Cranial morphology of early Americans from Lagoa Santa, Brazil: Implications for the settlement of the New World

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Comparative morphological studies of the earliest human skeletons of the New World have shown that, whereas late prehistoric, recent, and present Native Americans tend to exhibit a cranial morphology similar to late and modern Northern Asians (short and wide neurocrania; high, orthognatic and broad faces; and relatively high and narrow orbits and noses), the earliest South Americans tend to be more similar to present Australians, Melanesians, and Sub-Saharan Africans (narrow and long neurocrania; prognatic, low faces; and relatively low and broad orbits and noses). However, most of the previous studies of early American human remains were based on small cranial samples. Herein we compare the largest sample of early American skulls ever studied (81 skulls of the Lagoa Santa region) with worldwide data sets representing global morphological variation in humans, through three different multivariate analyses. The results obtained from all multivariate analyses confirm a close morphological affinity between South-American Paleoindians and extant Australo-Melanesians groups, supporting the hypothesis that two distinct biological populations could have colonized the New World in the Pleistocene/Holocene transition.

Paleoamericans | Paleoindian morphology | Paleoindians

Information derived from several comparative morphological studies of the earliest human skeletons of the continent has suggested a complex scenario in regards to the influx of humans to the New World (1, 2) (see *Supporting Text*, which is published as supporting information on the PNAS web site, for recent support of the use of cranial morphology as a legitimate tool to recover recent human evolutionary history). Whereas late prehistoric, recent, and present Native Americans tend to exhibit a cranial morphology similar to late and modern Northern Asians (short and wide neurocrania; high, orthognatic and broad faces; and relatively high and narrow orbits and noses) (3), the earliest South Americans tend to be more similar to present Australians, Melanesians, and Sub-Saharan Africans (narrow and long neurocrania; prognatic, low faces; and relatively low and broad orbits and noses) (2). The latter is known in the literature as Paleoamerican morphology. However, most studies carried out so far regarding the morphology of the first Americans were based on small cranial samples because human burials older than 8,000 years (8.0 kyr) are rarely found in the Americas, especially in North and Central America (1). In this paper, the morphological affinities of early South Americans are assessed by using the largest sample of early American skulls ever studied. All specimens were recovered in the Lagoa Santa region of central Brazil.

Because all human populations present a high degree of internal morphological variability, previous studies based on early Americans' cranial morphology were unable to completely rule out sampling anomalies or outliers as an explanation for the results they generated. Consequently, several specialists have questioned whether the peculiar cranial pattern described above for the first South Americans actually expressed the central tendency of this population (4, 5). This controversy could be addressed by the use of large samples of early Americans, if available.

Here we use a sample of 81 Late Pleistocene/Early Holocene specimens from the region of Lagoa Santa, central Brazil (described in Table 1) to explore the extracontinental morphological affinities of the first Americans. This unique sample results from a long-term research project led by W.A.N. involving a major program of curating and dating museum material, and fieldwork in Lagoa Santa. The Lagoa Santa karst, located near the center of the State of Minas Gerais (Fig. 1), has been known since the 1840s (6) as a key area for the study of the first Americans.

Chronology of the Specimens

Since the excavations of Peter Lund at Sumidouro Cave in 1842/1843, the human skeletal remains recovered in Lagoa Santa have been assumed to be of great antiquity (6). However, only very recently has this assertion proved to be correct. From the original excavations of Lund until 1969, the only indication of an early date for the human skeletons found in Lagoa Santa was the cooccurrence in Sumidouro Cave of human and megafauna skeletal remains apparently deposited in the same sedimentary levels (7). A similar phenomenon was also observed by Harold Walter in the inner chamber of Mortuaria cave in 1935 (8).

