, 19, 21, 22
	Alligatoridae Gray, 1844 indet.	Alligatorid / Aligatorídeo	6	0.067	9, 17, 18, 22, 26, 50
	Caiman latirostris (Daudin, 1802)	Broad-snouted caiman / Jacaré-do-papo-amarelo	14	0.157	1, 2, 29, 43, 45, 46, 47, 49, 50, 55, 56, 59, 60, 78
	Squamata Oppel, 1811 indet.	Squamate / Escamado	2	0.022	1, 2
	Teiidae Gray, 1827 indet.	Teiid / Teídeo	2	0.022	19, 20

	Salvator merianae Duméril & Bibron, 1839	Argentine black and white tegu / Teiú-gigante	21	0.236	1, 7, 11, 17, 19, 20, 22, 29, 33, 36, 38, 41, 43, 44, 45, 46, 47, 49, 50, 59, 81
	Serpentes Linnaeus, 1758 indet.	Snake / Serpente	4	0.045	2, 4, 5, 43
	Boa constrictor Linnaeus, 1758	Red-tailed boa / Jibóia	1	0.011	10
	Viperidae Oppel, 1811 indet.	Viperid / Viperídeo	1	0.011	43
	Bothrops sp. Wagler, 1824	Pit viper / Jararaca	1	0.011	29
Amphibians	Caeciliidae Rafinesque, 1814 indet.	Caecillid / Cecília	1	0.011	29
	Anura Duméril, 1806 indet.	Anuran / Anuro	6	0.067	4, 9, 45, 52, 67, 74
	Rhinella sp. Fitzinger, 1826	South American toad / Sapo	3	0.034	9, 16, 19
	Ceratophrys aurita (Raddi, 1823)	Brazilian horned frog / Sapo-boi	1	0.011	43

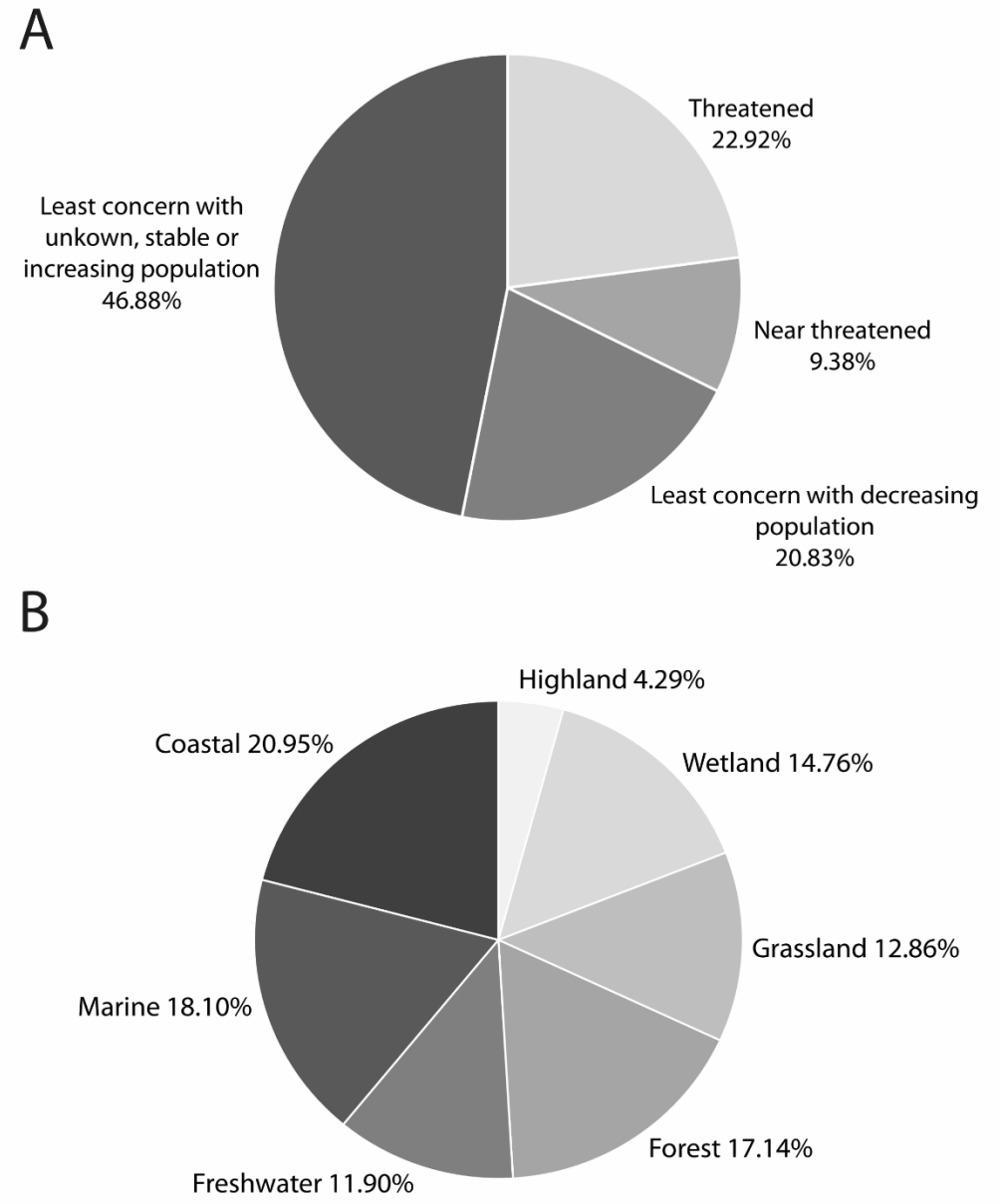

Figure 15. Data regarding conservation status (**A**) and habitats (**B**) of the inventoried species.

DISCUSSION

The inventory list

Zooarchaeological remains represent a sample of the fauna of the past. However, because they present cultural selectivity biases—due to food preferences, technological level of fishing and hunting artifacts, and funerary and ritualistic practices (Mendes et al., 2018)—many researchers believe that they cannot be used to make inferences about the biodiversity (Baisre, 2010; Rodrigues et al., 2016). However, several studies have shown that, despite their limitations, the records of these archaeological sites (i) are consistent with contemporary faunal records (i.e., they present the same taxa over time), (ii) act as indicators of past biodiversity, and (iii) can provide evidence on changes in species composition over time on a local scale (Faria et al., 2014; Souza et al., 2016; Silva et al., 2017; Mendes et al., 2018, 2020; Fossile et al. 2018, 2020).

The Atlantic Forest is one of the most important hotspots for biodiversity conservation on the planet (Myers et al., 2000), housing about 7.7% of the total tetrapod species of the world (Figueiredo et al., 2021). Regarding mammal diversity, for example, it has more than half of the total number of Brazilian species, 751 (Quintela et al., 2020), presenting a great diversity of orders, families and genres. This biome has 10 orders and 35 families of terrestrial mammals (Graipel et al., 2017), of which 8 orders and 21 families are represented in the sambaquis studied, demonstrating that, despite the selectivity biases in these archaeological sites, they have an expressive diversity of taxa.

The states of Rio de Janeiro and Santa Catarina were the ones with the highest number of sambaquis and zooarchaeological records, which agrees with Villagran (2013), who pointed out that they are the states with the most records of occupation by sambaquis builders on the south and southeast coasts. That author points out that, despite the fact that the states of Espírito Santo and Paraná have a significant amount of sambaquis, archaeological research in these places is less abundant. Until 2009 only 13 of the more than 300 archaeological sites in Paraná had been dated (Brochier, 2009; Villagran, 2013). In the 1960s, with the development of the National Archaeological Research Program (PRONAPA), research strategies focused on sambaquis from Paraná, Rio de Janeiro and Santa Catarina (Gaspar, 2004; Oliveira, 2010). DeBlasis and Gaspar (2009) discussed that in the mid-1990s, a research project on archaeological sites on the southern coast of Santa Catarina emerged as one of the most active shell mound working groups in Brazil, generating a large amount of well-documented records. Thus, several factors help to understand the predominance of research on sambaquis in certain areas of the country.

