An Acad Bras Cienc (2024) 96(2): e20230901 DOI 10.1590/0001-3765202420230901
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

PALEONTOLOGY

Tetrapod biodiversity in sambaquis from southern Brazil

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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 mollusks 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 biodiversity 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, analyzed them concerning fragmentation, and quantified the data for the number of identified specimens (NISP) and minimum number of individuals (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.

Key words: Brazilian Atlantic Forest, fishermen-hunter-gatherers, Holocene fauna, human-animal interactions, shell mounds, zooarcheology.

INTRODUCTION

The Brazilian coast displays several archeological sites (Figuti 1993, Bissa et al. 2000), with sambaquis being one of the most common and intensely studied (Villagran 2013, Scheel-Ybert 2019). 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), mainly in the south and southeast regions of the country (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 mollusks, but they also have sediments, charcoal, lithic material, mortuary and plant remains, and other faunal remains of echinoderms, crustaceans, fish and tetrapods that fishermen-hunter-gatherers exploited during the Holocene (Figuti 1993, Wagner et al. 2011, Mendes et al. 2014).

Zooarcheological 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, artifacts, ritualistic symbols or as part of their diet) (Gaspar 1998, Bigarella 2011). Despite this selectivity bias, 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 (Faria et al. 2014, Souza et al. 2016, Silva et al. 2017, Rodrigues et al. 2018, Mendes et al. 2018, 2020, Fossile et al. 2020, Lopes

et al. 2022). Even if incomplete, this data adds to that from other sources, such as Holocene subfossils, which suffer from preservational and collector biases. Moreover, zooarcheological data allows 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, 2023a, Ferreira et al. 2019).

Most studies aimed at researching specific groups of animals in sambaquis have been dedicated to analyzing mainly malacological (e.g. Mello & Coelho 1989, Souza et al. 2010, Gernet & Birckolz 2011, Faria et al. 2014, Beauclair et al. 2016, Arruda et al. 2019, Cardoso et al. 2020) and ichthyological (e.g. Gonzalez & Amenomori 2003, Costa et al. 2012, Barbosa-Guimarães 2013, Mendes et al. 2014, 2018, Lopes et al. 2016, Ferreira et al. 2019, Fossile et al. 2019, Wagner et al. 2020) records due to the abundance of those taxa in these archeological sites. Rather, we focused our research on the tetrapod fauna, a less studied group of animals in sambaquis (Fossile et al. 2020). Some faunal studies that include tetrapods remain unpublished, making access to zooarcheological data difficult. Therefore, there is a need for published and well-developed studies that present checklists that assist in the systematic documentation of the fauna present in archeological sites, contributing to the broad understanding of paleodiversity in Brazilian territory (Fossile et al. 2023b). 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 biodiversity of mammals, birds, reptiles and amphibians that were exploited by pre-Columbian populations.

MATERIALS 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 within the Paulista zoogeographical province (Figure 1), 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, therefore, presents a plurality of environments where, not coincidentally, the sambaquis communities have settled. These include transitional ecosystems between marine and freshwater habitats, characterized by notable biological productivity and a variety of resources (DeBlasis et al. 2007, FAO 2023). The southern region of Brazil stands out as the most studied area in terms of archeology, revealing numerous technological and cultural sets that are characterized by a general chronological framework spanning approximately 12,000 years BP (Noelli 1999, Gaspar et al. 2008, Wagner et al. 2011). Table I summarizes data on the studied sambaquis available in the literature.

Material

The analyzed material is deposited at the Museu de Arqueologia e Etnologia of Universidade Federal do Paraná (T51, GUA, and GUB; Curitiba, Brazil – see Table I 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

