Received: 10 December 2020 | Revised: 13 April 2021 | Accepted: 23 May 2021
DOI: 10.1002/ajpa.24342

RESEARCH ARTICLE

American Journal of PHYSICAL ANTHROPOLOGY
WILEY

Population history of Brazilian south and southeast shellmound builders inferred through dental morphology

Daniel Fidalgo[1,2] | **Mark Hubbe**[3,4] | **Veronica Wesolowski**[1]

[1]Museu de Arqueologia e Etnologia, Universidade de São Paulo, São Paulo, Brazil
[2]Centro de Investigação em Antropologia e Saúde, Universidade de Coimbra, Calçada Martim de Freitas, Coimbra, Portugal
[3]Department of Anthropology, Ohio State University, Columbus, Ohio, USA
[4]Instituto de Arqueología y Antropología, Universidad Católica del Norte, San Pedro de Atacama, Chile

Correspondence
Daniel Fidalgo, Museu de Arqueologia e Etnologia da Universidade de São Paulo, Av. Prof. Almeida Prado, 1466 - Butantã, São Paulo - SP, 05508-070, Brasil.
Email: danielfidalgo15@usp.br

Funding information
Universidade Federal do Paraná; Universidade de São Paulo; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: 001; Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Numbers: 2017/20637-4, 2019/18289-3

Abstract

Objective: The Southeast and South Coast of Brazil was inhabited during most of the Holocene by shellmound builders. Although there are cultural differences in the archaeological record between regions, it is still debatable how these differences may relate to different population histories. Here, we contribute to this discussion by exploring dental morphological affinities between several regional series.

Materials and Methods: Dental morphology of 385 individuals from 14 archaeological sites was analyzed using the Arizona State University Dental Anthropology System. Fifteen traits were used to explore morphological affinities among series through Euclidean distance, Mean Measure of Divergence, and Principal Component Analysis. Mantel matrix correlation and partial correlation tests were used to examine the association between biological, geographic, and chronological distances.

Results: Morphological affinities show that ceramic and nonceramic South Coast groups cluster and differ from most Southeast series. In contrast, Southeast coastal and riverine groups display high morphological variance, showing less biological coherence among them. These biological distances between regions are partially explained by geography, but not by chronology.

Conclusions: The results support that these coastal populations were low-mobility groups. Although interactions between individuals of different regions likely existed, gene flow occurred mostly among individuals from local or adjacent areas. The introduction of ceramic in the South Coast is not associated with changes in dental morphology patterns, suggesting its adoption is not exclusively associated with the arrival of different biological groups. Southeast coastal and riverine groups show high phenotypic diversity, suggesting a different history of human occupation and cultural development than observed in the South Coast.

KEYWORDS
archaeology, bioarchaeology, discrete traits, Itaipu tradition, Itararé-Taquara, Sambaquis

1 | INTRODUCTION

The South and Southeast Coast of Brazil were first inhabited by shellmound builders at least 8 kya (kya, thousand years ago) (Calippo, 2004, 2008; Lima et al., 2002). Initial settlements are hard to identify, as earlier evidence of human presence may now be submerged or destroyed due to sea level fluctuations throughout the Holocene (Calippo, 2004, 2010; Martin, 2003). Until ~1 kya, these groups built shellmounds (known locally as *sambaquis*), which are archaeological sites of variable size, constructed through the deliberate accumulation of shell-valves and vertebrate faunal remains (mainly fish), interspaced by soil levels, in a sequence of layers of varying composition and thickness. Sambaquis were used for many different purposes, and contain various artifacts, hearths, postholes, and human burials (DeBlasis et al., 1998; Gaspar, 2004; Lima, 2000). Similarities among the material culture found across the South and Southeast shellmounds suggests their builders shared a widespread archaeological culture (Gaspar, 2004). However, local variations within this larger spectrum also show the existence of regional cultural contexts, which were probably tied to unique histories of human occupation and cultural development. While these differences have been well documented in the archaeological literature (Gaspar, 2004; Lima, 2000; Villagran, 2013), and can be defined within specific geographic regions, the biological relationship between groups from different regional contexts is still unresolved (Bartolomucci, 2006; Filippini, 2004; Neves, 1988; Okumura, 2007).

In this study, we aim to contribute to the general discussion about the process of human occupation of the Brazilian coast by exploring how shellmound builders and other coastal populations were biologically related over space and time. To do so, we study the biological affinities among three well defined geographic units, with specific and well-recognized cultural differences: Southeast Coast (São Paulo and Rio de Janeiro states), South Coast (Santa Catarina and Paraná states), and Vale do Ribeira (a river valley that marks the border between the South and Southeast coast) (Figure 1).

We infer biological affinities through the analysis of dental nonmetric traits. Teeth are commonly the most preserved remains in the archaeological record due to their resistance to postmortem damage and taphonomic changes (Alt et al., 1998; Hillson, 2005). Their morphology is largely influenced by neutral evolutionary processes, showing high correlations to neutral genetic signatures, and therefore can be used to reconstruct past migratory events and population histories (Hubbard et al., 2015; Irish et al., 2020; Rathmann et al., 2017; Rathmann & Reyes-Centeno, 2020; Scott & Irish, 2013). Dental nonmetric traits have been successful in assessing biological relatedness between worldwide populations (Scott & Turner II, 1997), large migratory expansions (Greenberg et al., 1986; Scott et al., 2018; Turner II & Scott, 2013), and population dynamics within specific regional and historical contexts (Irish et al., 2017; Rathmann et al., 2019; Sutter, 2009).

So far, most studies that explore biological affinities among Brazilian coastal populations have focused on cranial analysis (Filippini, 2004; Filippini & Eggers, 2006; Hubbe et al., 2009; Neves, 1988; Neves et al., 2005; Neves & Okumura, 2005;