Comparing our results with already published sambaquis inventories, such as the one by Souza et al. (2011) for bivalves and gastropods from the southeast and south, and Mendes et al. (2018) for fish from the southeast region, the number of species in the present inventory is lower (352 bivalve and gastropod species in 578 sambaquis, and 142 fish species in 68 sambaquis respectively, from the aforementioned references). This result is expected, due to the abundance of these taxa at the sites.

The high frequency of lowland paca (*C. paca*) and lowland tapir (*T. terrestris*) can be explained (i) by their geographic distribution: these species have a wide distribution in South America, occurring in all states of southeast and south regions of Brazil and inhabit various habitats such as forests and wetlands (Oliveira-Santos et al., 2009; Michalski and Norris, 2011; Ferreguetti et al., 2019), and (ii) the selectivity of fishermen-gatherers-hunters: it is likely that these animals were target species of sambaqui builders as they provide a significant proportion of bushmeat for hunters, and they are still today targets of subsistence hunting (Novaro et al., 2000; El Bizri et al. 2018). The inventoried species inhabit a great diversity of habitats, corroborating observations made by Lima (1999-2000) and DeBlasis et al. (2007), who highlighted the variety of environments explored by fishermen-gatherers-hunters.

Conservation

The inclusion of zooarchaeological data in conservation studies has been encouraged in recent years to broaden the temporal spectrum of analyses and thus understand the history of threatened species and human-species interaction on a large temporal scale (Lopes et al., 2016; Mendes et al., 2018; Fossile et al., 2018, 2020; Mendes et al., 2020). For *Tapirus terrestris* (F = 36), *Tayassu pecari* (22), *Ozotoceros bezoarticus* (7), *Eubalaena australis* (7), and *Chelonia mydas* (5) (threatened species recorded as primary data in this work), zooarchaeological data contribute to the understanding of local extinctions and possible overexploitation of this fauna even in pre-colonial times.

The lowland tapir, identified in T51, GUB, IE2, and CO1 sambaquis, is categorized as VU on a national scale, but as EN in the state lists of Paraná and Santa Catarina (Medici et al., 2018). In Paraná, *Tapirus terrestris* occurred in virtually all biomes, however, in recent decades it has been disappearing due to deforestation and especially illegal hunting (Vidolin et al., 2011). Another species that suffers from illegal hunting is *Tayassu pecari*, also categorized as VU by the national red list but as CR by the state lists of Paraná and Santa Catarina (Keuroghlian et al., 2018). The high frequency

of occurrence of lowland tapirs and peccaries in sambaquis indicates a high consumption of these mammals and suggest that they may have been under pressure from hunting for thousands of years.

Overhunting, reduction of their natural habitat, and diseases are the main reasons why *Ozotoceros bezoarticus* is currently in the VU category in both Santa Catarina and Brazil red lists (Duarte et al., 2018). The present distribution of pampas deer populations in SC is virtually limited to interior grasslands and highlands (Bôlla et al., 2017; IUCN, 2020). Records of that species in coastal or near to coastal cities in SC are mostly historical, from the 1980s (Cherem et al., 2004), and prehistorical from sambaquis. This indicates that this species was probably more common in coastal areas in southern Brazil in the past, corroborating Fossile et al. (2018) who suggested a wider distribution in the past based on records of a sambaqui in Babitonga Bay (SC), and Mazzolli and Benedet (2009) who indicated a drastic reduction in the distribution of pampas deers in Paraná, previously widely distributed, and highlighted two local extinctions in the SC plateau due to illegal hunting and absence of protected areas.

Hunting is an exploratory activity that also affects marine species. Southern right whales were severely exploited by commercial whaling from the 18th through the early 20th centuries, and in southern Brazilian waters they were subjected to intensive commercial whaling until 1973, when their population appeared to be locally extinct in the region (Groch et al., (2005). In the early 1980s, specimens of *Eubalaena australis* were “rediscovered” in the south region, and they are today in the EN category in Brazilian and Paraná lists and VU in the Santa Catarina and Rio Grande do Sul lists (Groch et al., 2018). Regarding green sea turtles, extractive use of *Chelonia mydas* for eggs, meat, and other products in the 18th and 19th centuries is probably the major reason for the species being globally endangered in the early 2000s (Tröeng and Rankin, 2005). Currently, these factors, added to pollution, increased fishing activity and disorderly coastal development, make green sea turtles globally endangered and nationally vulnerable (Almeida et al., 2018).

These five species are examples of how exploratory hunting interferes with population size and geographical distribution and can often lead to local extinction. Data on species found in sambaquis help to understand how they may have been exploited for thousands of years, placing a long-term framework on human-fauna interactions. Exploitation by fishermen-gatherer-hunters of sambaquis may have been of great proportions. Lima (1999–2000), for example, suggested that there was a crisis in mollusc

and fish exploitation due to their depletion, caused by the intense collecting of specimens coveted by sambaquis communities. Lopes et al. (2016), in their study of sambaquis from Rio de Janeiro, indicated that the variation of fishing resources by sambaqui builders was a consequence of the threat of local extinction of certain species due to over-exploitation. Likewise, Fossile et al. (2019) considered that the sambaqui fishermen-gatherer-hunters from Babitonga Bay might have extracted volumes of fish biomass higher than or comparable to historical subsistence fisheries in the region, evidencing how exploratory fishing can lead to a significant decrease or local extinction of resources.

CONCLUSIONS

From an extensive bibliographic survey and primary data, here we present the first complete inventory of tetrapod fauna from sambaquis in the southeastern and southern regions of Brazil. In total we inventoried 188 taxa in 89 sambaquis, 96 at species level. Most of these species (51.06%) are at some level of concern regarding their conservation status. Thus, we expect that the fauna inventory presented in this study will contribute to future conservation research, since reference taxonomic inventories are fundamental to the establishment of baselines, that become more accurate when they include not only current data but also historic and prehistoric (sub-fossil and fossil) data as well. More complete and accurate baselines enable a large-scale temporal approach which recognises tendencies in species composition along deep time, and an understanding of the life history of a particular community, especially its extinctions. Baselines are particularly well-used in ecological restoration where they determine the ecosystem present before human influence and are important tools to understand biodiversity patterns as well as to guide conservation and management initiatives. Therefore, data here presented are useful for archaeological, environmental, ecological, and biogeographic studies, as well as for conservation of tetrapods species of Atlantic Forest and coastal-marine ecosystems in Brazilian southeast and south regions.

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FINAL REMARKS

This doctoral dissertation presents data on mammal, bird, reptile, and amphibian fauna from a total of 89 sambaquis distributed in the three coastal states of the Southeast region and the three southern states, covering about 2,000 km of the Brazilian coastline. The zooarchaeological material from ten sambaquis in the southern region had never been studied before. Thus, the information contained in this research is valuable for the understanding of the tetrapod fauna of sambaquis, an understudied group for these sites in relation to molluscs and fish.

We identified 46 taxa in the ten sambaquis of the southern region. Most remains were from marine animals, mainly cetaceans, otariids, and Magellanic penguins. Sambaqui fishermen-hunter-gatherers exploited these seasonal resources in an opportunistic and selective manner, given the significant number of juvenile fur seals and southern right whales recorded. Despite the diversity of the fauna recorded, the data pointed to the great relevance of marine tetrapod fauna as a resource for sambaqui builders.

The human modification vestiges on the bones support the importance of marine fauna for ancient sambaqui societies. Cut marks were identified mainly on the bones of otariids, cetaceans, and penguins, and most artefacts were made from cetacean bones. Sambaqui builders manufactured various types of bone artefacts, processed carcasses aimed at selecting meaty parts, and used fire for cooking.

The inventory of tetrapods from sambaquis of the South and Southeast regions recorded 188 taxa, 96 of them at the species level. The most frequent species were lowland paca and tapir, mammals that even today suffer from overhunting. Most of the species inventoried are now under some level of threat. This checklist is a powerful tool for understanding diversity on a long-term evolutionary time scale (allowing, for example, the study of local extinctions) and can provide baselines for more accurate conservation and management measures.

Therefore, the data presented here provide a broad understanding of the biodiversity of tetrapods from sambaquis from cultural (builders-fauna interactions) and evolutionary-conservationist perspectives, being useful for biological (zoology, osteology, ecology, biogeography) and archaeological (zooarchaeology, taphonomy), studies.