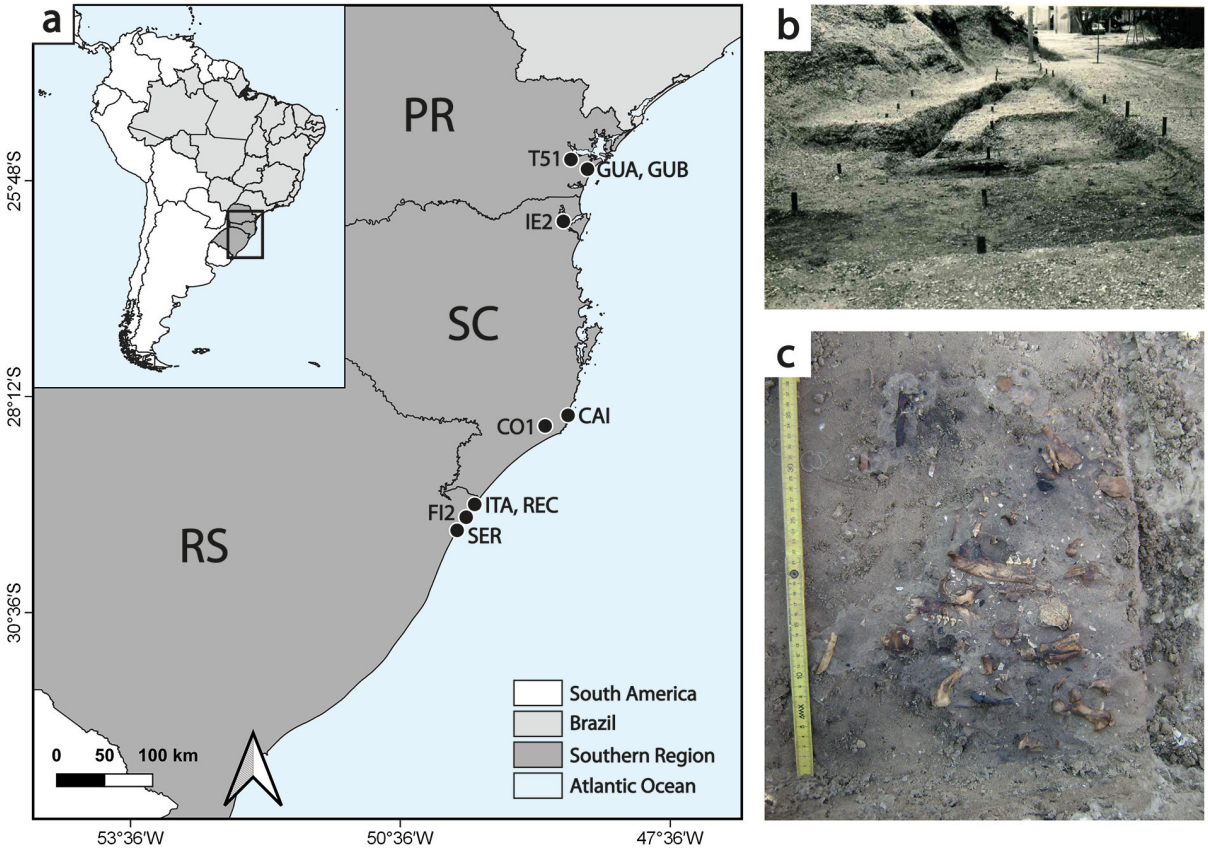

Figure 1. a: Map of the southern region of Brazil with the sambaquis' locations. b: Ilha dos Espinheiros II (IE2) excavation (Photo: Museu Arqueológico de Sambaqui de Joinville); c: *In situ* otariid remains in Figueira II (FI2) (Photo: Laboratório de Pesquisas Arqueológicas of Museu de Ciências e Tecnologia of Pontifícia Universidade Católica do Rio Grande do Sul).

Universidade Católica do Rio Grande do Sul (ITA, REC, FI2, and SER; Porto Alegre, Brazil).

As collection effort and methods differed between different sambaquis, we did not compare data between different sites. Still, detailed data on the collection methods for each site is available, as we opted to work with sambaquis that had the most accurate information (excavation and dating methodology) present in the literature or field reports (e.g. Laming-Emperaire 1968, Menezes 1968, Beck 1969, Hurt 1974, Andreatta & Menezes 1975, Wagner 2012; see references in Table I), with preference to the ones with remains of vertebrates previously sorted and washed. Moreover, no examined material had previously been submitted to zooarcheological identification analysis, which include anatomical and taxonomical identification, as well as quantification of the remains (see more below). Most of the material was stored in bags labelled "animal bones", therefore we processed it to exclude fish and modern animals as cattle and domestic pigs, and even human remains.

Most sites do not have published data on tetrapod fauna, with the exception of ITA, which has published results concerning material excavated in the 1980s (Jacobus & Gil 1987, Gazzeano et al. 1989, Rosa 1996). For ITA, we only analyzed artefacts from this excavation that had not undergone previous taxonomic analyses, as

well as material from excavations conducted in the 1990s (Hilbert L.M., unpublished data).