The first professional archaeological excavations in Lagoa Santa were carried out by Wesley Hurt and Oldemar Blasi in 1956 (9). They were unable to find any association between human and megafauna remains in the seven rock-shelters excavated by them at Cerca Grande, the largest limestone outcrop in the region. However, many years after their fieldwork, two radiocarbon dates were reported by them (10). These two dates (9,720 ± 128 and 9,028 ± 120), obtained in Rock-Shelter 6, were the first direct evidence that a large number of human skeletons found in that area, including those uncovered by Hurt and Blasi in Cerca Grande, could be in fact of final Pleistocene/Early Holocene age.

The next contribution toward an improved chronological framework for the Lagoa Santa human skeletal remains came from the excavations of Lapa Vermelha IV, in the mid-1970s (11). The now famous "Luzia" skeleton was uncovered by the excavators 12 m below the surface of the rock-shelter, in a sedimentary deposit estimated by ^{14}C dates on charcoal to be of final Pleistocene age (12).

Since the work of Lund in Sumidouro Cave in 1842/1843 until the mid-1970s when Luzia was found, at least 250 ancient human skeletons were recovered in Lagoa Santa by naturalists, amateurs, and professional archaeologists. Because the majority of the excavations were reported in Portuguese in local publications, few North American and European physical anthropologists were aware of

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Abbreviations: kyr, thousand years; PCo1 and PCo2, principal coordinates 1 and 2.

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ANTHROPOLOGY

Table 1. Archaeological sites from which the Lagoa Santa specimens were collected, number of measured skulls per site, chronological range, and chief archaeologist responsible for the exhumation of the human remains

Site	No. of males	No. of females	Chronological range, years B.P.	Institutions	Chief archaeologists
Lapa da Amoreira	1	—	≈7,000*	MNRJ	Padberg Drenkpol
Lapa de Carrancas	2	—	≈8,000*	MNRJ	Bastos d'Ávila
Lapa Mortuária (Rockshelter)	2	2	7,000–9,000*	MNRJ	Padberg Drenkpol
Santana do Riacho	2	4	8,000–9,500*	MHN-UFMG	André Prous
Cerca Grande 6	2	3	8,000–8,500*	MNRJ	Wesley Hurt and Oldemar Blasi
Cerca Grande 7	—	1	≈9,000*	MNRJ	Wesley Hurt and Oldemar Blasi
Lapa Mortuária (Cave)	1	—	11,000–12,000*	MHN-UFMG	Harold Walter
Escrivânia 3	—	1	≈7,700	ZMUC	Peter Lund
Sumidouro	17	14	>8,000†	ZMUC/MNH/IHG	Peter Lund
Cerca Grande 2	1	—	8,000–8,500†	MNRJ	Wesley Hurt and Oldemar Blasi
Cerca Grande 5	2	—	8,000–8,500†	MNRJ	Wesley Hurt and Oldemar Blasi
Lapa do Caetano	1	1	8,000–8,500†	MNRJ	Padberg Drenkpol and Cássio Lanari
Lapa D'Água	—	1	8,000–8,500†	MNRJ	Padberg Drenkpol
Harold Walter Collection¶	11	11	8,000–8,500§	MHN-UFMG	Harold Walter
Lapa Vermelha IV	—	1	11,000–11,500§	MNRJ	Annete Emperaire
Total	42	39			

B.P., before present; ZMUC, Zoology Museum of the University of Copenhagen; MNH, Museum of Natural History, London; IHG, Instituto Histórico e Geográfico Brasileiro (Brazilian Historic and Geographic Institute, Rio de Janeiro); MHN-UFMG, Museum of Natural History of the Federal University of Minas Gerais (Belo Horizonte, Brazil); MNRJ, National Museum of the Federal University of Rio de Janeiro.

*Based on dates of human bones and/or charcoal directly associated to the burials.

†Minimum date.

†Based on stratigraphic analogy with geologically similar well dated sites and burial pattern.

§Based on stratigraphic dates on charcoal.