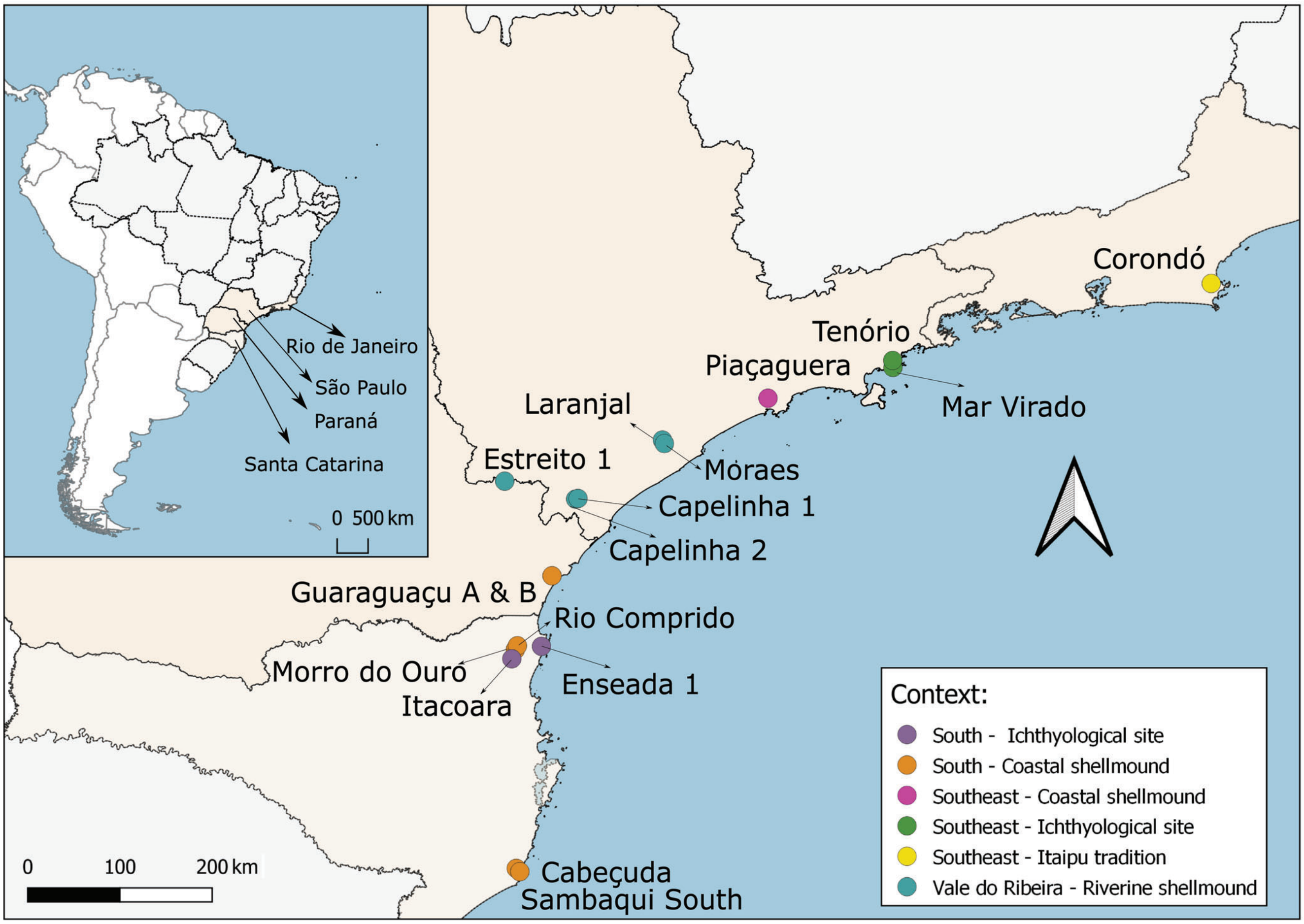


FIGURE 1 Geographic units and archaeological sites included in this study. Map made using QGIS desktop 3.12.2 (QGIS, 2020)

Okumura, 2007, 2014). However, as we know from previous cranial and dental studies, results are not always consilient between both methods (Scott et al., 2018). To aggravate this, dental morphological studies focusing specifically on shellmound builders are still very scarce. Only one dissertation on regional biological variation exists, focusing on riverine and coastal populations of the South Coast, but without comparative series for the Southeast Coast (Bartolomucci, 2006). Other works involving dental morphology of Brazilian shellmound builders usually focus on broader topics, such as the peopling of the Americas (Greenberg et al., 1986; Huffman, 2014; Turner II & Scott, 2013). As a consequence, little attention has been paid to how the analysis of dental nonmetric traits contributes to regional debates that drive regional archaeological and anthropological inquiries.

Therefore, to contribute to dental morphological studies focusing on regional and local discussions, our goal is to test the hypothesis that cultural distinctions among the three geographic regions studied are correlated to the biological differentiation among their populations. In other words, this study tests whether the different cultural patterns observed in the archaeological record of these regions are the result of biological isolation, or if they developed independently of biological contact and gene flow.

1.1 | The geographic context of coastal populations

1.1.1 | South coast

The South Coast comprises coastal archaeological series from the states of Paraná and Santa Catarina (Figure 1). The South Coast can be divided into two different archaeological contexts: an earlier one defined by the construction of large shellmounds, and a later phase characterized by shallow ichthyological sites. The shellmound builder phase lasted from ~7 to 1 kya, and is defined by the presence of fisher-hunter-gatherer populations that built shellmounds in ecotone environments around lagoons, estuarine bays, and coastal islands (DeBlasis et al., 2007; Giannini et al., 2010). They were highly adapted to marine-related environments and have been inferred to be low-mobility groups, given their continuous occupation for thousands of years of several shellmounds, which could reach up to 30 m of height (Bastos, 2009; DeBlasis et al., 1998, 2007; Kneip et al., 2018). Here, we focus on shellmound builders from the states of Santa Catarina and Paraná, which have been included in several studies of morphological affinities in the past (Hubbe, 2006; Hubbe et al., 2009; Neves, 1988; Okumura, 2007). Overall, these studies suggest that these populations share strong morphological affinities among local populations (Hubbe, 2006; Hubbe et al., 2009; Okumura, 2007), with some studies showing that the Paraná groups also share similarities with Southeast Coast populations when craniometric data is considered (Okumura, 2007), and with riverine shellmound builders from Vale do Ribeira when dental traits are explored (Bartolomucci, 2006). Such affinities can be partially explained by the geographic location of the Paraná coast, as it borders both Vale do Ribeira and the Southeast Coast (Figure 1).

The second archaeological context is represented by shallow sites that start to appear around 1.7 kya, which show noteworthy differences from previous sites on the South Coast (Giannini et al., 2010). These later sites can be best described as ichthyological sites, characterized by a mixture of dark-colored sediment, fish remains, and only a small portion of shell-valves (Giannini et al., 2010; Nishida, 2001; Uchôa, 1973; Villagran, 2012), suggesting that shell-valve accumulation was less important for constructive purposes in this context (Giannini et al., 2010). Some of these sites appear as layers on top of preexisting shellmounds, showing a reappropriation of the former sites (Bandeira, 1992; Bandeira et al., 2013; Beck, 1972; Bryan, 1977; Klokler, 2008). In the South Coast, some ichthyological sites have human burials associated with pottery, closely related to the Taquara-Itararé tradition (Bandeira, 1992, 2004; Bandeira et al., 2013; Beck, 1972). This tradition is associated with Jê speaking groups, that expanded from the inland plateau into the South Coast around 1 kya, although it is not clear how and to what degree they interacted with previously established coastal groups (Beck, 1972; DeBlasis et al., 2014). Based on archaeological data, some authors argue that this event did not involve a significant cultural change for coastal societies (Bryan, 1977), while others defend that the appearance of ceramic in the coast is the result of a large-scale migration from inland groups (Beck, 1972; Schmitz, 1984). Previous morphological studies have supported a change in the genetic make-up of coastal groups with the appearance of ceramic (Neves, 1988; Okumura, 2007).

1.1.2 | Southeast coast

The Southeast Coast comprises archaeological series from the Brazilian Southeast states of São Paulo and Rio de Janeiro. This geographic unit region is marked by three discernible archaeological contexts. The earliest and longest one is associated with shellmound builders, who occupied the area between ~8 and 1 kya (Calippo, 2004, 2010; Lima et al., 2002). Like South Coast shellmound builders, they built shellmounds around ecotone environments such as lagoons, bays, mangroves, and coastal islands (Afonso, 2017). However, unlike the South, where shellmounds reached monumental dimentions, most Southeast Coast shellmound have around 2 or 3 m of maximum height (Lima, 2000). Cranial morphological studies suggest Southeast shellmound builders form a cluster that contrasts with South Coast shellmound builders and coastal ceramic groups (Okumura, 2007). But their relationship to riverine shellmound builders is still a matter of debate, as some craniometric studies suggest they share similar phenotypic patterns (Neves & Okumura, 2005; Okumura, 2007), while cranial nonmetric studies support the hypothesis that riverine and coastal populations are two distinct biological components (Filippini, 2004; Filippini & Eggers, 2006).

The second archaeological context observed in the Southeast is represented by ichthyological sites, which are very similar to those described for the South Coast, and usually have around 1 m of maximum height (Amenomori, 2005; Nishida, 2001). However, they have a very important difference from their South counterparts, which is the lack of ceramic associated to their original builders (Uchôa, 1973, 2009). As a result, any relationship to inland societies is not evident in the archaeological record. Southeast ichthyological sites appear around 3.8 kya (Uchôa, 2009) and co-existed with shellmounds of the coast of São Paulo, until both practices ceased ~600 years ago (Afonso, 2017). Few studies have focused on the biological affinities of individuals from Southeast ichthyological sites. According to craniometrics, these groups were closely related to Southeast shellmound builders (Okumura, 2007), but cranial nonmetric studies support closer affinities to shellmound builders from both the Southeast and South Coast (Filippini, 2004).