Zooarcheological 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); Laboratório de Mamíferos Aquáticos of Universidade Federal de Santa Catarina (Florianópolis, Brazil); Museu Arqueológico de Sambaqui de Joinville (Joinville, Brazil); Museu de Ciências e Tecnologia of Pontifícia Universidade Católica do Rio Grande do Sul (Porto Alegre, Brazil); and Universidade Federal do Espírito Santo (Vitória, Brazil). When necessary, specialized literature and online databases also were consulted to aid identification (Supplementary Material - Table SI). One of us (ABM) took measurements with a digital caliper.

The majority of faunal remains in sambaquis are commonly found altered due to pre- and/or post-depositional processes, and to investigate this phenomenon, we made taphonomic analyses concerning the degree of fragmentation (Lyman 1994a, Fernández-Jalvo & Andrews 2016). We classified the fragmentation state according to Huisman et al. (2009), who categorized bones as (1) strong and complete; (2) fragile but

Table I. 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 & 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 & 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 & Menezes 1975, Parellada & Neto 1993
Ilha dos Espinheiros II	IE2	Joinville, SC	7.090.076 721.825	1980–1989	Partially destroyed	1,170 ± 200 (Gif-6166), charcoal	Oliveira M.S.C. unpublished data, Farias & Kneip 2010
						2,730 ± 80 (Gif-6167), charcoal	
						3,000 ± 95 (St-8413), charcoal	
						3,015 ± 130 (St-8414), charcoal	
Caieira	CAI	Laguna, SC	6.848.627 717.962	1966	Partially destroyed	2,770 ± 100 (I-2628S), shell	Hurt 1974, Farias & Kneip 2010
						3,230 ± 155 (I-1618C), charcoal	
Congonhas I	CO1	Tubarão, SC	6.843.010 694.930	1967	Very destroyed	3,165 ± 55 (Az-10650), charcoal	Beck 1969, Fish et al. 2000, Farias & Kneip 2010
						3,350 ± 85 (Az-10650), charcoal	
Itapeva	ITA	Torres, RS	6.748.814 620.357	1982 / 1996	Preserved	3,130 ± 40 (Beta-248226), charcoal	Wagner G.P. unpublished data, Wagner 2012
Recreio	REC	Torres, RS	6.745.799 617.757	2007 / 2010	Partially destroyed	3,350 ± 50 (Beta-232731), charcoal	Wagner 2012, Wagner et al. 2020
						3,540 ± 50 (Beta-283771), charcoal	
Figueira II	FI2	Arroio do Sal, RS	6.738.441 612.305	2010	Partially destroyed	3,660 ± 40 (Beta-263432), charcoal	Rogge & 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

complete; (3) disintegrated, fragmented; and (4) completely decayed (here referred as heavily, instead of completely, decayed). In the case of marine mammals, we also analyzed ontogeny. Therefore, 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 & Chang 2019).

Data quantification and richness analysis

We used traditional indices in zooarcheological 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 that correspond to a specific taxon (Lyman 2008). Although NISP is considered a good index to quantifying taxonomic abundance (Lyman 2018), 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 represents the minimum count of individual animals required to account for specimens of a particular taxon. It was calculated by pairing the most representative and paired elements of the body, primarily long bones, while considering laterality, size, and age. The final value was determined as the highest number achieved for that specific element (Reitz & Wing 2008). MNE, on the other hand, is defined as the smallest number of skeletal elements required to account for a skeletal part. It was calculated by pairing bone fragments, considering factors such as laterality, size, age, and the region of the bone (Lyman 1994b). Finally, taxonomic richness (number of taxa present in a site) and frequency of occurrence (number of sambaquis in which a given taxon occurs) were analyzed following the methodology outlined by Mendes et al. (2018).

RESULTS

A total of 3,682 remains were analyzed from ten sambaquis located in Paraná, Santa Catarina, and Rio Grande do Sul spanning 4.220 +/- 200 years BP (see references in Table I). 90.33% of these remains are represented by mammals (n = 3,326), followed by birds (6.60%, n = 243), reptiles (1.38%, n = 51), and an amphibian (0.03%, n = 1). CAI was the sambaqui that presented the highest taxonomic richness, with 22 taxa. Conversely, SER recorded the lowest richness, with only one taxon (Table II).