SUPPLEMENTARY MATERIAL

Supplementary Table 1. Supporting literature and databases used for anatomical and taxonomic identification.

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Laridae	Mayr, G., 2011. The phylogeny of charadriiform birds (shorebirds and allies) – reassessing the conflict between morphology and molecules. Zoological Journal of the Linnean Society 161, 916–934. https://doi.org/10.1111/j.1096-3642.2010.00654.x Olson, S.L., 2011. A new genus and species of unusual tern (Aves: Laridae: Anoinae) from the Middle Miocene Calvert Formation of Virginia. Proceedings of the Biological Society of Washington 124, 270–279. https://doi.org/10.2988/11-16.1 Pietri, V.L., Costeur, L., Güntert, M., Mayr, G., 2011. A revision of the Lari (Aves, Charadreformes) from the Early Miocene of Saint-Gérand-Le-Puy (Allier, France). Journal of Vertebrate Paleontology 31, 812–828. https://doi.org/10.1080/02724634.2011.586663 Shufeldt, R.W., 1890. Contributions to the comparative osteology of arctic and sub-arctic waterbirds. Part VIII. Journal of Anatomy and Physiology 25, 60–77. Watanabe, J., 2017. Ontogeny of macroscopic morphology of limb bones in modern aquatic birds and their implications for ontogenetic ageing Contribuciones del MACN 7, 183–220.
Rynchopidae	Mayr, G., 2011. The phylogeny of charadriiform birds (shorebirds and allies) – reassessing the conflict between morphology and molecules. Zoological Journal of the Linnean Society 161, 916–934. https://doi.org/10.1111/j.1096-3642.2010.00654.x Olson, S.L., 2011. A new genus and species of unusual tern (Aves: Laridae: Anoinae) from the Middle Miocene Calvert Formation of Virginia. Proceedings of the Biological Society of Washington 124, 270–279. https://doi.org/10.2988/11-16.1 Shufeldt, R.W., 1890. Contributions to the comparative osteology of arctic and sub-arctic waterbirds. Part VIII. Journal of Anatomy and Physiology 25, 60–77.
Charadriidae	Mayr, G., 2011. The phylogeny of charadriiform birds (shorebirds and allies) – reassessing the conflict between morphology and molecules. Zoological Journal of the Linnean Society 161, 916–934. https://doi.org/10.1111/j.1096-3642.2010.00654.x Schäfer, F., Schmitz, G., Skull identification key for Central European shorebirds (Aves: Charadriiformes: Scolopaci and Charadrii). Stuttgarter Beiträge zur Naturkunde A 9, 267–282. https://doi.org/10.18476/sbna.v9.a16 Stewart, J.R., Jacobi, R.M., 2015. The long term response of birds to climate change: new results from a cold stage avifauna in Northern England. Plos One 10, e0122617. https://doi.org/doi:10.1371/journal.pone.0122617

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Sulidae	Carlos, C.J., Alvarenga, J.G., Mazzochi, M.S., 2017. Osteology of the feeding apparatus of Magnificent Frigatebird *Fregata magnificens* and Brown Booby *Sula leucogaster* (Aves: Suliformes). Papéis Avulsos de Zoologia, Museu de Zoologia da Universidade de São Paulo 57, 265–274. https://doi.org/10.11606/0031-1049.2017.57.20 Mayr, G., Hazevoet, C.J., Dantas, P., Cachão, M., 2008. A sternum of a very large bony-toothed bird (Pelagornithidae) from the Miocene of Portugal. Journal of Vertebrate Paleontology 28, 762–769. https://doi.org/10.1671/0272-4634(2008)28[762:ASOAVL]2.0.CO;2 Smith, N.D., 2010. Phylogenetic analysis of Pelecaniformes (Aves) based on osteological data: implications for waterbird phylogeny and fossil calibration studies. Plos One 5, e13354. https://doi.org/10.1371/journal.pone.0013354 Smith, N.D., Grande, L., Clarke, J.A., 2013. A new species of Threskiornithidae-like bird (Aves, Ciconiiformes) from the Green River Formation (Eocene) of Wyoming. Journal of Vertebrate Paleontology 33, 363–381. https://doi.org/10.1080/02724634.2012.722898 Stucchi, M., 2013. The skull of the peruvian booby *Sula variegata* (Aves, Sulidae). The Biologist 11, 15–32.
Phalacrocoracidae	Noriega, J.I., Piña, C.I., 2004. Nuevo material de *Macranhinga paranensis* (Aves: Pelecaniformes: Anhingidae) del Mioceno Superior de la Formación Ituzaingó, provincia de Entre Ríos, Argentina. Ameghiniana 41, 115–118. Smith, N.D., 2010. Phylogenetic analysis of Pelecaniformes (Aves) based on osteological data: implications for waterbird phylogeny and fossil calibration studies. Plos One 5, e13354. https://doi.org/10.1371/journal.pone.0013354 Stucchi, M., 2013. The skull of the peruvian booby *Sula variegata* (Aves, Sulidae). The Biologist 11, 15–32. Watanabe, J., 2017. Ontogeny of macroscopic morphology of limb bones in modern aquatic birds and their implications for ontogenetic ageing. Contribuciones del MACN 7, 183–220.
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Rallidae	Alves, T.R., 2012. Análise filogenética de ralídeos neotropicais (Aves: Rallidae) com base em caracteres osteológicos. Master dissertation, Universidade de São Paulo, São Paulo, Brazil. Kirchman, J.J., Steadman, D.W., 2006. New species of rails (Aves: Rallidae) from an archaeological site on Huahine, Society Islands. Pacific Science, 60, 281–297. https://doi.org/10.1353/psc.2006.0007 Mayr, G., 2006. A rail (Aves, Rallidae) from the early Oligocene of Germany. Ardea 94, 23–31.
Cracidae	Holman, J.A., 1964. Osteology of gallinaceous birds. Quarterly Journal of the Florida Academy of Sciences 27, 230–252. Marceliano, M.L.V., Posso, S.R., Donatelli, R.J., 2007. Osteologia craniana de *Penelope superciliaris* Temminck, 1815 (Galliformes: Cracidae). Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais 2, 55–67.
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Accipitridae	Migotto, R., 2013. Filogenia de Accipitridae (Aves: Accipitriformes) com base em caracteres osteológicos. PhD dissertation, Universidade de São Paulo, São Paulo, Brazil. Stewart, J.R., Jacobi, R.M., 2015. The long term response of birds to climate change: new results from a cold stage avifauna in Northern England. Plos One 10, e0122617. https://doi.org/doi:10.1371/journal.pone.0122617 Zhang, Z., Feduccia, A., James, H.F., 2012. A Late Miocene accipitrid (Aves: Accipitriformes) from Nebraska and its implications for the divergence of Old World vultures. Plos One 7, e48842. https://doi.org/10.1371/journal.pone.0048842
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Alligatoridae	Bona, P., Desojo, J.B., 2011. Osteology and cranial musculature of *Caiman latirostris* (Crocodylia: Alligatoridae). Journal of Morphology 272, 780–795. https://doi.org/10.1002/jmor.10894 Romão, M.F., Santos, A.L.Q., Lima, F.C., 2012. Skeletal anatomy of the pectoral girdle, stylopodium and zeugopodium of *Caiman latirostris* (Daudin, 1802) (Crocodylia: Alligatoridae). International Journal of Biology 4, 40–45. https://doi.org/10.5539/ijb.v4n4p40 Vieira, L.G., Santos, A.L.Q., Lima, F.C., Mendonça, S.H.S.T., Menezes, L.T., Sebben, A., 2016. Osteologia de *Melanosuchus niger* (Crocodylia: Alligatoridae) e a evidência evolutiva. Pesquisa Veterinária Brasileira 36, 1025–1044. https://doi.org/10.1590/S0100-736X2016001000018
Lissamphibia	Duellman, W.E., Trueb, L., 1994. Biology of Amphibians. The Johns Hopkins University Press, Baltimore.
Anura	Araújo-Júnior, H.I., Moura, G.J.B., 2014. Anuros (Amphibia, Anura) do Pleistoceno Final-Holoceno Inicial de Itapipoca, estado do Ceará, Brasil: taxonomia, paleoecologia e tafonomia. Revista Brasileira de Paleontologia 17, 373–388. https://doi.org/10.4072/rbp.2014.3.08 Bailon, S., 1999. Différenciation ostéologique des anoures (Amphibia, Anura) de France. Association pour la Promotion et la Diffusion des Connaissances en Archéologie Série C: Varia, 1–40. Trueb. L., 1977. Osteology and anuran systematics: intrapopulational variation in *Hyla lanciformis*. Systematic Biology 26, 165–184. https://doi.org/10.1093/sysbio/26.2.165 Vélez-Rodríguez, C.M., 2005. Osteology of *Bufo sternosignatus* Günther, 1858 (Anura: Bufonidae) with comments on phylogenetic implications. Journal of Herpetology 39, 299–303. https://doi.org/10.1670/31-04W

Supplementary Table 2. NISP and MNI of identified taxon of each sambaqui. We used em dashes (—) when it was not possible to calculate the NMI due to the extremely fragmented level of material, making it impossible to identify the anatomical elements.