Finally, the third archaeological context mentioned for the Southeast Coast is found in the coast of Rio de Janeiro, starting at ~4 kya (Dias, 1975; Machado, 1984; Schmitz, 1987). It is often associated to the Itaipu tradition, a term currently used to describe coastal sites possibly related to incipient plant cultivation in Rio de Janeiro (Dias, 1975; Gaspar, 1996). One of its most emblematic sites is Corondó, dated to between 4 and 3 kya (Machado, 1984). In terms of dental morphology, individuals from Corondó differ from coastal shellmound builders (Turner II & Scott, 2013). While shellmound builders have an intermediate dental complex between North and South Native Americans, Corondó has a dental pattern clearly related to South Americans (Turner II & Scott, 2013). On the other hand, based on cranial morphology, Corondó is closely related to Southeast shellmound builders (Okumura, 2007). Therefore, dental and cranial morphology show conflicting results about the biological affinities between individuals of the Itaipu tradition and shellmound builders.

1.1.3 | Vale do Ribeira

From the state of Rio de Janeiro to Santa Catarina, the meridional inland plateau is separated from the Atlantic coast by a complex of mountain ranges known as Serra do Mar (Dominguez, 2006). This complex is only transposable through river valleys such as Vale do Ribeira, which is known to be inhabited since the early Holocene (Barreto, 1988; DeBlasis, 1988;Figuti, 2004; Figuti et al., 2013). Vale do Ribeira is also the geo-political landmark which divides the South and Southeast states of Brazil (Figure 1).

The earliest evidences of human occupation in Vale do Ribeira is associated with riverine shellmounds that, similarly to coastal sites, were often used as burial grounds (Collet, 1985; Collet & Prous, 1977; Figuti, 2004). As riverine shellmounds are located within the Atlantic Forest, they were built through the accumulations of terrestrial gastropods instead of coastal shell valves (Figuti, 2004; Plens, 2007, 2009). Their size is usually around 2 m of height, similar in size to coastal shellmounds of the Southeast Coast (Figuti, 2004).

The earliest human skeleton from Vale do Ribeira is a male young-adult found within burial 2 of the riverine shellmound Capelinha 1, dated to the early Holocene (Figuti, 2004; Figuti et al., 2013). However, his association to the riverine shellmound culture is not uncontested, as his funerary practices differ from every other individual found in the site (Alves, 2008; Eggers et al., 2011; Figuti, 2004). Also, he shares stronger phenotypic affinities with early Holocene inland groups of Lagoa Santa than with other riverine shellmound builders (Neves et al., 2005; Neves & Okumura, 2005). These characteristics, combined with the fact that there is a chronological gap of almost 3000 years between him and other burials from the same site (Figuti, 2004; Figuti et al., 2013), suggests this individual from Capelinha I may not represent the initial occupation of the river valley by shellmound builders. Instead, he probably represents an earlier occupation of the Ribeira de Iguape by inland groups with a Paleoamerican cranial morphology, which was replaced by the arrival of shellmound builders during the Holocene (Neves et al., 2005; Neves & Okumura, 2005). For these reasons, in this study we exclude burial 2 from our analyses.

Apart from this outlier, riverine shellmound builders are usually perceived as a homogenous biological group by genetics, cranial, and dental morphology (Bartolomucci, 2006; Filippini, 2004; Filippini & Eggers, 2006; Neves & Okumura, 2005; Posth et al., 2018; Strauss et al., 2015). They inhabited Vale do Ribeira until ~1 kya, while also maintaining some contact with coastal groups, as represented by artifacts made from marine animals (e.g., punctured shark teeth) found within riverine sites (Figuti et al., 2013; Plens, 2007). Despite the cultural similarities in the structure of sites, and the evidence of some degree of contact between the riverine and coastal groups, their biological relationship is still largely unresolved. Some dental morphological and craniometric studies indicate a strong affinity between them (Bartolomucci, 2006; Hubbe et al., 2014; Neves & Okumura, 2005; Okumura, 2007), while cranial nonmetric suggests stronger biological affinities with inland groups from the early Holocene (Filippini, 2004; Filippini & Eggers, 2006).

2 | MATERIALS AND METHODS

The dental morphology of 385 individuals from 14 sites was analyzed by the first author (DF) using the Arizona State University Dental Anthropology System (ASUDAS) (Turner II et al, 1991). A brief description of each site and sample can be consulted in Data S1. As skeletal remains were mostly fragmented, series are usually characterized by collections of individuals represented by partially recovered material. Furthermore, although teeth are well preserved within the archaeological record, sample sizes were affected because many teeth with severe dental wear were not scored (Burnett et al., 2013). This limitation is particularly relevant when studying past Brazilian coastal societies, which are often marked by severe and sometimes atypical dental wear patterns (Cunha & Cunha, 1960; Machado, 1984; Turner II & Machado, 1983; Wesolowski, 2007). Therefore, due to limited sample sizes, individuals from different sites but with similar cultural background and chronology were pooled into combined series, resulting in a total of nine series representing the three geographical regions explored. As previously mentioned, burial 2 from Capelinha 1 was excluded from this study due to its archaeological, chronological,

TABLE 1 Coordinates in Universal Transverse Mercator (UTM), sample sizes, and radiocarbon data of each series. Radiocarbon dates were calibrated with OxCal v4.4.3 Bronk Ramsey (2009), using calibration curve SHCal20 (Hogg et al., 2020) for terrestrial samples and Marine20 (Heaton et al., 2020) for marine samples. Human skeletal remains from coastal sites were calibrated using a mixed curve (50/50 SHCal20 and Marine20). Conventional and calibrated dates are in Before Present (BP) time scale.

Series (coord. UTM)	N	Sites	Context	Material	Sample	Conventional BP	Cal. BP (95.4%)	Reference
Guaraguaçu (22 J 754110 7,166,741)	69	Guaraguaçu A	South–Coastal shellmound	-	-	4220 ± 200	-	Menezes (1968)
		Guaraguaçu A		-	-	4134 ± 134	-	Posse (1978)
		Guaraguaçu B		Charcoal (Layer 9)	-	4128 ± 134	4962–4156	Laming-Emperaire (1968)
Joinville (22 J 730952 7,084,846)	54	Enseada 1	South–Ichthyological site	-	CAMS-53144	1390 ± 50	-	DeMasi (2001)
		Itacoara		Ceramic[a]	ITA-1/ LVD876	550 ± 55	-	Bandeira (2004)
		Itacoara		Charcoal	KIA-21796	1570 ± 20	1512–1354	Bandeira (2004)
		Itacoara		Bone (Sep.2)	-	1250 ± 30	1049–812	Wesolowski et al. (2010)
Morro do Ouro (22 J 716896 7,087,669)	70	Morro do Ouro	South–Coastal shellmound	Bone (Sep.80)	-	3870 ± 40	4151–3876	Wesolowski et al. (2010)
		Morro do Ouro		Bone (Sep.28)	Beta-93,152	4030 ± 40	4401–4096	Wesolowski (2007)
		Morro do Ouro		Bone (Sep.22)	AA-104768	4086 ± 42	4440–4151	Filippini et al. (2019)
		Morro do Ouro		Bone (Sep.2)	Beta-444,034	4200 ± 30	4583–4318	Filippini et al. (2019)
		Morro do Ouro		Bone (Sep.59)	AA-104770	3938 ± 55	4294–3908	Filippini et al. (2019)
		Morro do Ouro		Bone (Sep.31)	-	4300 ± 50	4805–4442	Wesolowski et al. (2010)
		Morro do Ouro		Teeth (Sep.13)	AA-104767	4425 ± 39	4867–4610	Pezo-Lanfranco et al. (2018)
Rio Comprido (22 J 718965 7,091,882)	48	Rio Comprido	South–Coastal shellmound	-	SI-1579	2170 BC[b]		Prous and Piazza (1977)
		Rio Comprido		-	SI-1580	2490 BC[b]		Prous and Piazza (1977)
		Rio Comprido		-	SI-1581	2665 BC[b]		Prous and Piazza (1977)
		Rio Comprido		-	SI-1583	2865BC[b]		Prous and Piazza (1977)
		Rio Comprido		Bone (Sep.4A)	Beta-444,032	1140 ± 30	916–737	Pezo-Lanfranco et al. (2018)
		Rio Comprido		Wood	GIF-3646	4560 ± 110	5465–4864	Martin et al. (1984)
		Rio Comprido		Bone (Sep.68)	Beta-444,033	5090 ± 30	5682–5474	Pezo-Lanfranco et al. (2018)
		Rio Comprido		Bone (Sep.3)	Beta-448,933	3820 ± 30	4077–3841	Pezo-Lanfranco et al. (2018)
		Rio Comprido		Bone (Sep.1A)	Beta-448,932	3510 ± 30	3682–3445	Pezo-Lanfranco et al. (2018)
		Rio Comprido		Bone (Sep.6)	AA-104771	4320 ± 61	4824–4446	Pezo-Lanfranco et al. (2018)
Cabeçuda (22 J 713668 6,851,761)	12	Cabeçuda (locus6)	South–Coastal shellmound	Bone (Sep.5)	Beta-383,565	2990 ± 30	3026–2780	Farias & DeBlasis et al. (2014)
		Cabeçuda (locus6)		Bone (Sep.15)	Beta-383,566	3030 ± 30	3098–2843	Farias & DeBlasis et al. (2014)
		Cabeçuda (locus6)		Bone (Sep.20)	Beta-383,567	2920 ± 30	2924–2749	Farias & DeBlasis et al. (2014)