We identified a total of 46 taxa, 44 of them at a level more inclusive than Class. Marine fauna was more abundant (Cetacea indet., NISP = 1,696; Mysticeti indet., NISP = 811; Otariidae indet., NISP = 53; *Arctocephalus* sp., NISP = 193; Magellanic penguin, *Spheniscus magellanicus*, NISP = 34; and Cheloniidae indet., NISP = 41). However, terrestrial animals were also recorded and some of them frequently, such as the South American tapir, *Tapirus terrestris* (NISP = 81) and Tayassuidae indet. (NISP = 36). Only 61 remains (1.66%) could not be identified in any taxon other than Tetrapoda (Table III and Table SII). The number of elements of unidentified taxa and the taxonomic identification at less inclusive levels than families (e.g. Mammalia, Aves and Cetacea) can be explained by their high degree of fragmentation and a large amount of non-diagnostic anatomical elements. 91.66%

Table II. NISP by Class and taxonomic richness (TR) of analyzed material per sambaqui.

Sambaqui	NISP						TR
	Mammalia	Aves	Reptilia	Lissamphibia	Not id.	Total	
Toral 51 (T51)	51	20	0	0	9	80	10
Guaraguaçu A (GUA)	2,053	0	8	0	3	2,064	8
Guaraguaçu B (GUB)	421	13	39	0	14	487	16
Ilha dos Espinheiros II (IE2)	57	3	1	0	4	65	15
Caieira (CAI)	328	24	3	1	19	375	22
Congonhas I (CO1)	30	110	0	0	1	141	19
Itapeva (ITA)	125	0	0	0	0	125	5
Recreio (REC)	20	1	0	0	0	21	4
Figueira II (FI2)	219	72	0	0	11	302	10
Sereia do Mar (SER)	22	0	0	0	0	22	1
Total	**3,326**	**243**	**51**	**1**	**61**	**3,682**	

of the remains were fragmented, 3.29% heavily decayed, 2.93% strong and complete bones, and 2.12% fragile but complete bones. Moreover, only 16 out of 2,556 cetacean remains could be identified at the species level.

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 contrast, excavation on CO1 had a mitigation aspect and lasted 23 days (Beck 1969). In SER, a total of 18 m² were excavated during 3 samplings that were conducted in 47 days of work, with an average depth of the archeological layer of 0.75 m (Wagner 2012). All these differences in the methodologies used in each sambaqui provide a different volume of material for taxonomic identification.

The identification of zooarcheological remains depends on many factors such as the researcher's analytical skill level, completeness of modern comparative osteological collections, and fragmentation level of the archeological material (Grayson 1984, Lyman 2008, 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 (NISP = 333, see Table IV and Table SIII). 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. Fragmentation is a taphonomic process that directly impacts the identifiability of archeological vestiges, and consequently the abundance of identified taxa (Lyman 1994a), especially when they have fragile bones, such as amphibians (Stoetzel et al. 2012). As in our study, Pavei et al. (2015) also recorded only one remain of Anura indet. in Sambaqui Papagaio, Santa Catarina, and suggest that these animals were not appreciated by sambaqui builders for food consumption. However, it is

Table III. NISP, MNI, frequency of occurrence (F), and material weight of identified taxa. See Table I for sambaquis' codes. See Table SII 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) White-lipped peccaries	11	0.30	6	4.11	3	GUB, CAI, CO1	71.398
	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

Table III. Continuation.

	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 Black skimmers	2	0.05	1	0.68	1	CO1	0.942
	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

Table III. Continuation.

	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**

Table IV. NISP and MNE of identified anatomical elements grouped by axial cranial, axial post-cranial, shoulder girdle, pelvic girdle, stylopodia, zeugopodia, and autopodia zones. See Table SIII 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**

unlikely that the sambaqui builders did not consume amphibians, given that Anura indet. and *Rhinella* sp. have already been recorded in six and three sambaquis, respectively (Mendes A.B., unpublished data). Thus, the small amount of remains of this class in sambaquis is probably due to the fragility of their bones.