Taxon	Paraná						Santa Catarina						Rio Grande do Sul								Total	
	T51		GUA		GUB		IE2		CAI		CO1		ITA		REC		FI2		SER			
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Mammalia indet.	24	—	23	—	64	—	8	—	111	—	18	—	17	—	1	—	68	—	0	0	334	—
Didelphis sp.	0	0	0	0	0	0	4	2	1	1	0	0	0	0	0	0	0	0	0	0	5	3
Dasypodidae indet.	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Alouatta sp.	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	3	1
Rodentia indet.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1
Hydrochoerus hydrochaeris	0	0	0	0	2	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	4	3
Cuniculus paca	3	2	0	0	6	4	2	1	0	0	0	0	0	0	0	0	0	0	0	0	11	7
Otariidae indet.	0	0	0	0	0	0	0	0	38	3	1	1	1	1	0	0	13	4	0	0	53	9
Otaria flavescens	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	2	1
Arctocephalus sp.	5	2	3	1	0	0	1	1	66	10	0	0	2	1	0	0	116	7	0	0	193	22
Nasua nasua	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Felidae indet.	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1
Tapirus terrestris	2	1	0	0	76	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	81	5
Tayassuidae indet.	15	4	0	0	12	1	0	0	7	2	1	1	0	0	1	1	0	0	0	0	36	9
Tayassu pecari	0	0	0	0	1	1	0	0	8	4	2	1	0	0	0	0	0	0	0	0	11	6
Dicotyles tajacu	2	2	0	0	0	0	0	0	5	2	1	1	0	0	0	0	0	0	0	0	8	5
Cervidae indet.	0	0	0	0	4	1	1	1	1	1	0	0	0	0	0	0	1	1	0	0	7	4
Mazama sp.	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	2	1
Ozotoceros bezoarticus	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	3	1
Cetacea indet.	0	0	1,423	—	176	1	27	1	66	1	0	0	0	0	0	0	4	1	0	0	1,696	—
Odontoceti indet.	0	0	9	1	3	1	2	1	10	1	0	0	0	0	0	0	17	1	0	0	41	5
Delphinidae indet.	0	0	3	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	4	3
Tursiops truncatus	0	0	0	0	0	0	4	1	1	1	0	0	0	0	0	0	0	0	0	0	5	2
Mysticeti indet.	0	0	584	3	74	1	0	0	9	1	0	0	104	1	18	1	0	0	22	1	811	8
Eubalaena australis	0	0	8	6	2	2	0	0	0	0	0	0	1	1	0	0	0	0	0	0	11	9

Aves	15	—	0	0	6	—	3	—	1	—	83	—	0	0	1	—	52	—	0	0	161	—
Procellariidae indet.	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	2	1
Puffinus sp.	0	0	0	0	0	0	0	0	0	0	4	1	0	0	0	0	0	0	0	0	4	1
Thalassarche sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	0	0	3	2
Laridae indet.	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1
Larus dominicanus	0	0	0	0	0	0	0	0	1	1	3	1	0	0	0	0	0	0	0	0	4	2
Rynchops niger	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	2	1
Charadriidae indet.	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	2	1
Sula leucogaster	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	2	1
Nannopterum brasilianus	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1
Ardea sp.	0	0	0	0	0	0	0	0	0	0	10	2	0	0	0	0	0	0	0	0	10	2
Spheniscus magellanicus	0	0	0	0	6	2	0	0	19	6	0	0	0	0	0	0	9	2	0	0	34	10
Aramides sp.	2	1	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	4	2
Penelope sp.	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1
Amazona sp.	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1
Accipitridae indet.	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Cathartidae indet.	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	7	1	0	0	8	2
Cheloniidae indet.	0	0	0	0	38	1	0	0	3	1	0	0	0	0	0	0	0	0	0	0	41	2
Chelonia mydas	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Caiman latirostris	0	0	8	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	2
Anura indet.	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Not identified	9	—	3	—	14	—	4	—	19	—	1	—	0	0	0	0	11	—	0	0	61	—
Total	**80**	**14**	**2,064**	**14**	**487**	**20**	**65**	**14**	**375**	**41**	**141**	**19**	**125**	**4**	**21**	**2**	**302**	**20**	**22**	**1**	**3,682**	**145**

Supplementary Table 3. NISP and MNE of identified anatomical elements of each sambaqui.

	Element	Paraná						Santa Catarina						Rio Grande do Sul								Total	
		T51		GUA		GUB		IE2		CAI		CO1		ITA		REC		FI2		SER			
		NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
Mammalia	Temporal bone	0	0	12	7	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	13	8
	Tympanic bulla	0	0	23	14	3	3	0	0	0	0	0	0	2	2	0	0	0	0	0	0	28	19
	Upper jaw	0	0	0	0	0	0	0	0	6	4	1	1	0	0	0	0	1	1	0	0	8	6
	Lower jaw	1	1	3	2	72	8	3	3	19	16	0	0	2	1	0	0	7	4	0	0	107	35
	Jaw indet.	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	3	3
	Incisor tooth	3	3	0	0	5	5	0	0	4	4	1	1	0	0	0	0	17	17	0	0	30	30
	Canine tooth	4	4	0	0	1	1	0	0	22	22	1	1	0	0	0	0	22	22	0	0	50	50
	Post-canine tooth	1	1	0	0	0	0	0	0	4	4	0	0	0	0	0	0	56	56	0	0	61	61
	Premolar tooth	0	0	0	0	2	2	0	0	3	3	0	0	0	0	1	1	0	0	0	0	6	6
	Molar tooth	1	1	0	0	1	1	0	0	1	1	2	2	0	0	0	0	0	0	0	0	5	5
	Cervical vertebra	0	0	1	1	3	3	0	0	15	15	0	0	0	0	0	0	5	5	0	0	24	24
	Thoracic vertebra	1	1	2	2	8	7	0	0	22	21	1	1	1	1	0	0	4	3	0	0	39	36
	Lumbar vertebra	0	0	1	1	2	2	0	0	1	1	0	0	0	0	1	1	3	3	0	0	8	8
	Caudal vertebra	0	0	2	2	1	1	6	6	1	1	0	0	0	0	0	0	0	0	0	0	10	10
	Vertebra indet.	0	0	116	17	6	4	0	0	8	2	0	0	3	3	11	6	18	18	0	0	162	50
	Rib	3	3	3	2	1	1	0	0	10	10	2	2	0	0	0	0	13	12	0	0	32	30
	Scapula	0	0	0	0	11	2	3	3	9	8	1	1	0	0	0	0	0	0	0	0	24	14
	Pelvis	0	0	0	0	0	0	2	1	5	5	0	0	0	0	0	0	1	1	0	0	8	7
	Humerus	4	3	0	0	6	6	3	3	18	18	0	0	0	0	0	0	3	3	0	0	34	33
	Femur	6	5	2	2	6	6	7	7	17	17	1	1	0	0	0	0	10	7	0	0	49	45
	Radius	0	0	1	1	0	0	0	0	13	13	0	0	0	0	0	0	9	9	0	0	23	23
	Ulna	2	2	3	2	0	0	2	2	1	1	2	2	0	0	0	0	3	3	0	0	13	12
	Tibia	2	2	0	0	5	4	0	0	7	6	3	1	0	0	0	0	3	1	0	0	20	14