¶Refers to human remains derived from six undifferentiated rock-shelters of the Lagoa Santa region (only the highly fossilized specimens were included).

this important material. For the same reason, until recently, none of these human skeletons had been directly dated by accelerator mass spectrometry to confirm their antiquity.

Because of the importance of this unique material to the debate on the settlement of the New World, W.A.N. has directed an extensive operation since 1994 to generate a reliable chronological framework for the human skeletons of Lagoa Santa. This operation has involved four complementary lines of action: dating directly as many human skeletons as possible by accelerator mass spectrometry; generating minimum dates for some of the human skeletal collections by dating cristaline calcite layers sealing archaeological and paleontological deposits; excavating new archaeological sites to increase the number of human specimens and to understand the details of the local stratigraphic sequence; and visiting classical sites looking for remnants of the original sediments to reconstruct the original archaeological sequences. Few specimens could in fact be directly dated by accelerator mass spectrometry, because absence of collagen in the bones is the norm in Lagoa Santa.

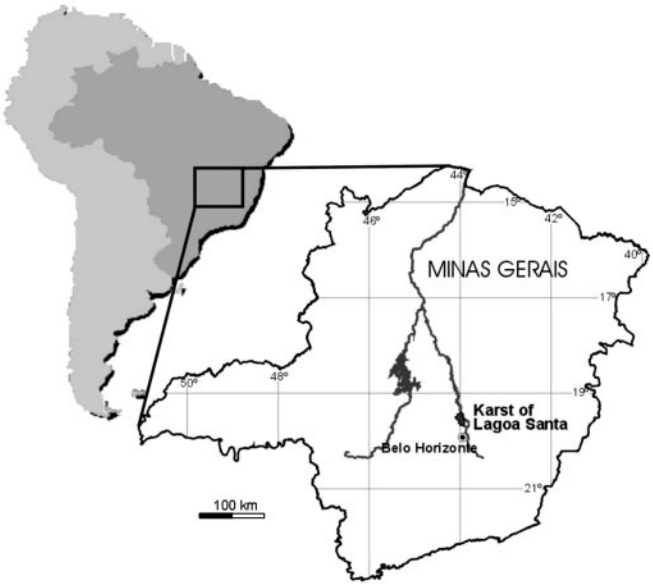

Fig. 1. Geographic location of Lagoa Santa, Brazil.

In conjunction, these four lines of research have allowed for the construction of a very solid chronological framework for the specimens used in this work. Table 2, which is published as supporting information on the PNAS web site, presents the absolute dates obtained for 22 human skeletons uncovered from 11 classical sites in Lagoa Santa. Most of the specimens are dated to Early Holocene, specifically between 8.5 and 7.5 kyr. Because these specimens can be assumed to represent a random sample of the total universe of already institutionalized human skeletal remains from Lagoa Santa, they can be taken to represent the burial distribution along time in the region as a whole.

A few human skeletal remains dated to Late Holocene (last 2.0 kyr) were also found in the rock-shelters of Lagoa Santa (data not shown). This late material, very fragmented, was found, however, on the surface of the shelters (sometimes deposited in urns) and not in stratigraphy, as the early ones, and can be easily sorted out from the Early Holocene specimens by means of taphonomical characteristics.

Because of its homogeneity, the burial pattern of the early settling of Lagoa Santa can also be used as a complementary indicator of the chronology of the human remains uncovered when neither stratigraphic control nor direct methods of dating were available (13). In general, the corpses were deposited in hyperflexed position in very shallow graves topped by small blocks of limestone or quartz. Sometimes, these blocks were also used to cover the lateral walls of the grave pits. A small hearth was always established adjacent to the top of the pit, and burning charcoals were thrown into the pit, before sealing. Secondary burials were also popular in ancient days in the region. Red pigment was vastly used in these cases. Because most naturalists and amateurs described the burial conditions of the human skeletons they recovered in Lagoa Santa, these descriptions can also be used, as a last resource, to help to contextualize the old material in time.