The presence of cetaceans in the sambaquis we studied is remarkable (Table III and Figures 2 and 3). Their zooarcheological 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. This determination was made possible through the analysis of tympanic bullae, which provide species-level diagnostics in Mysticeti (Ekdale et al. 2011). Unlike other bones, tympanic bullae are relatively well-preserved in the archeological 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 & Chang (2019): relatively large size

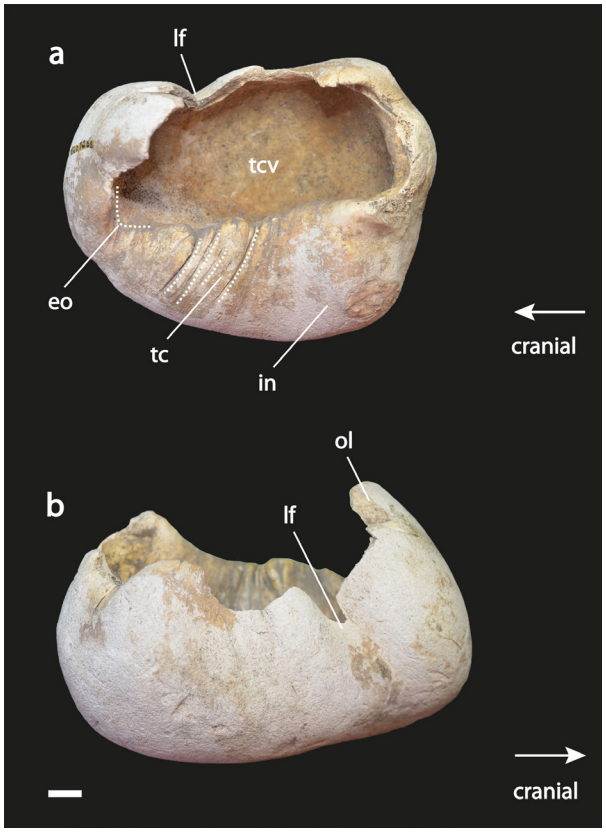

Figure 2. Right tympanic bulla of *Eubalaena australis* (Guaraguaçu A, GUA) in dorsal (a) and lateral (b) views. Abbreviations: eo, Eustachian outlet; in, involucrum; lf, lateral furrow; ol, outer lip; tc, transverse creases; tcv, tympanic cavity. Scale bar: 1 cm. Photos of remain: A.B.M. Source of remain: Collection of Museu de Arqueologia e Etnologia of Universidade Federal do Paraná (Curitiba, Paraná).

(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 2).

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), and may have been a seasonal resource for fisherman-hunter-gatherers. 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).

In the analyzed sambaquis' records, five individuals were small cetaceans (Delphinidae and the common bottlenose dolphins, *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, Fossile et al. 2023a), they had the necessary toolkit to actively hunt smaller-sized cetaceans, in the same way that they also exploited a diversity of sharks and rays, exemplifying hunt/fisheries of large/medium specimens/individuals (Lopes et al. 2016, Fossile et al. 2020). 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