(Continues)

TABLE 1 (Continued)

Series (coord. UTM)	N	Sites	Context	Material	Sample	Conventional BP	Cal. BP (95.4%)	Reference
Piaçaguera (23 K 360843 7,359,863)	34	Piaçaguera	Southeast–Coastal shellmound	Bone (Sep.15)	AA-109293	6342 ± 34	7151–6848	Filippini et al. (2019)
		Piaçaguera		Bone (Sep.5)	AA-109292	5437 ± 31	6112–5884	Filippini et al. (2019)
		Piaçaguera		Marine shell	Isotopes 4480	4890 ± 110	5429–4828	Uchôa (1973)
		Piaçaguera		Marine shell	Isotopes 4481	4980 ± 110	5528–4883	Uchôa (1973)
Ubatuba (23 K 484604 7,397,729)	45	Mar Virado	Southeast–Ichthyological site	Urchin spicules	Beta - 154,722	2640 ± 70	2562–2042	Nishida (2001)
		Mar Virado		Urchin spicules	Beta - 154,721	2570 ± 70	2443–1949	Nishida (2001)
		Mar Virado		Charcoal	CSIC-1803	3465 ± 31	3828–3575	Uchôa (2009)
		Tenório		Bone (Sep.20)	AA-109201	2050 ± 26	1879–1696	Filippini et al. (2019)
		Tenório		Bone (Sep.7)	AA-109200	1983 ± 26	1808–1590	Filippini et al. (2019)
		Tenório		-	Beta-202,532	570 ± 60	-	Afonso (2017)
		Tenório		-	Isotopes-5306	1875 ± 90	-	Uchôa (1973)
Moraes (23 J 256907 7,313,340)	32	Moraes	Vale do Ribeira–Riverine shellmound	Bone (Sep.25)	KIA 20844	4511 ± 32	5298–4971	Figuti et al. (2013)
		Moraes		Bone (Sep.13)	KIA 15561	5895 ± 45	6791–6503	Figuti et al. (2013)
		Moraes		Bone (Sep.5)	MAMS 34575	5092[b]	5910–5660[b]	Posth et al. (2018)
		Moraes		Bone (Sep.5)	KIA 15562	4985 ± 35	5852–5590	Figuti et al. (2013)
		Moraes		Bone (Sep.37)	KIA 20843	5420 ± 30	6287–6007	Figuti et al. (2013)
Ribeira do Iguape (22 J 798179 7,291,837)	21	Estreito 1	Vale do Ribeira–Riverine shellmound	Bone (Sep.1)	KIA 20845	4124 ± 27	4814–4442	Figuti et al. (2013)
		Estreito 1		Bone (Sep.6)	KIA 20846	3655 ± 26	4079–3835	Figuti et al. (2013)
		Capelinha 2		Terrestrial shell	Beta 189,332	5000 ± 70	5896–5588	Figuti et al. (2013)
		Laranjal		Terrestrial shell	Beta 189,337	6980 ± 90	7945–7613	Figuti et al. (2013)
		Laranjal		Bone (Sep.2)	MAMS 34572	6485[b]	6660–6450[b]	Posth et al. (2018)
		Laranjal		Bone (Sep.3)	MAMS 34573	6849[b]	6900–6680[b]	Posth et al. (2018)
		Capelinha 1		Bone (Sep.5)	Beta 184,619	6090 ± 40	7153–6748	Figuti et al. (2013)

[a] Thermoluminescence.

[b] Insufficient data for recalibration: MAMS 34572, MAMS 34573, MAMS 34575, SI-1579, SI-1580, SI-1581, and SI-1583 stand as published originally by the authors in the references.

and biological differences from other individuals found at the same site.

Available chronological and geographic information for each series is presented in Table 1. All radiocarbon dates were obtained from previously published studies, as referenced in Table 1. For this study, when sufficient information was available, we recalibrated the radiocarbon dates with OxCal v4.4.3 Bronk Ramsey (2009), using the calibration curve SHCal20 (Hogg et al., 2020) for terrestrial samples and Marine20 (Heaton et al., 2020) for marine samples. Skeletal remains from coastal sites were calibrated using a mixed curve (50/50 SHCal20 and Marine20). Different R values accounting for regional reservoir effects of marine samples were taken for the State of São Paulo (E. Alves et al., 2015), Paraná and north region of Santa Catarina (Angulo et al., 2005) and south of Santa Catarina (Angulo et al., 2005; DeMasi, 1999).

We complement our dataset with two Brazilian precolonial coastal series analyzed by Christy Turner II: Corondó and Sambaqui South (Scott & Irish, 2017). The summary data on both series is available in Scott and Irish (2017). We acknowledge some potential inter-observer error may be caused by pooling series analyzed by two different observers. However, both series are important for this work because they provide new insights about the population history of precolonial coastal societies in Brazil on a regional scale. For the Sambaqui South series, we have no specific information about which individuals were included, although we know this series is composed by South shellmound builders curated at the National Museum of Rio de Janeiro (Scott & Irish, 2017), and therefore are most likely from Cabeçuda, the largest South shellmound collection in the museum at the time (de Mello e Alvim & Soares, 1984). There were other series of South shellmound builders in the National Museum of Rio de Janeiro: Forte Marechal Luz (Santa Catarina) and shellmound builders from the Paraná state. However, if they were included in the series, they most likely represent a small number of individuals, as other samples at the National Museum were very small compared to Cabeçuda. The trait frequencies and sample sizes of these Sambaqui South and Corondó are available in Scott and Irish (2017).

In order to compare our series with both Corondó and Sambaqui South series, we used 27 ASUDAS traits available for these series (Corondó has 29 published traits, Sambaqui South has 27 traits, missing Interruption Groove UI2 and Tuberculum dentale UI2) (Scott & Irish, 2017). We narrowed the selection to 22 traits after excluding five (Winging UI1, Distal accessory Ridge UC, Parastyle UM3 and Tome's root UP3, Deflecting Wrinkle LM1) due to extremely low sample sizes (no observations, or only one or two observations) in some of our series. After that, two other traits were removed because they are absent in all the series (Uto-Aztecan UP3 and Root Number LC), reducing our final number of variables to 20 ASUDAS traits.

To assess the trait frequencies, we followed the individual counting method: if available, both antimeres were analyzed, and if asymmetry between antimeres was apparent, only the highest degree of expression was considered. If only one tooth was available, it was still considered for analysis (Turner II & Scott, 1977).

Trait were dichotomized as present/absent based on the different threshold grades of each trait as suggested by Scott and Irish (2017). And we calculated the intra-observer error for each dichotomized trait. 127 individuals were analyzed twice by the first author (DF), with ~1 month interval between them. The agreement coefficient was calculated using Cohen's Kappa coefficient agreement (Cohen, 1960). All morphological traits reached substantial agreement or higher (kappa >0.6; see results in Data S2). However, the difference of the trigonid crest precision between sessions was 15%. Therefore, this variable was assumed to be problematic and excluded from the analyses.