The chronology assumed for the Lagoa Santa skulls used in this work is also supported by what is known about cultural continuity and change in the region. Humans were present in Lagoa Santa earlier than or at least as early as Clovis in North America (14). However, only two skulls in the studied sample date back to the final Pleistocene. Dry climatic conditions apparently did now allow for a real human settlement within the karst of Lagoa Santa during that period. As it is widely known, karsts in general are rich in subterranean streams but poor in surface water. During the last two millennia of the Pleistocene, humans were not formally buried. Apparently, when a group was crossing the area or sporadically exploring it, eventual casualties were expediently treated: the corpse was simply laid down in extended position in a natural protected niche within caves and cavities. This was the case of Luzia (13) and possibly Confins Man (8).

From ≈10.0 to 7.5 kyr, more humid conditions allowed for an intense settlement within the karst itself, with the great majority of the local rock-shelters already occupied by 9.6 kyr ago. For still unknown reasons, formal burying in the rock-shelters started only around 8.5 kyr ago and would be intensively practiced only until around 7.5 kyr ago. Except for this, the other elements of the local lifestyle and material culture did not change significantly. This phase of intensive use of the karst by humans was followed by what is now known elsewhere in South America as the "archaic gap." Also because of drier conditions, humans almost completely aban-

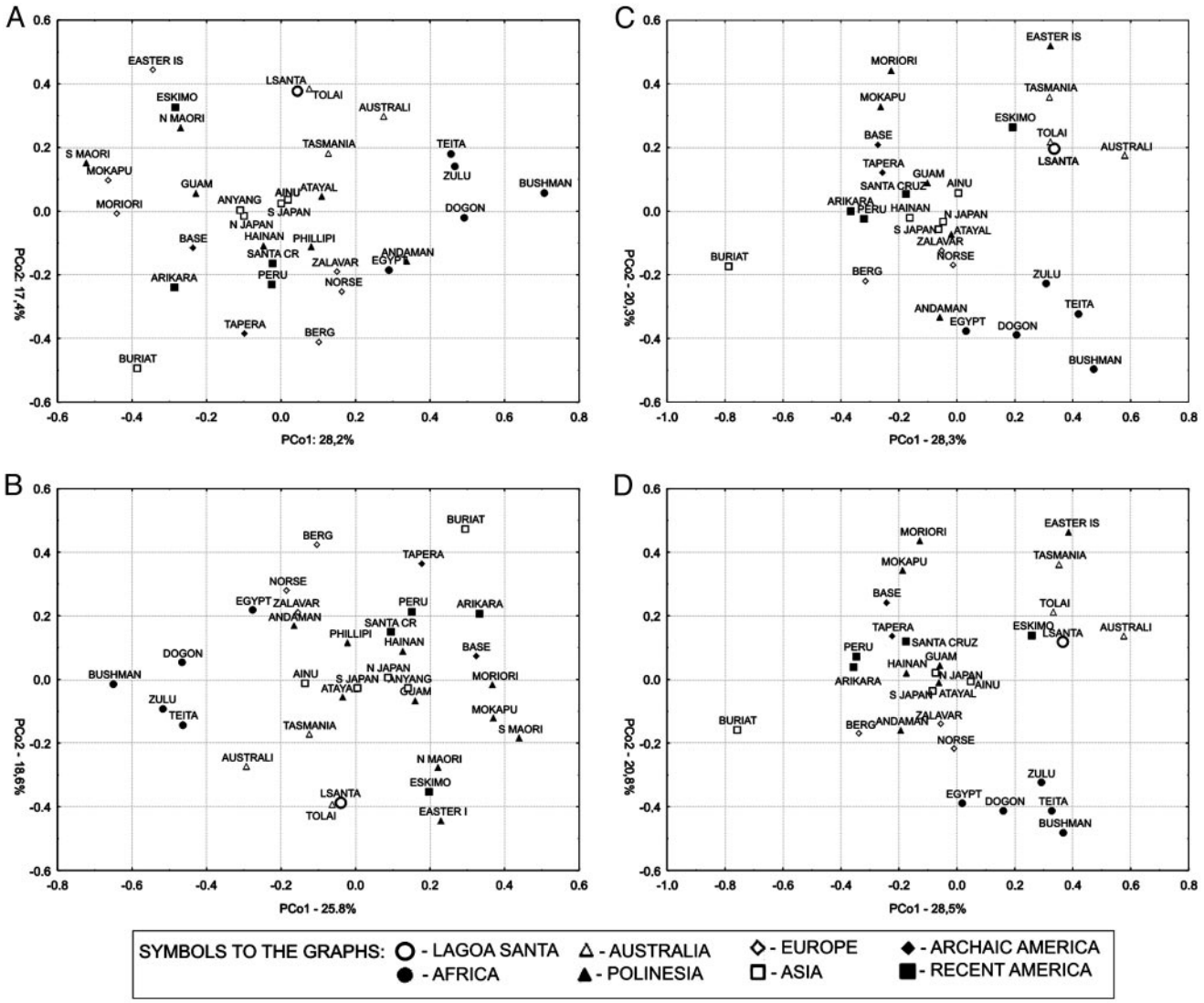

Fig. 2. Graphs showing the morphological affinities of the samples as seen through the first two principal coordinates (PCo1 and PCo2) extracted from matrices when heritability was equal to 0.55. The percentages accompanying each axis represent the amount of the original variance explained by each axis. (*A*) Analysis of males, with size and shape considered. (*B*) Analysis of males with size effect corrected. (*C*) Analysis of females, with size and shape considered. (*D*) Analysis of females with size effect corrected. Only the 55 best preserved skulls were included.

doned the region during the Middle Holocene. Again, the rock-shelters were occupied only sporadically, as in the final Pleistocene, and no human burial dated to between 7.0 and 3.0 kyr has ever been found in Lagoa Santa.