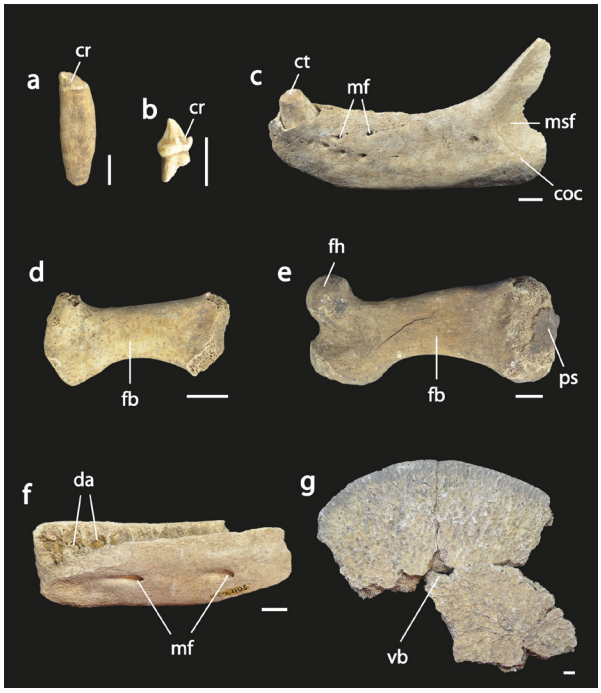

Figure 3. Remains of marine mammals. a: upper incisor tooth of *Otaria flavescens* (Caieira, CAI) in labial view; b: postcanine tooth of *Arctocephalus* sp. (Figueira II, FI2) in lingual view; c: left mandible of *Arctocephalus* sp. (Caieira, CAI) in lateral view; d: right femur of juvenile *Arctocephalus* sp. (Caieira, CAI) in anterior view; e: right femur of adult *Arctocephalus* sp. (Caieira, CAI) in anterior view; f: distal portion of left mandible of Delphinidae indet. (Guaraguaçu A, GUA) in lateral view; g: vertebral disc of Mysticeti (Guaraguaçu, 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. Photos of remains: A.B.M. Source of remains: Collections of Museu de Arqueologia e Etnologia of Universidade Federal do Paraná (Curitiba, Paraná), Museu de Arqueologia e Etnologia of Universidade Federal de Santa Catarina (Florianópolis, Santa Catarina), and Laboratório de Pesquisas Arqueológicas of Museu de Ciências e Tecnologia of Pontifícia Universidade Católica do Rio Grande do Sul (Porto Alegre, Rio Grande do Sul).

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 3). Fur seals, mainly *Arctocephalus australis*, and sea lions (*Otaria flavescens*) are frequent in archeological sites on the South American coast (e.g. Schiavini 1993, Castilho & Simões-Lopes 2008, Borella 2014). 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* sp..

There are currently three species of *Arctocephalus* in Brazil: the South American fur seal (*A. australis*), the Subantarctic fur seal (*A. tropicalis*), and the Antarctic fur seal (*A. gazella*) (Monteiro-Filho et al. 2013). As in some previous studies on the fauna of southern Brazilian sambaquis (e.g. Bandeira D.R., unpublished data, 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 analyzed 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-canines for *A. tropicalis*, and unicuspid with flat fifth and sixth post-canines for *A. gazella* (Repenning et al. 1971, Pinedo et al. 1992). 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).

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 & 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 according to the authors. 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 bycatch (Figure 4), as they are in fishery activities nowadays (Žydelis et al. 2013).

The fishermen-hunter-gatherers also exploited terrestrial environments. The hunting of white-lipped peccaries (*Tayassu pecari*) and collared peccaries (*Dicotyles tajacu*), here identified by dental characteristics—*D. tajacu* has slenderer, more elongate, and more hypsodont lower canine teeth (Woodburne 1968; Figure 5)—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 (*Caiman latirostris*, Figure 6) suggests that environments such as swamps and wetlands were also exploited.

Five currently threatened species according to Brazilian Red List of Threatened Species (ICMBio 2018) are present in our inventory: the South American tapir (*Tapirus terrestris*), the white-lipped peccary (*Tayassu pecari*), the pampas deer (*Ozotoceros bezoarticus*), the southern right whale (*Eubalaena australis*), and the green sea turtle (*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

Figure 4. Seabird remains. a: proximal and middle portions of right humerus of *Puffinus* sp. (Congonhas I, CO1) in anterior view; b: middle and distal portions of left humerus of *Larus dominicanus* (Congonhas I, CO1) in posterior view; c: right femur of *L. dominicanus* (Congonhas I, CO1) in posterior view, d: distal portion of left tarsometatarsus of *Thalassarche* sp. (Figueira II, FI2) in anterior view; e: right coracoid of *Spheniscus magellanicus* (Guaraguaçu B, GUB) in ventral view; f: right humerus of *S. magellanicus* (Caieira, CAI) in lateral view; g: right femur of *S. magellanicus* (Caieira, CAI) in posterior view; h: distal portion of tibiotarsus of *S. magellanicus* (Figueira II, 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; dfv, 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. Photos of remains: A.B.M. Source of remains: Collections of Museu de Arqueologia e Etnologia of Universidade Federal do Paraná (Curitiba, Paraná), Museu de Arqueologia e Etnologia of Universidade Federal de Santa Catarina (Florianópolis, Santa Catarina), and Laboratório de Pesquisas Arqueológicas of Museu de Ciências e Tecnologia of Pontifícia Universidade Católica do Rio Grande do Sul (Porto Alegre, Rio Grande do Sul).

from sambaquis (Bandeira D.R., unpublished data, 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 and 2020) based on records of a sambaqui in Babitonga Bay, SC. Land resources, such as Tayassuidae, also were exploited by sambaquis' builders in the Lagoa dos Freitas (Santos et al. 2018) and Içara 06 (Rosa 2006, Teixeira 2006), both located in Santa Catarina, demonstrating a high exploitation of peccaries. *T. terrestris* was also registered in other sambaquis in the Brazilian south region (Bandeira D.R., unpublished data, Bryan 1993, Pavei et al. 2015, Santos et al. 2018), as well *E. australis* (Castilho 2008) and *C. mydas* (Ramos Junior M., unpublished data). 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.