	Fibula	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2	2
	Talus	1	1	0	0	1	1	1	1	4	4	0	0	0	0	0	0	0	0	0	0	7	7
	Calcaneus	0	0	0	0	0	0	0	0	4	4	1	1	0	0	0	0	1	1	0	0	6	6
	Metatarsal	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	3	3
	Metacarpal	7	7	0	0	2	2	1	1	5	5	1	1	0	0	0	0	1	1	0	0	17	17
	Phalanx	1	1	0	0	2	2	1	1	26	26	4	4	0	0	0	0	9	9	0	0	43	43
	Autopod bone indet.	8	8	16	6	16	7	0	0	18	18	0	0	3	2	0	0	25	24	0	0	86	65
	Not identified	6	1	1,867	1	265	1	27	1	81	1	9	1	114	1	7	1	8	1	21	1	2,405	10
	Total	**51**	**44**	**2,053**	**61**	**421**	**71**	**57**	**30**	**328**	**234**	**30**	**20**	**125**	**10**	**20**	**9**	**219**	**201**	**22**	**2**	**3,326**	**682**
Aves	Cervical vertebra	7	7	0	0	1	1	0	0	0	0	2	2	0	0	0	0	5	5	0	0	15	15
	Thoracic vertebra	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	1	1	0	0	4	4
	Rib	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	Coracoid	0	0	0	0	1	1	0	0	0	0	3	3	0	0	0	0	2	2	0	0	6	6
	Scapula	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1
	Synsacrum	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	2	2
	Humerus	5	4	0	0	5	4	0	0	8	8	21	20	0	0	0	0	14	6	0	0	53	42
	Femur	2	2	0	0	3	3	0	0	8	8	10	10	0	0	0	0	2	2	0	0	25	25
	Radius	2	2	0	0	0	0	0	0	0	0	5	5	0	0	0	0	6	4	0	0	13	11
	Ulna	0	0	0	0	0	0	0	0	1	1	25	19	0	0	0	0	4	4	0	0	30	24
	Tibiotarsus	1	1	0	0	1	1	0	0	5	3	14	13	0	0	0	0	11	6	0	0	32	24
	Carpometacarpus	1	1	0	0	1	1	0	0	0	0	7	6	0	0	0	0	1	1	0	0	10	9
	Tarsometatarsus	0	0	0	0	0	0	0	0	0	0	7	7	0	0	0	0	4	3	0	0	11	10
	Phalanx	2	2	0	0	0	0	0	0	0	0	1	1	0	0	1	1	2	2	0	0	6	6
	Not identified	0	0	0	0	0	0	3	1	0	0	11	1	0	0	0	0	20	1	0	0	34	3
	Total	**20**	**19**	**0**	**0**	**13**	**12**	**3**	**1**	**24**	**22**	**110**	**91**	**0**	**0**	**1**	**1**	**72**	**37**	**0**	**0**	**243**	**183**
Reptilia	Lower jaw	0	0	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1
	Tooth	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3
	Carapace	0	0	0	0	37	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37	2

	Cervical vertebra	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
	Coracoid	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
	Humerus	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	2
	Femur	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
	Ulna	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	Total	**0**	**0**	**8**	**4**	**39**	**4**	**1**	**1**	**3**	**3**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**51**	**12**
Lissamphibia	Tibiofibula	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
	Total	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**
Not id.		9	1	3	1	14	1	4	1	19	1	1	1	0	0	0	0	11	1	0	0	61	7
Total		**80**	**64**	**2,064**	**65**	**487**	**88**	**65**	**33**	**375**	**261**	**141**	**112**	**125**	**10**	**21**	**10**	**302**	**239**	**22**	**2**	**3,682**	**885**

Supplementary Table 4. Biomass calculated for each taxon. Abbreviations: **T**, terrestrial animal; **M**: marine animal.

Taxon		MNI				Average body weight (kg)	% Consumable meat	Weight of consumable meat (kg)	Biomass (kg)			
		PR	SC	RS	Total				PR	SC	RS	Total
Mammalia	*Didelphis* sp. (T)	0	5	0	5	1.42	70	0.98	0	4.9	0	4.9
	Alouatta sp. (T)	0	1	0	1	5.81	50	2.9	0	2.9	0	2.9
	Hydrochoerus hydrochaeris (T)	1	2	0	3	50.00	65	32.5	32.5	65	0	97.5
	Cuniculus paca (T)	6	1	0	7	9.30	70	6.51	39.06	6.51	0	45.57
	Otaria flavescens (M)	0	1	0	1	1744.00	56	976.64	0	976.64	0	976.64
	Arctocephalus sp. (M)	2	12	7	21	117.40	56	65.52	131.04	786.24	458.64	1375.92
	Nasua nasua (T)	0	1	0	1	5.10	50	2.55	0	2.55	0	2.55
	Tapirus terrestris (T)	1	1	0	2	260.00	50	130	130	130	0	260
	Tayassu pecari (T)	1	5	0	6	35.00	70	24.5	24.5	122.5	0	147
	Pecari tajacu (T)	2	3	0	5	26.00	70	18.2	36.4	54.6	0	91
	Mazama sp. (T)	0	1	0	1	24.86	50	12.43	0	12.43	0	12.43
	Ozotoceros bezoarticus (T)	0	1	0	1	35.00	50	17.5	0	17.5	0	17.5
	Tursiops truncatus (M)	0	2	0	2	280.00	63	176.4	0	352.8	0	352.8
Aves	*Puffinus* sp. (M)	0	1	0	1	0.65	70	0.45	0	0.45	0.45	0.9
	Thalassarche sp. (M)	0	0	2	2	3.46	70	2.42	0	0	4.84	4.84
	Larus dominicanus (M)	0	2	0	2	1.05	70	0.73	0	1.46	1.46	2.92
	Rynchops niger (M)	0	1	0	1	0.30	70	0.21	0	0.21	0.21	0.42
	Sula leucogaster (M)	0	1	0	1	1.35	70	0.94	0	0.94	0.94	1.88
	Nannopterum brasilianus (M)	0	1	0	1	1.30	70	0.91	0	0.91	0.91	1.82
	Ardea sp. (M)	0	2	0	2	1.20	70	0.84	0	1.68	1.68	3.36
	Spheniscus magellanicus	2	6	2	10	5.25	70	3.67	7.34	22.02	36.7	66.06
	Aramides sp. (T)	1	1	0	2	0.45	70	0.31	0.31	0.31	0.62	1.24
	Penelope obscura (T)	0	1	0	1	1.00	70	0.7	0	0.7	0.7	1.4
	Amazona sp. (T)	1	0	0	1	0.38	70	0.26	0.26	0	0.26	0.52
Reptilia	*Chelonia mydas* (M)	0	1	0	1	147.41	50	73.7	0	73.7	0	73.7
	Caiman latirostris (T)	2	0	0	2	33.75	70	23.62	47.24	0	0	47.24

Supplementary Table 5. Data on remains with cut marks. Each line corresponds to one vestige with cut mark identified.