Afterwards, the remaining 19 traits (Table 2) were tested for possible sex-bias using multiple chi-square tests, comparing the dichotomized dental nonmetric traits from 204 individuals with their available sex estimations. We found no significant differences ($p > 0.05$) in all tests (Data S3). As many individuals are in a bad state of preservation due to postmortem damage, we were unable to estimate age-at-death with enough confidence to test the association between dental traits and age.

Finally, we calculated trait frequencies by dividing the number of times a trait was scored as present by the total number of valid observations. Inter-trait correlation of the 19 morphological traits was assessed using Spearman correlation coefficient. Four traits were excluded from multivariate analysis due to high correlations (>0.7): Metaconule LM1, Lingual cusp number LP4, Entoconulid LM1, and Odontome UP/LP (Data S4). Although we acknowledge Spearman correlations above 0.6 may still be considered strong, removing such traits would make us remove five more variables, reducing the amount of information available for the series. Nonetheless, to guarantee the results presented here are not affected by the moderate-high correlation among some traits, we repeated all analyses also with the reduced set of 10 traits. These results are presented in Data S5 and they show no meaningful differences from the results obtained for 15 variables.

Multivariate statistical analyses were based on the average trait frequencies of each series, and biological distances were calculated through Euclidean distances and mean measure of divergence (MMD) (Sjøvold, 1977). The original MMD was used to calculate a distance matrix and check for significant distances between series, which can be consulted on Data S6. However, for the analyses done between pair of series, to explore the relative affinities among the series, we used a modified version of MMD. The original version of MMD includes a correction factor for sample sizes, in the form of a term that is subtracted from the arc differences between trait frequencies (Sjøvold, 1977). This term, $(1/N_A + 1/N_B)$, results in smaller sample sizes having distance values closer to 0 than larger sample sizes. The original reason for the sample size correction factor proposed by Sjøvold (1977) was to create conservative tests of significance of the distance between pair of samples, where the null hypothesis is that MMD $= 0$. In this context, the sample size correction is added to the MMD calculations to make the significance tests more conservative, reducing the chance of making type I errors as a result of low sample sizes and the consequent poor inferences of population parameters

TABLE 2 Dental morphological traits and key tooth, threshold, sample size, and frequency for each archaeological series

			Ribeira de Iguape		Moraes		Piaçaguera		Ubatuba		Guaraguaçu		Morro do Ouro		Rio Comprido		Joinville		Cabeçuda	
Trait	Key tooth	Threshold	N	f	N	f	N	f	N	f	N	f	N	f	N	f	N	f	N	f
Shoveling	UI	3–7	5	1.000	11	1.000	12	1.000	14	0.833	16	0.750	25	0.760	11	0.818	5	0.800	3	0.667
Double shoveling	UI	2–6	5	0.800	9	0.222	7	0.286	14	1.000	15	0.867	25	0.760	13	0.769	5	0.600	3	0.667
Bushman	UC	1–3	7	0.000	10	0.100	8	0.000	12	0.000	14	0.000	29	0.069	15	0.067	10	0.000	4	0.250
Root number	UP3	2–3	3	0.000	12	0.250	8	0.125	19	0.200	24	0.000	30	0.100	16	0.188	3	0.000	4	0.250
Metaconule	UM1	1–5	6	0.000	14	0.000	10	0.100	13	0.000	10	0.300	16	0.125	10	0.200	8	0.000	4	0.000
Carabelli cusp	UM1	2–7	6	0.333	17	0.176	15	0.000	17	0.125	16	0.438	34	0.235	16	0.375	10	0.100	4	0.000
Enamel extension	UM1	2–3	8	0.375	13	0.385	19	0.789	19	0.375	24	0.375	41	0.415	20	0.350	16	0.188	7	0.286
Hypocone	UM2	2–6	9	0.889	15	0.933	22	0.909	20	0.917	24	0.917	45	0.933	17	0.824	22	0.864	7	1.000
Root number	UM2	3	4	0.250	12	0.917	11	0.545	18	0.600	30	0.633	39	0.744	20	0.800	13	0.923	5	0.800
Peg/reduced/missing	UM3	1–3	5	0.200	11	0.000	25	0.080	28	0.214	48	0.063	50	0.120	22	0.182	31	0.097	7	0.143
Lingual cusp number	LP4	2–3	4	0.250	8	0.125	9	0.222	12	0.250	13	0.385	26	0.269	19	0.316	17	0.235	5	0.400
Protostylid	LM1	2–7	7	0.000	17	0.059	13	0.000	12	0.200	15	0.133	26	0.000	15	0.067	15	0.000	5	0.000
Metaconulid	LM1	1–4	6	0.167	15	0.067	11	0.182	11	0.250	20	0.000	28	0.143	19	0.211	22	0.182	6	0.000
Entoconulid	LM1	1–5	6	0.167	15	0.400	7	0.000	6	0.500	10	0.300	22	0.227	13	0.385	11	0.273	4	0.250
Root number	LM1	3	3	0.000	16	0.063	11	0.000	23	0.000	37	0.000	42	0.071	31	0.065	19	0.000	4	0.000
Groove pattern	LM2	Y	4	0.250	7	0.000	16	0.250	19	0.250	17	0.176	38	0.079	26	0.115	18	0.056	7	0.286
Hypoconulid	LM2	1–5	4	0.500	6	0.667	11	0.636	15	0.600	13	1.000	27	0.852	20	0.800	12	0.750	5	1.000
Root number	LM2	1	5	0.000	10	0.200	6	0.167	27	0.167	31	0.129	43	0.093	32	0.125	16	0.063	6	0.167
Odontome	UP/LP	1	11	0.000	12	0.083	14	0.000	20	0.000	20	0.000	47	0.021	27	0.074	27	0.074	8	0.000

from small samples. However, when considering multiple pairs of distances simultaneously to estimate the morphological affinities among series, the sample size correction of the MMD adds a component of error that is not independent and randomly distributed across samples (since it depends on the intrinsic size of the sample) in the morphospace. This error can bias significantly the relationship between series, making series that have smaller samples gravitate closer to each other. When comparing the relative morphological affinities of multiple pairs of series, the hypothesis that $\mathrm{MMD}_{\mathrm{AxB}} = 0$ is not relevant, since the analyses explore the relative hierarchy of distances among pairs. In this analytical design, the inclusion of the sample size correction factor becomes inappropriate as there is no formal Null Hypothesis being tested for each distance calculated, but there is the expectation that the error resulting from population parameter estimations are independent from the series samples, which the correction factor violates.

Consequently, to remove this bias in the multivariate analyses we calculated the MMD without the size correction term. Evidently, the removal of the size correction term does not mean that the distances observed are less biased, just that any biases in the distances is now solely a product of the poor inference of the original population trait frequencies as a function of the sample size, a significant limitation that must be taken into account when discussing the reliability of the inferences derived from our analyses. This limitation is particularly relevant for the series that have smaller sample size in our analyses (Cabeçuda and Ribeira do Iguape). Moreover, the use of the adapted MMD in this context precludes the direct comparison of the values obtained here with values reported in other studies (Irish, 2010; Irish et al., 2017). While this limitation does not affect our results, as all our distances are calculated using the same approach, the MMD values reported here should not be directly compared with MMD values obtained in previous studies. For authors interested in a direct comparison, the values presented in Data S6 will be more appropriate.

The morphological affinities among series, as measured by Euclidean distances and the modified MMD (without size correction), were represented using two-dimensional Kruskal nonmetric multidimensional scaling (MDS) (Cox & Cox, 2001). To complement the distance based analyses, the average trait frequencies for each series was also analyzed through principal component analysis (PCA), and the morphological affinities among series were represented in a scatterplot of the two first principal components. The morphological affinities are presented here only through the two most informative PCs to offer a comparative and complementary analyses to the distances. Because distances invariably take the information of all the variables and, in the case of MMD and Euclidean distance, variables are all equally weighted, they are prone to be more affected by outlier values in one or few variables. PCA analyses, on the other hand, explores the most relevant axes of covariance among all variables, which results in the noise caused by outliers in one or few variables to not be present in the most important PCs (see a similar discussion in Hubbe et al., 2020). Therefore, the PCA offers a check for the reliability of distance analyses and complement well the analyses based on pairwise distances.