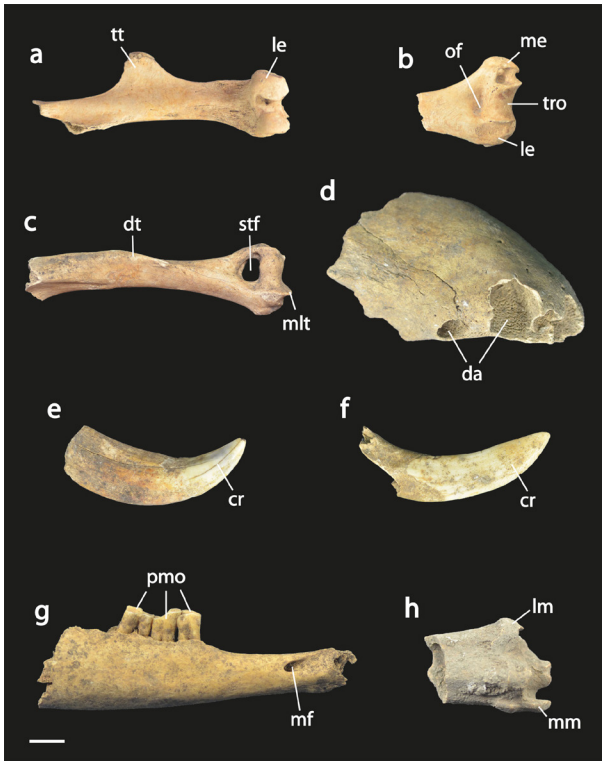

Figure 5. Remains of terrestrial mammals. **a**: middle and distal portions of right femur of Dasypodidae indet. (Ilha dos Espinheiros II, IE2) in anterior view; **b**: distal portion of left humerus of *Alouatta* sp. (Ilha dos Espinheiros II, IE2) in posterior view; **c**: middle and distal portions of left humerus of *Cuniculus paca* (Guaraguaçu B, GUB) in anterior view; **d**: distal portion of right maxilla of *Tapirus terrestris* (Congonhas I, CO1) in lateral view; **e**: right lower canine tooth of *Tayassu pecari* (Caieira, CAI) in labial view; **f**: right lower canine tooth of *Dicotyles tajacu* (Caieira, CAI) in labial view; **g**: distal portion of right mandible of *Mazama* sp. (Caieira, CAI) in lateral view; **h**: distal portion of left tibia of *Ozotoceros bezoarticus* (Congonhas I, 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; **mlt**, 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. Photos of remains: A.B.M. Source of remains: Collections of Museu de Arqueologia e Etnologia of Universidade Federal do Paraná (Curitiba, Paraná), Museu Arqueológico de Sambaqui de Joinville (Joinville, Santa Catarina), and Museu de Arqueologia e Etnologia of Universidade Federal de Santa Catarina (Florianópolis, Santa Catarina).