Cut mark identification	Sambaqui	Taxonomic identification	Anatomical identification	Bone zone
Skinning	T51	Not identifiable	Not identifiable	—
Skinning	T51	*Tapirus terrestris*	Phalanx	Epiphysis
Defleshing	GUA	Cetacea indet.	Not identifiable	—
Skinning	GUA	Mysticeti indet.	Autopod bone	Diaphyses
Skinning	GUA	Mysticeti indet.	Not identifiable	—
Skinning	GUA	Mysticeti indet.	Autopod bone	Diaphyses
Defleshing	GUA	Mysticeti indet.	Temporal bone	—
Defleshing	GUA	Mysticeti indet.	Temporal bone	—
Defleshing	GUA	*Arctocephalus* sp.	Radius	Diaphyses
Skinning	GUA	*Arctocephalus* sp.	Femur	Diaphyses
Skinning	GUB	*Cuniculus paca*	Lower jaw	—
Defleshing	GUB	Not idenfiable	Not idenfiable	—
Skinning	GUB	Mammalia indet.	Tibia	Diaphyses
Skinning	GUB	Mammalia indet.	Not idenfiable	—
Disarticulation	IE2	*Alouatta* sp.	Femur	Epiphysis
Disarticulation	CAI	Mammalia indet.	Pelvis	—
Skinning	CAI	Otariidae indet.	Phalanx	Diaphyses
Disarticulation	CAI	Mammalia indet.	Tibia	Epiphysis
Skinning	CAI	Mammalia indet.	Fibula	Diaphyses
Skinning	CAI	*Didelphis* sp.	Lower jaw	—
Skinning	CAI	*Spheniscus magellanicus*	Femur	Diaphyses
Skinning	CAI	*Arctocephalus* sp.	Femur	Diaphyses
Skinning	CAI	Cetacea indet.	Not identifiable	—
Disarticulation	CAI	Mammalia indet.	Thoracic vertebra	—
Defleshing	CAI	*Arctocephalus* sp.	Femur	Epiphysis
Skinning	CAI	Mammalia indet.	Lower jaw	—
Defleshing	CAI	*Arctocephalus* sp.	Lower jaw	—
Skinning	CAI	*Arctocephalus* sp.	Radius	Diaphyses
Defleshing	CAI	Mammalia indet.	Scapula	—

Skinning	CAI	Odontoceti indet.	Autopod bone	Diaphyses
Disarticulation	CAI	*Arctocephalus* sp.	Femur	Diaphyses
Defleshing	CAI	*Arctocephalus* sp.	Radius	Diaphyses
Defleshing	CAI	Cheloniidae indet.	Coracoid	—
Disarticulation	CAI	*Arctocephalus* sp.	Humerus	Diaphyses
Disarticulation	CAI	*Spheniscus magellanicus*	Humerus	Epiphysis
Skinning	CAI	*Spheniscus magellanicus*	Tibiotarsus	Diaphyses
Skinning	CAI	*Spheniscus magellanicus*	Tibiotarsus	Diaphyses
Disarticulation	CAI	*Spheniscus magellanicus*	Femur	Epiphysis
Defleshing	FI2	*Spheniscus magellanicus*	Coracoid	—
Disarticulation	FI2	*Thalassarche* sp.	Tarsometatarsus	Epiphysis
Disarticulation	FI2	*Spheniscus magellanicus*	Tibiotarsus	Epiphysis
Skinning	FI2	*Thalassarche* sp.	Tarsometatarsus	Diaphyses
Defleshing	FI2	*Arctocephalus* sp.	Femur	Diaphyses
Disarticulation	FI2	Cervidae indet.	Femur	Epiphysis
Defleshing	FI2	*Arctocephalus* sp.	Lower jaw	—
Disarticulation	FI2	*Spheniscus magellanicus*	Tibiotarsus	Epiphysis
Defleshing	FI2	Not identifiable	Not identifiable	—
Disarticulation	FI2	Aves indet.	Ulna	Epiphysis

Supplementary Table 6. Number of artefacts registered in each sambaqui by its taxonomic identification. Abbreviations: **Cet**, Cetacea indet.; **Eaus**, *Eubalaena australis*; **Mam**, Mammalia indet.; **Mys**, Mysticeti indet.; **Tay**, Tayassuidae indet.; **Tter**, *Tapirus terrestris*.

Artefact	T51		GUA				GUB				CAI	ITA					Total
	Mam	Tay	Mam	Cet	Mys	Eaus	Mam	Mys	Eaus	Tay	Cet	Mam	Cet	Mys	Eaus	Tter	
Beveled object	0	0	0	2	18	7	0	1	2	0	2	0	7	32	1	0	72
Piercing object	2	1	5	0	1	0	2	0	0	1	0	3	2	0	0	0	17
Perforated object	0	0	0	0	5	0	0	0	0	0	0	0	0	1	0	1	7
Double point hook	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	12
Grooved double point hook	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Symmetric composite hook	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	5
Asymmetric composite hook (stem)	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	5
Asymmetric composite hook (point)	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	6
Sphere	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Zoomorphic item	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Total	**2**	**1**	**5**	**2**	**24**	**7**	**2**	**2**	**2**	**1**	**2**	**27**	**10**	**38**	**1**	**1**	**127**

Supplementary Table 7. Consulted databases, and libraries and institutions visited for data collection and inventory construction.

Online Databases	Website
Periódicos CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior)	https://www.periodicos.capes.gov.br
Scientific Electronic Library Online - SciELO	https://www.scielo.org
Google Scholar	https://www.scholar.google.com
Catálogo de Teses e Dissertações - CAPES	https://www.catalogodeteses.capes.gov.br
Libraries	**Location**
Central Library of Universidade Federal do Espírito Santo	Vitória, ES, Brazil
Library of Instituto de Geociências of Universidade Federal Fluminense	Niterói, RJ, Brazil
Library of Pós-Graduação em Geoquímica of Universidade Federal Fluminense	Niterói, RJ, Brazil
Library of Escola de Arquitetura e Urbanismo of Universidade Federal Fluminense	Niterói, RJ, Brazil
Library of Centro de Memória Fluminense of Universidade Federal Fluminense	Niterói, RJ, Brazil
Central Library of Valonguinho of Universidade Federal Fluminense	Niterói, RJ, Brazil
Central Library of Gragoatá of Universidade Federal Fluminense	Niterói, RJ, Brazil
Library of Museu de Arqueologia de Itaipu	Niterói, RJ, Brazil
Central Library of Pontifícia Universidade Católica of Rio de Janeiro	Rio de Janeiro, RJ, Brazil
Library of Museu Nacional of Universidade Federal do Rio de Janeiro	Rio de Janeiro, RJ, Brazil
Library of Museu de Arqueologia e Etnologia of Universidade de São Paulo	São Paulo, SP, Brazil
Library of Museu de Arqueologia e Etnologia of Universidade Federal do Paraná	Curitiba, PR, Brazil
Library of Centro de Estudos e Pesquisas Arqueológicas of Universidade Federal do Paraná	Curitiba, PR, Brazil
Library of Centro de Humanas of Universidade Federal do Paraná	Curitiba, PR, Brazil
Library of Ciências Biológicas of Universidade Federal do Paraná	Curitiba, PR, Brazil
Central Library of Pontifícia Universidade Católica of Paraná	Curitiba, PR, Brazil
Library of Círculo de Estudos Bandeirantes of Pontifícia Universidade Católica do Paraná	Curitiba, PR, Brazil
Romário Martins Library of Museu Paranaense	Curitiba, PR, Brazil
Library of Museu Arqueológico de Sambaqui de Joinville	Joinville, SC, Brazil
Central Library of Universidade Federal de Santa Catarina	Florianópolis, SC, Brazil
Library of Museu de Arqueologia e Etnologia of Universidade Federal de Santa Catarina	Florianópolis, SC, Brazil
Library of Museu Homem do Sambaqui	Florianópolis, SC, Brazil
Library of Instituto Anchietano de Pesquisas	São Leopoldo, RS, Brazil
Central Library of Pontifícia Universidade Católica of Rio Grande do Sul	Porto Alegre, RS, Brazil
Library of Laboratório de Pesquisas Arqueológicas of Pontifícia Universidade Católica of Rio Grande do Sul	Porto Alegre, RS, Brazil

Library of Instituto de Biociências of Universidade Federal do Rio Grande do Sul	Porto Alegre, RS, Brazil
Library of Ciências Sociais e Humanidades of Universidade Federal do Rio Grande do Sul	Porto Alegre, RS, Brazil
Library of Instituto de Geociências of Universidade Federal do Rio Grande do Sul	Porto Alegre, RS, Brazil
Institutions	**Location**
Instituto do Patrimônio Histórico e Artístico Nacional do Espírito Santo	Vitória, ES, Brazil
Instituto do Patrimônio Histórico e Artístico Nacional de São Paulo	São Paulo, SP, Brazil

Supplementary Table 8. Datations of the 73 inventoried sambaquis from the Brazilian southeast and south regions.