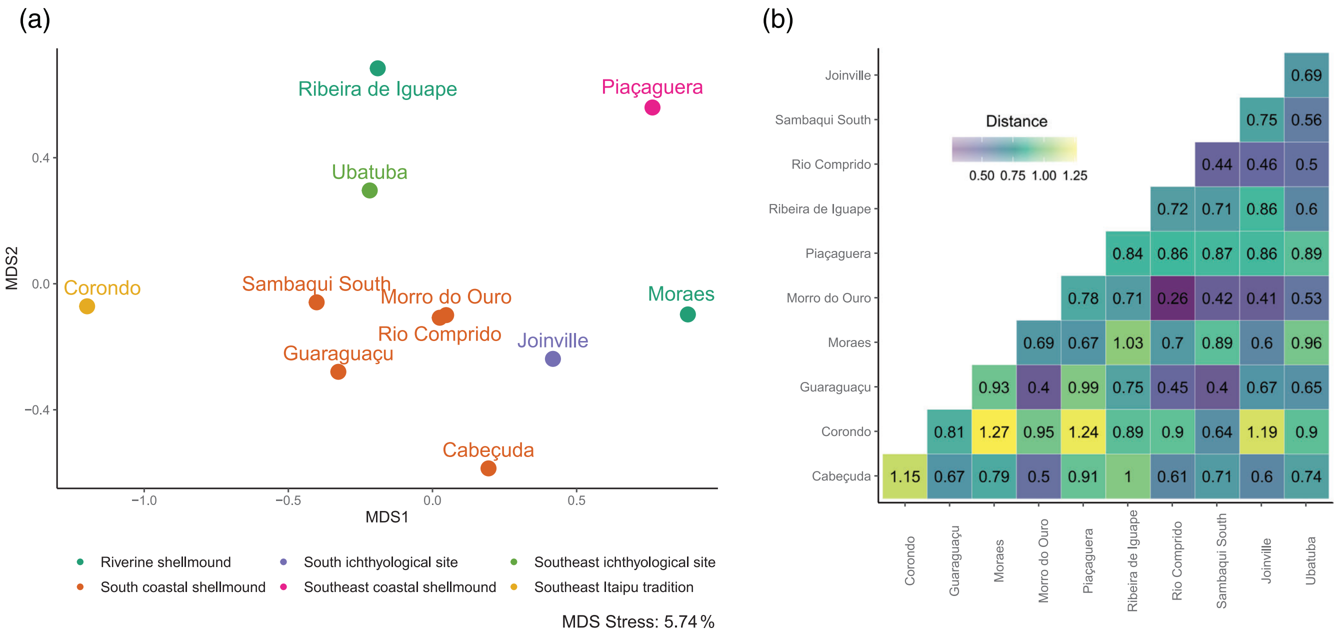
To test if the distances between series are structured across space and/or time, we applied Mantel matrix correlation tests between biological and geographic/chronological distances (Mantel, 1967). Geographic distances were calculated based on the approximate coordinates of each site (Table 1). For series composed of multiple sites, a geographic mid-point of the sites was used. For Turner's Sambaqui South series, we used the geographic coordinate of Cabeçuda to calculate the geographic distance matrix, given the likely provenience of the material. Chronologic distances between series were estimated using a dissimilarity matrix based on the average radiocarbon dates of each series. For the Sambaqui South series, we followed the timeframe provided by Scott and Irish (2017). Finally, we also performed a Mantel partial-correlation test among the biological distance matrices and geographic distance matrix, using the chronological distance matrix as a covariate (Hubbe et al., 2014; Pinhasi & von Cramon-Taubadel, 2009; Rathmann et al., 2019) to control for the impact of chronological distances in the biological differentiation among series.

All multivariate analyses were performed in R (R Core Team, 2020), with functions written by MH and DF, and complemented with the following R packages: *irr* (Gamer et al., 2012), *MASS* (Venables & Ripley, 2002), *vegan* (Oksanen et al., 2013), *ggplot2* (Wickham, 2016), *ggfortify* (Tang et al., 2016), and *RColorBrewer* (Neuwirth, 2014).

3 | RESULTS

The MDS based on Euclidean distance (Figure 2(a)) and MMD (Figure 3(b)) show a central cluster composed by South Coast series, with series from the other geographic regions surrounding it without a clear contextual pattern. Joinville is closely related to other sites from the South (Figures 2(b) and 3(b)), supporting the evidence for regional continuity between nonceramic and ceramic periods. Cabeçuda is partially distant from other South Coast series, which can be due to a larger geographic distance, as it is the southern most series from our study, or the result of the small sample size of this series. Morro do Ouro, Rio Comprido, and Guaraguaçu are sites that share a very similar archaeological, geographic, and chronological contexts, so it is not surprising to see them sharing a close biological relationship as well. Turner's Sambaqui South series is closely related to the remaining South series, supporting that there is little inter-observer error between the data collection protocols of the first author (DF) and Christy Turner II. Their distance from Cabeçuda can be partially explained by significant differences in sample sizes, or the fact that the Sambaqui South series possibly includes individuals from sites other than Cabeçuda.

The Southeast Coast series have a much higher phenotypic variation and no clear clustering pattern among them (Figures 2 and 3). Piaçaguera, Ubatuba, and Corondó are very different from each other, showing that the Southeast Coast may have been inhabited by different biological populations in different geographic areas and chronological periods. The most evident outlier is Piaçaguera, which seems



	Corondo	Guaraguaçu	Moraes	Morro do Ouro	Piaçaguera	Ribeira de Iguape	Rio Comprido	Sambaqui South	Joinville	Ubatuba
Joinville										0.69
Sambaqui South									0.75	0.56
Rio Comprido								0.44	0.46	0.5
Ribeira de Iguape							0.72	0.71	0.86	0.6
Piaçaguera						0.84	0.86	0.87	0.86	0.89
Morro do Ouro					0.78	0.71	0.26	0.42	0.41	0.53
Moraes				0.69	0.67	1.03	0.7	0.89	0.6	0.96
Guaraguaçu			0.93	0.4	0.99	0.75	0.45	0.4	0.67	0.65
Corondo		0.81	1.27	0.95	1.24	0.89	0.9	0.64	1.19	0.9
Cabeçuda	1.15	0.67	0.79	0.5	0.91	1	0.61	0.71	0.6	0.74

FIGURE 2 (a) Kruskal nonmetric multidimensional scaling based on Euclidean distances. (b) Euclidean distance matrix

to share more biological affinities with riverine populations than to any other coastal populations. Corondó also appears as an outlier when compared to most shellmound builders, something that was already visible in a previous study (Turner II & Scott, 2013: Figure 3), and supports the idea that the Itaipu tradition represents a different biological component that co-existed with other coastal societies during precolonial times. It must be noted that this difference could be the result of inter-observer errors between Turner, who analyzed Corondó, and the first author. However, we find the outlier nature of Corondó unlikely to be the result of interobserver error, since the Sambaqui South series is well integrated within the South Coast cluster.

The riverine shellmound builders from Vale do Ribeira show patterns of morphological affinities that are not easy to define. Ribeira do Iguape appears between Piaçaguera and Ubatuba, which may partially support some degree of biological relationship with people from the Southeast Coast. On the other hand, individuals from Moraes appear closer to series from the South Coast, particularly the ceramic ichthyological series from Joinville. Given the geographic position of Vale do Ribeira, which divides the South and Southeast Coast, it seems possible that series can be related to either South of Southeast populations depending on the series included in the analyses. However, due to our limitations in terms of sample sizes, further research is required.