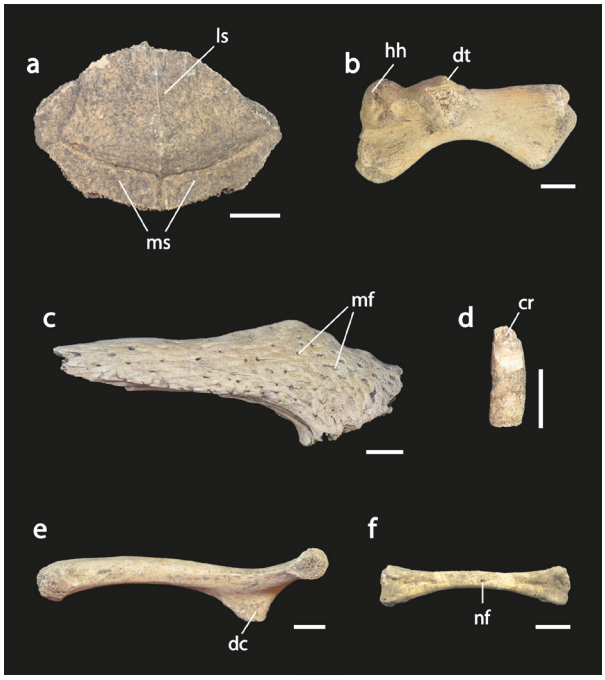

Figure 6. Remains of herpetofauna. **a**: distal portion of carapace of Cheloniidae indet. (Guaraguaçu B, GUB) in dorsal view; **b**: left humerus of *Chelonia mydas* (Ilha dos Espinheiros II, IE2) in ventral view; **c**: distal portion of right mandible of *Caiman latirostris* (Guaraguaçu A, GUA) in ventral view; **d**: lower tooth of *C. latirostris* (Guaraguaçu A, GUA) in labial view; **e**: left humerus of *C. latirostris* (Guaraguaçu B, GUB) in medial view; **f**: left tibiofibula of Anura indet. (Caieira, 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. Photos of remains: A.B.M. Source of remains: Collections of Museu de Arqueologia e Etnologia of Universidade Federal do Paraná (Curitiba, Paraná), Museu Arqueológico de Sambaqui de Joinville (Joinville, Santa Catarina), and Museu de Arqueologia e Etnologia of Universidade Federal de Santa Catarina (Florianópolis, Santa Catarina).

Terrestrial animals were also exploited, especially *Tayassu pecari* and *Dicotyles tajacu* (peccaries), but we also recorded *Cuniculis paca* (lowland pacas), *Tapirus terrestris* (south american tapirs), *Mazama* sp. and *Ozotoceros bezoarticus* (deers), and *Caiman latirostris* (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 zooarcheological 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 remains of sambaquis never studied before in a taxonomic approach and, focusing on tetrapod fauna—a relatively less studied group of animals in these archeological sites—, contributes to a greater understanding of the Holocene biodiversity, sambaqui culture, and builders-animals' interactions.

Acknowledgments

We would like to thank everyone who contributed to access sambaquis' material [S.P. Carmo Junior (MAE-UFPR); R.M.M. Veiga, A.M.P. Santos, D.R. Bandeira (MASJ); L.Z. Scherer, A.L. Trivia (MArquE-UFSC); K. Hilbert, L.M. Hilbert, C.E.F. Melchiades (LPA-MCT-PUCRS)] and osteological collections [J. Oliveira, S.M. Vaz (Mammalogy MN-UFRJ); M.A. Raposo, T.G. Capdeville, G.G. Araujo (Ornithology MN-UFRJ); P. Passos, M.W. Cardoso (Herpetology MN-UFRJ); P.C. Simões-Lopes (Mammalogy UFSC); C.S. Fontana (Mammalogy and Ornithology MCT-PUCRS); Y.R.L. Leite, M.P. Nascimento, J.Z. Nodari, E.B. Guerra (Mammalogy UFES)]. We are also very grateful to all researchers who helped in the taxonomic and anatomic identifications of mammals [M. Laeta (MN-UFRJ); P.C. Simões-Lopes, M.E. Graipel (LAMAQ-UFSC); F.A. Machado (UMass); S. Ferrasso (IAP); P.V. Castilho (UDESC); N.R. Chimento (CONICET), F.M.M. Mejía (INAH), A. Chahud (USP), and D.C.S. Borges (FPM and FCJ)], birds [G.R.R. Brito (UFSC)], reptiles [L.G. Souza (FEA); T.F. Mariani (MN-UFRJ); G.S. Ferreira (SHEP); B.M. Hörmanseder (UFES)], and amphibian [I.S.N. Silva-Filho (UNESP); M.W. Cardoso (MN-UFRJ)], as well as E.P. Silva and M.R. Duarte (UFF) for helpful comments on an earlier version of this manuscript, and R. Buchmann (UFES) for helping to edit the figures in this paper. Finally, we thank the two reviewers for the evaluations that were sent. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001 (A.B. Mendes' PhD scholarship).

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SUPPLEMENTARY MATERIAL

Table SI-SIII.

How to cite
MENDES AB & RODRIGUES T. 2024. Tetrapod biodiversity in sambaquis from southern Brazil. An Acad Bras Cienc 96: e20230901. DOI 10.1590/0001-3765202420230901.

Manuscript received on August 14, 2023;
accepted for publication on February 4, 2024

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