Sambaqui	Code	Datation (Years BP)	
		Oldest	Most recent
Lagoa Bonita 17	1	5,580	5,377
Suruaca 20	2	6,118	3,867
Campus 2	6	1,515	1,355
Ilha de Santana	7	1,590	930
Geribá II	8	5,260	5,040
Corondó	9	4,335	2,930
Boca da Barra	10	3,940	1,160
Forte	11	5,640	2,100
Meio	12	5,260	5,100
Salina Peroano	13	4,530	1,785
Ponta da Cabeça	15	3,340	2,040
Beirada	16	5,595	3,635
Madressilva	17	3,690	3,590
Manitiba I	18	4,515	3,695
Moa	19	3,890	3,420
Pontinha	20	2,240	1,740
Saco	21	3,590	3,490
Saquarema	22	4,200	2,100
Camboinhas	23	8,182	1,275
Arapuan	24	3,530	2,740
Amourins	25	3,840	3,320
Rio das Pedrinhas	26	4,280	3,100
Sernambetiba	28	2,570	1,760
Galeão	29	5,677	5,270
Embratel	30	2,140	1,800
Zé Espinho	31	2,420	1,010
Guaíba	32	1,580	1,460
Algodão	33	4,414	2,345
Bigode	34	3,525	3,223

Caieira I	35	2,175	1,875
Major	37	900	675
Peri	38	1,140	890
Couves 1	40	2,240	2,160
Mar Virado	41	2,710	2,500
Tenório	42	1,965	1,785
Buracão	43	2,150	1,850
Maratuá	44	3,690	3,310
Mar Casado	45	4,530	4,270
COSIPA 1	46	4,300	4,120
COSIPA 2	47	1,240	1,120
COSIPA 3	48	3,900	3,680
COSIPA 4	49	2,670	2,510
Piaçaguera	50	5,040	4,780
Ramal	51	6,645	4,950
Ilha das Pedras	52	1,890	820
Macedo	53	3,552	3,245
Guaraguaçu A	55	4,420	4,020
Guaraguaçu B	56	4,262	3,994
Bupeva II	58	2,350	2,300
Enseada I	59	3,960	1,350
Forte Marechal Luz	60	4,420	750
Espinheiros II	61	3,030	1,115
Ilha dos Espinheiros II	62	3,145	970
Morro do Ouro	63	4,070	3,990
Laranjeiras I	66	3,960	3,670
Armação do Sul	69	2,760	2,580
Pântano do Sul	70	4,570	4,415
Porto do Rio Vermelho	71	5,030	5,010
Porto do Rio Vermelho II	72	1,735	1,067
Caieira	74	3,385	2,670
Cabeçuda	75	4,240	1,150
Congonhas I	76	3,435	3,110

Encantada III	77	4,470	4,280
Jabuticabeira II	78	6,375	1,810
Içara 06	79	3,410	3,270
Lagoa do Freitas	80	1,360	1,275
Itapeva	81	3,170	3,090
Recreio	82	3,590	3,300
Arroio Seco V	83	3,350	3,270
Figueira II	84	3,700	3,620
Marambaia 1	85	3,090	3,010
Sereia do Mar	87	2,420	2,300
Serra Azul 2	88	3,350	3,270

Supplementary Table 9. Conservation status of 96 inventoried species according to IUCN and ICMBio. LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, DD = data deficient.

Species	IUCN		ICMBio/MMA
	Status	Population Trend	Status
Chironectes minimus (Zimmermann, 1980)	LC	Decreasing	DD
Didelphis aurita Wied-Neuwied, 1826	LC	Stable	LC
Didelphis marsupialis Linnaeus, 1758	LC	Stable	LC
Lutreolina crassicaudata (Desmarest, 1804)	LC	Unknown	LC
Philander opossum (Linnaeus, 1758)	LC	Stable	LC
Cabassous unicinctus (Linnaeus, 1758)	LC	Unknown	LC
Dasypus septemcinctus Linnaeus, 1758	LC	Unknown	LC
Dasypus novemcinctus Linnaeus, 1758	LC	Stable	LC
Euphractus sexcinctus (Linnaeus, 1758)	LC	Stable	LC
Tamandua tetradactyla (Linnaeus, 1758)	LC	Unknown	LC
Alouatta guariba (Humboldt, 1812)	LC	Decreasing	VU
Brachyteles arachnoides (É. Geoffroy Saint-Hilaire, 1806)	CR	Decreasing	EN
Sylvilagus brasiliensis (Linnaeus, 1758)	EN	Decreasing	LC
Cavia aperea Erxleben, 1777	LC	Stable	LC
Cavia fulgida Wagler, 1831	LC	Stable	LC
Hydrochoerus hydrochaeris (Linnaeus, 1766)	LC	Stable	LC
Holochilus brasiliensis (Desmarest, 1819)	LC	Stable	LC
Ctenomys minutus Nehring, 1887	DD	Stable	VU
Cuniculus paca (Linnaeus, 1766)	LC	Stable	LC
Dasyprocta azarae Lichtenstein, 1823	DD	Decreasing	LC
Dasyprocta leporina (Linnaeus, 1758)	LC	Stable	LC
Myocastor coypus (Molina, 1782)	LC	Decreasing	LC
Phyllomys pattoni Emmons, Leite, Kock and Costa, 2002	LC	Unknown	LC
Leopardus pardalis (Linnaeus, 1758)	LC	Decreasing	LC
Leopardus geoffroyi (d'Orbigny and Gervais, 1844)	LC	Stable	VU
Panthera onca (Linnaeus, 1758)	NT	Decreasing	VU
Puma concolor (Linnaeus, 1771)	LC	Decreasing	VU
Puma yagouaroundi (É. Geoffroy Saint-Hilaire, 1803)	LC	Decreasing	VU

Eira barbara (Linnaeus, 1758)	LC	Decreasing	LC
Lontra longicaudis (Olfers, 1818)	NT	Decreasing	NT
Arctocephalus australis (Zimmermann, 1783)	LC	Increasing	-
Arctocephalus tropicalis (J. E. Gray, 1872)	LC	Stable	-
Otaria flavescens (Shaw, 1800)	LC	Stable	LC
Nasua nasua (Linnaeus, 1766)	LC	Decreasing	LC
Procyon cancrivorus (G. Cuvier, 1798)	LC	Decreasing	LC
Tapirus terrestris (Linnaeus, 1758)	VU	Decreasing	VU
Blastocerus dichotomus (Illiger, 1815)	VU	Decreasing	VU
Mazama gouazoubira (G. Fischer [von Waldheim], 1814)	LC	Decreasing	LC
Mazama americana (Erxleben, 1777)	DD	Unknown	DD
Ozotoceros bezoarticus (Linnaeus, 1758)	NT	Decreasing	VU
Pecari tajacu (Linnaeus, 1758)	LC	Stable	LC
Tayassu pecari (Link, 1795)	VU	Decreasing	VU
Eubalaena australis (Desmoulins, 1822)	LC	Unknown	EN
Megaptera novaeangliae (Borowski, 1781)	LC	Increasing	NT
Delphinus delphis Linnaeus, 1758	LC	Unknown	DD
Globicephala macrorhynchus Gray, 1846	LC	Unknown	LC
Globicephala melas (Traill, 1809)	LC	Unknown	LC
Orcinus orca (Linnaeus, 1758)	DD	Unknown	LC
Pseudorca crassidens (Owen, 1846)	NT	Unknown	LC
Sotalia fluviatilis (Gervais and Deville, 1853)	EN	Decreasing	NT
Sotalia guianensis (van Bénéden, 1864)	NT	Unknown	VU
Stenella frontalis (G. Cuvier, 1829)	LC	Unknown	DD
Steno bredanensis (G. Cuvier in Lesson, 1828)	LC	Unknown	LC
Tursiops truncatus (Montagu, 1821)	LC	Unknown	DD
Pontoporia blainvillei (Gervais and d'Orbigny, 1844)	VU	Decreasing	CR
Tinamus solitarius (Vieillot, 1819)	NT	Decreasing	NT
Amazonetta brasiliensis (Gmelin, 1789)	LC	Decreasing	LC
Cairina moschata (Linnaeus, 1758)	LC	Decreasing	LC
Aburria jacutinga (Spix, 1825)	EN	Decreasing	EN
Podilymbus podiceps (Linnaeus, 1758)	LC	Stable	LC
Spheniscus magellanicus (Forster, 1781)	NT	Decreasing	NT