Figure 4 shows the morphological affinities among series and the variables most correlated with each axis of the principal component analysis. The first two principal components explain 61.97% of the variance, with PC1 explaining 41.95% of the variation, and PC2 explaining 20.02% (see Data S7 for additional information). The results are very similar to those obtained with Euclidean distance and MMD, supporting the patterns of morphological affinities presented above. PC2 clearly separates all South Coast series (negative values on y-axis) from the Southeast Coast and Vale do Ribeira (positive values on the y-axis). The most important variables separating the Southeast Coast and Vale do Ribeira from South Coast series are shoveling UI1 and enamel extensions UM1, which are particularly high among Piaçaguera and Ribeira do Iguape. Conversely, South Coast groups have a higher frequency of double Shoveling UI1, hypoconulid LM2, and three-rooted UM2. Along the first principal component, the outlier position of Corondó is the result of this site having high frequencies of one-rooted LM2 and peg/reduced/missing UM3, which further supports the unique biological component of this site when compared to other Southeast populations.

Mantel correlation tests using Euclidean distances and MMD (Table 3) show that geography explains a significant portion of the variance in the biological distances ($r = 0.4491$, $p = 0.019$ for Euclidean distances; and $r = 0.3955$ $p = 0.023$ for MMD), which supports the north–south pattern of separation observed in the PCA. The chronological difference between series is not significantly correlated with morphological distances, which supports regional biological continuities in these regions (i.e., over time morphologies remained similar in each region). Finally, the correlation with geography is not affected by the chronological differences between sites, as the partial partial-Mantel results correcting for chronology do not differ significantly from the values of the initial Mantel test.

4 | DISCUSSION

The results of our analyses show differences in the process of biological differentiation in the three geographic regions analyzed. There is a geographic structure to the biological differences, with a clear Southeast—South separation and series from Vale do Ribeira showing

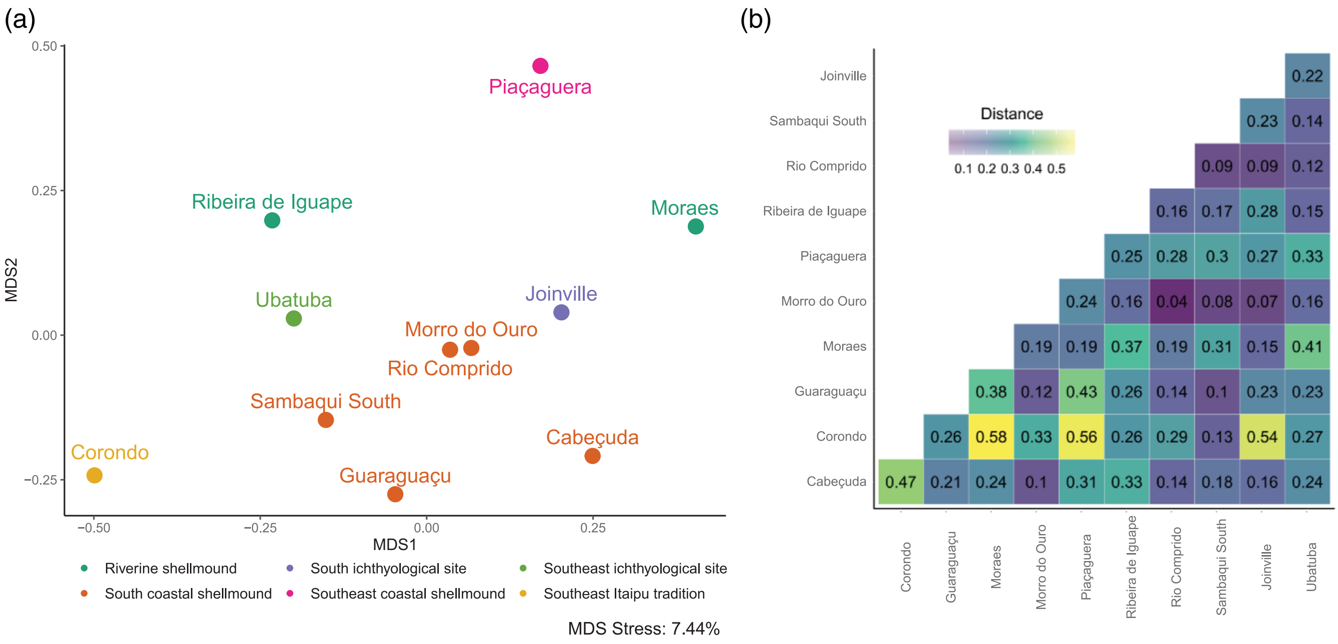
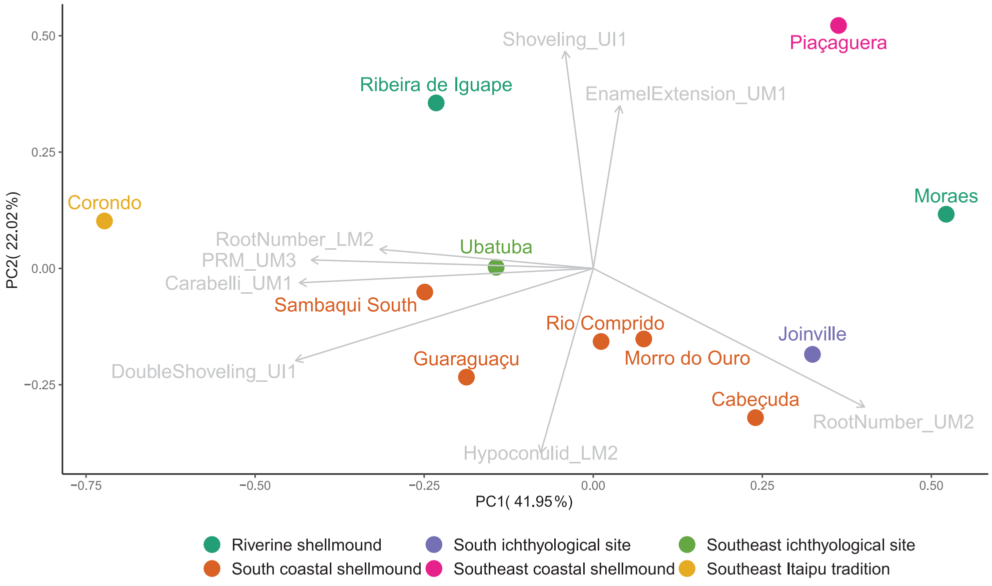


FIGURE 3 (a) Kruskal nonmetric multidimensional scaling based on Mean Measures of Divergence. (b) Mean Measure of Divergence distance matrix

FIGURE 4 Morphological affinities according to the first two principal components extracted from the data. Gray arrows show variables most correlated (*r* > |0.5|) with each PC axis



variable patterns of morphological affinity with Southeast and South series. On a broad scale, this geographic structure in the biological variance is expected on low-mobility populations, whereas stronger correlations with time would be expected in high-mobility populations (Loog et al., 2017). Therefore, the geographic structure observed in our analyses supports that most coastal societies were low-mobility groups. This statement corroborates previous suggestions based on the archaeological record that the occupation of the Brazilian coast was largely defined by low-mobility or even semi-sedentary populations (Bastos, 2009; DeBlasis et al., 1998; DeMasi, 2009; Kneip et al., 2018). This low-mobility pattern is also consistent with the high morphological diversity among Brazilian precolonial coastal populations (Hubbe, 2006; Hubbe et al., 2014; Neves, 1988; Okumura, 2007), as isolation between populations accentuates the accumulation of differences between regions over time (Relethford, 2004).

South Coast series are the ones that show the highest morphological similarities among them, sharing a very similar dental morphological pattern over time. As suggested by previous studies, shellmound builders from Paraná (Guaraguaçu) and Santa Catarina (Morro do Ouro, Rio Comprido) probably share a common evolutionary history (Hubbe et al., 2009; Okumura, 2007).

The Joinville series, composed of individuals from South ceramic ichthyological sites, is closely associated to shellmound builders of the same region. This suggests that even after the increase of interactions with inland groups, the overall phenotypic characteristics of preceramic coastal populations was seemingly maintained. Studies that examined other South ichthyological sites besides Itacoara and Enseada have suggested that the incorporation of ceramic to the coast may have combined both demic and cultural diffusion (Neves, 1988; Okumura, 2007, 2014). That scenario would explain why in some instances ceramic sites show clear biological distinctions from preceramic populations (Okumura, 2014), while in other cases, like the case of Joinville reported here, we observe no discontinuity in the biological characteristics of populations after the appearance of ceramic. Demic diffusion presumes a large-scale migration of a population into another territory, often resulting in the incorporation and admixture with a preexisting population (Cavalli-Sforza et al., 1993; Pinhasi & von Cramon-Taubadel, 2009) and, given this complex outcome of human dispersion events, it is to be expected that different samples may show different association patterns. This is clearly a possibility that must be further explored in the future, by comparing in more details the biological charateristics of ceramic ichtyological sites in the region.

In the Southeast Coast, there is an almost complete lack of biological similarities among series, especially when compared to the South Coast. Our analyses show a high dental phenotypic variation among groups from São Paulo and Rio de Janeiro. Piaçaguera, our only sample of Southeast coastal shellmound builders, is a noteworthy outlier, since it is only relatively closer to riverine shellmound builders of Vale do Ribeira. Piaçaguera is also one of the earliest sites in the coast and São Paulo, so its position may suggest that there were biological changes over time in the region. Unfortunately, the samples available at this point are not sufficient to explore these possibilities in more detail.

The second outlier in our analyses is Corondó, related to the Itaipu tradition. These results go against some archaeological narratives, as this tradition is often considered part of the wide range of settlements made by shellmound builders of the Southeast coast (Gaspar, 2004). In fact, previous studies of cranial morphology found strong biological affinities between individuals buried in Corondó and Southeast shellmound builders (Okumura, 2007). Our results seem consistent with the biological differences found between Corondó and shellmound builders when analyzing dental nonmetric traits (Turner II & Scott, 2013), and reinforces the idea that individuals exhumed from Corondó show a clear deviation from the dental patterns found in other Brazilian coastal groups (Turner II & Scott, 2013). Unfortunately, this study lacks shellmound builders from Rio de Janeiro, and therefore it is not possible to discuss the relationship of Itaipu sites with local shellmound populations.

Finally, the relationship between Vale do Ribeira and other regions is not resolvable with our samples and analyses. On one hand, the series of Ribeira do Iguape occupies the same general space as other Southeast Coast series of the state of São Paulo (Ubatuba and Piaçaguera). However, this association must be seen with caution, since Riberia do Iguape is one of the smallest samples in our study, and the morphological affinities are probably biased by this factor. On the other hand, Moraes shows similar morphological distances to both the late ceramic ichthyological series of Joinville, and the early southeast shellmound of Piaçaguera. As Vale do Ribeira reaches the sea at the south coast of São Paulo, geographically it occupies an intermediate position dividing the southeast and south geographic units. Thus, it is quite possible that the contact between riverine shellmound builders involved populations from both the South and Southeast Coast (Bartolomucci, 2006;Neves & Okumura, 2005; Okumura, 2007), although the nature of this contact cannot yet be properly elucidated.

Other studies on phenotypic traits also showed conflicting results when it comes to the phenotypic variation of riverine shellmound builders, although unlike us, they considered them to be a homogenous biological group (Bartolomucci, 2006; Filippini, 2004; Filippini & Eggers, 2006; Neves & Okumura, 2005; Posth et al., 2018; Strauss et al., 2015). Some studies based on cranial nonmetric traits argued that riverine shellmound builders from Vale do Ribeira are related to inland populations (Filippini, 2004; Filippini & Eggers, 2006), and others based on dental nonmetric traits (Bartolomucci, 2006) and craniometrics suggested that they bear stronger morphological affinities with coastal shellmound builders (Neves & Okumura, 2005; Okumura, 2007). Our results suggest a high phenotypic variation within the geographic unit of Vale do Ribeira, meaning that riverine shellmound builders may not be a homogenous biological group, despite having similar archaeological contexts. However, once again, we must take into account the possible bias due to small sample sizes of the many riverine shellmound sites pooled into the Ribeira de Iguape series.

TABLE 3 Mantel correlation and partial correlation results (based on 999 permutations)

Model	Euclidean	MMD		
	r	*p*-value	r	*p*-value
Dental variation explained by the geographic distance among populations.	0.4491	**0.019**	0.3955	**0.023**
Dental variation explained by the geographic populations, controlled for chronology.	0.461	**0.02**	0.4092	**0.029**
Dental variation between series is a product of genetic differentiation by chance over time.	0.1415	0.293	0.163	0.206

Note: Bold values denote statistically significant correlations.
Abbreviation: MMD, mean measure of divergence.

In conclusion, the analyses of the dental morphology of coastal and riverine archaeological sites from three distinct geographic regions in southern Brazil show that the occupation of the coast was probably the result of low-mobility populations that occupied each of these regions for long periods of time, without showing evidence of significant biological changes over time. These results support the hypotheses of relative isolation between the South and Southeast Coast (Okumura, 2007), despite the overall cultural similarities on a broad scale of analysis (Gaspar, 2004).

Our results also point out to large morphological diversity among Southeast coastal and riverine groups, which suggests the Southeast region may have been characterized by more complex population dynamics than usually presented. In that way, our analyses speaks directly to regional archaeological and bioanthropological studies focused on reconstructing the history of human occupation in coastal Brazil.

Nevertheless, our results must be taken with caution, as the low samples sizes in some of the archaeological series included may make the patterns of morphological affinities unreliable. This is particularly true for the series Ribeira de Iguape, Moraes, Piaçaguera, Joinville, and Cabeçuda. Therefore, while our results suggest broad patterns of regional differentiation, small scale associations between series must be seen as tentative and will require further analyses before they can be considered reliable. Nevertheless, we hope to have open new possibilities to be tested regarding the population history of Brazilian precolonial coastal societies, by adding the information of the less-explored dental nonmetric traits to the discussions.

ACKNOWLEDGMENTS

This study is funded by Fundação de Amparo à Pesquisa do Estado de São Paulo, grants 2017/20637-4 and 2019/18289-3. It was also partially funded by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Funding Code 001, between November 2017 and March 2018. We would like to thank everyone at the following institutions for granting access to the skeletal series and for helping during their analyses: Museu de Arqueologia e Etnologia da Universidade de São Paulo (MAE-USP), Museu de Arqueologia e Etnologia da Universidade Federal do Paraná (MAE-UFPR), Museu Arqueológico de Sambaqui de Joinville (MASJ), and Grupo de Pesquisa em Educação Patrimonial e Arqueologia da Universidade do Sul de Santa Catarina (GRUPEP-UNISUL).

CONFLICT OF INTEREST

All authors declare there are no conflicts of interest.

AUTHOR CONTRIBUTIONS

Daniel Filipe Fidalgo: Conceptualization; data curation; formal analysis; funding acquisition; investigation; resources; visualization; writing-original draft. **Mark Hubbe:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing-original draft; writing-review & editing. **Veronica Wesolowski:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; visualization; writing-original draft; writing-review & editing.

DATA AVAILABILITY STATEMENT

Trait frequencies used for correlation tests and multivariate analysis of all the series analyzed by the first author are available in Table 2. The Sambaqui South and Corondó frequencies can be consulted in Scott and Irish (2017). Radiocarbon dates and geographic coordinates used for mantel correlation tests are available in Table 1.

ORCID

Daniel Fidalgo https://orcid.org/0000-0001-7175-1686
Mark Hubbe https://orcid.org/0000-0003-4433-3942
Veronica Wesolowski https://orcid.org/0000-0002-4685-1500

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How to cite this article: Fidalgo, D., Hubbe, M., & Wesolowski, V. (2021). Population history of Brazilian south and southeast shellmound builders inferred through dental morphology. *American Journal of Physical Anthropology*, 1–16. https://doi.org/10.1002/ajpa.24342