Thalassarche melanophris (Temminck, 1828)	LC	Increasing	NT
Calonectris borealis (Cory, 1881)	LC	Unknown	LC
Macronectes giganteus (Gmelin, 1789)	LC	Increasing	LC
Procellaria aequinoctialis Linnaeus, 1758	VU	Decreasing	VU
Puffinus gravis (O'Reilly, 1818)	LC	Stable	LC
Puffinus griseus (Gmelin, 1789)	NT	Decreasing	LC
Puffinus puffinus (Brunnich, 1764)	LC	Unknown	LC
Ciconia maguari (Gmelin, 1789)	LC	Stable	LC
Jabiru mycteria (Lichtenstein, 1819)	LC	Unknown	LC
Mycteria americana Linnaeus, 1758	LC	Decreasing	LC
Fregata magnificens Mathews, 1914	LC	Decreasing	LC
Sula leucogaster (Boddaert, 1783)	LC	Decreasing	LC
Nannopterum brasilianus (Gmelin, 1789)	LC	Increasing	LC
Anhinga anhinga (Linnaeus, 1766)	LC	Decreasing	LC
Eudocimus ruber (Linnaeus, 1758)	LC	Decreasing	LC
Cathartes aura (Linnaeus, 1758)	LC	Stable	LC
Buteogallus meridionalis (Latham, 1790)	LC	Increasing	LC
Urubitinga urubitinga (Gmelin, 1788)	LC	Stable	LC
Aramides cajaneus (Statius Muller, 1776)	LC	Decreasing	LC
Aramides saracura (Spix, 1825)	LC	Decreasing	LC
Rallus longirostris Boddaert, 1783	LC	Decreasing	LC
Jacana jacana (Linnaeus, 1766)	LC	Stable	LC
Larus dominicanus Lichtenstein, 1823	LC	Increasing	LC
Thalasseus acuflavidus (Cabot, 1847)	-	-	LC
Rynchops niger Linnaeus, 1758	LC	Decreasing	LC
Amazona aestiva (Linnaeus, 1758)	NT	Decreasing	NT
Ara chloropterus Gray, 1859	LC	Decreasing	NT
Caretta caretta (Linnaeus, 1758)	VU	Decreasing	EN
Chelonia mydas (Linnaeus, 1758)	EN	Decreasing	VU
Eretmochelys imbricata (Linnaeus, 1766)	CR	Decreasing	CR
Dermochelys coriacea (Vandelli, 1761)	VU	Decreasing	CR
Caiman latirostris (Daudin, 1802)	LC	Stable	LC
Salvator merianae Duméril & Bibron, 1839	LC	Stable	LC

Boa constrictor Linnaeus, 1758	-	-	LC
Ceratophrys aurita (Raddi, 1823)	LC	Decreasing	LC

APPENDIX

XXVI Congresso Brasileiro de Paleontologia

O LEGADO DO TEMPO E AS LIÇÕES DOS FÓSSEIS

21 a 25 outubro 2019

UBERLÂNDIA - MG

CERTIFICADO

Certificamos que **Augusto Barros Mendes** apresentou na forma de pôster o trabalho **"TETRAPODS IN SAMBAQUIS OF SANTA CATARINA STATE, BRAZIL"**, de autoria de **Augusto Barros Mendes, Taissa Rodrigues**, na sessão temática **Forma: Morfologia e Descrições**, durante o ***XXVI Congresso Brasileiro de Paleontologia***, realizado de 21 a 25 de outubro de 2019 em Uberlândia, MG, Brasil.

Renato Pirani Ghilardi
Presidente da Sociedade Brasileira de Paleontologia

Douglas Santos Riff
Presidente da Comissão Organizadora

Promoção — Realização — Patrocínio

UFU Universidade Federal de Uberlândia

CAPES

UNIVERSITY OF BERGEN
University Museum of Bergen

To Whom It May Concern,

This is to state that Augusto Barros Mendes (Laboratório de Paleontologia, Universidade Federal do Espírito Santo, Vitória, Brazil) attended the 10th Meeting of the International Council for Archaeozoology (ICAZ) Bird Working Group on 5-6 June 2021, and presented their presentation entitled **Seabirds as seafood: bird remains in sambaquis of southern Brazil**.

With kind regards, the Organizing Committee

Dr. Hanneke J.M. Meijer
Prof. Dr. Anne Karin Hufthammer
Dr. Samuel J. Walker
Dr. Liselotte Takken-Beijersbergen
Olaug Flatnes Bratbak
Dr. Ramona Harrison

Zooarqueología, sociedades tradicionales, biodiversidad y cambios climáticos: integrando perspectivas entre pasado y futuro.

CERTIFICADO

IV Reunión Académica del NZWG-ICAZ

En homenaje a Luz Segura

Certificamos que el trabajo, SEAFOOD AND SEA TOOLS: WHY FISHERMEN-HUNTER-GATHERERS OF SAMBAQUIS IN SOUTHERN BRAZIL EXPLOITED TETRAPODS, de los autores **Augusto Barros MENDES, Klaus HILBERT, Taissa RODRIGUES**, fue presentado en la IV Reunión Académica del Grupo de Trabajo de Zooarqueología Neotropical del International Council for Archaeozoology (NZWG-ICAZ), "Zooarqueología, sociedades tradicionales, biodiversidad y cambios climáticos: integrando perspectivas entre pasado y futuro". En homenaje a Luz Segura.

Certificamos que o trabalho, SEAFOOD AND SEA TOOLS: WHY FISHERMEN-HUNTER-GATHERERS OF SAMBAQUIS IN SOUTHERN BRAZIL EXPLOITED TETRAPODS, dos autores **Augusto Barros MENDES, Klaus HILBERT, Taissa RODRIGUES,** foi apresentado durante a IV Reunião Acadêmica do Neotropical Zooarchaeology Working Group do International Council for Archaeozoology (NZWG-ICAZ), "Zooarqueologia, sociedades tradicionais, biodiversidade e mudanças climáticas: integrando perspectivas entre passado e futuro". Em homenagem a Luz Segura.

Dr. Caroline Borges
Departamento de História - UFRPE

Dr. Pablo Marcelo Fernández
CONICET - INAPL - UBA

27-29 octubre 2021
Recife - Pernambuco - Brasil

La reunión tuvo lugar entre el 27 y 29 de octubre de 2021 y fue organizada por NZWG-ICAZ y el Núcleo de Educación e Investigación Arqueológica (NEPARQ), Departamento de Historia y Programa de Posgrado en Historia de la Universidad Federal Rural de Pernambuco (UFRPE), Brasil.

A reunião aconteceu entre os dias 27 e 29 de outubro de 2021 e foi organizada pelo NZWG-ICAZ conjuntamente com o Núcleo de Estudo e Pesquisa Arqueológica (NEPARQ), o Departamento de História e o Programa de Pós-graduação em História da Universidade Federal Rural de Pernambuco – UFRPE, Brasil.

Neotropical Zooarchaeology Working Group — International Council for ArchaeoZoology
ICAZ — International Council for Archaeozoology
UNIVERSIDADE FEDERAL RURAL DE PERNAMBUCO — Departamento de História
Programa de Pós-graduação em História
NEPARQ — Núcleo de Ensino e Pesquisa Arqueológica
CAPES

XXVII Congresso Brasileiro de Paleontologia

I Simpósio Brasileiro de Paleometria
I Simpósio sobre Biotas do Cretáceo do Brasil
II Simpósio Brasileiro de Paleontologia Antártica
1st Gondwana Devonian Symposium

02 a 06 de maio de 2022
Cuiabá - MT
Universidade Federal de Mato Grosso

CERTIFICADO

Certificamos que **Augusto Barros Mendes** realizou a apresentação do trabalho **ELECTING ELEMENTS: PREFERENCES IN CONSUMPTION OF MARINE TETRAPODS CARCASSES BY SAMBAQUI BUILDERS** de autoria de **Augusto Barros Mendes e Taissa Rodrigues Marques da Silva**, durante o **27º Congresso Brasileiro de Paleontologia - Exposição de poster.**

Cuiabá, 05 de maio de 2022

Hermínio Ismael de Araújo Júnior
Presidente da Sociedade Brasileira de Paleontologia

Silane A. F. da Silva Caminha
Presidente da Comissão Organizadora

REALIZAÇÃO PATROCÍNIO PROMOÇÃO APOIO