With a local increase in humidity during the Late Holocene, the Lagoa Santa Karst was again intensively occupied by human groups, this time with a very different material culture and settlement-subsistence pattern when compared to the Paleoindians. Slash-and-burn agriculture and pottery making were part of the cultural repertory of the newcomers. Their dead were buried mainly in urns, some of them deposited on the surface of the rock-shelters.

In summary, although most of the human skeletons used in this work were not directly dated by accelerator mass spectrometry (primarily because no collagen was preserved in these specimens), one can surely assume that the 81 human crania (42 males and 39 females) used here pertain to one same breeding population bracketed in time between 7.5 and 11.0 kyr (Table 2), with the vast majority (74 skulls) dating to between 8.0 and 8.5 kyr. Taking into account the biological and cultural continuity during this time interval, the term Late Paleoindians is adopted in this work to refer to these specimens collectively.

Materials and Methods

All specimens were measured by a single individual (W.A.N.), using W. W. Howells' protocol as craniometric standard (15), and the original data can be found in Data Set 1, which is published as supporting information on the PNAS web site. Howells' database (16) was used as comparative material to assess the extracontinental morphological affinities of the Lagoa Santa skulls. Howells' cranial measurements and database have been extensively used in the literature for similar purposes because all 2,524 individuals were measured by Howells himself and the database contains skeletal samples from the five continents. Two fairly recent Brazilian coastal samples from the late archaic period [Tapera and Base Aérea; measured by Myia Pereira da Silva (Musée de l'Homme, Paris) and W.A.N.] were also added to the analysis to increase the number of comparative series from South America.

To assess the morphological affinities of Lagoa Santa, three different multivariate tests were applied: (*i*) principal coordinates on heritability corrected data, (*ii*) principal components of the individual data of Lagoa Santa and Howells centroids, and (*iii*) principal components of Lagoa Santa and Howells cen-

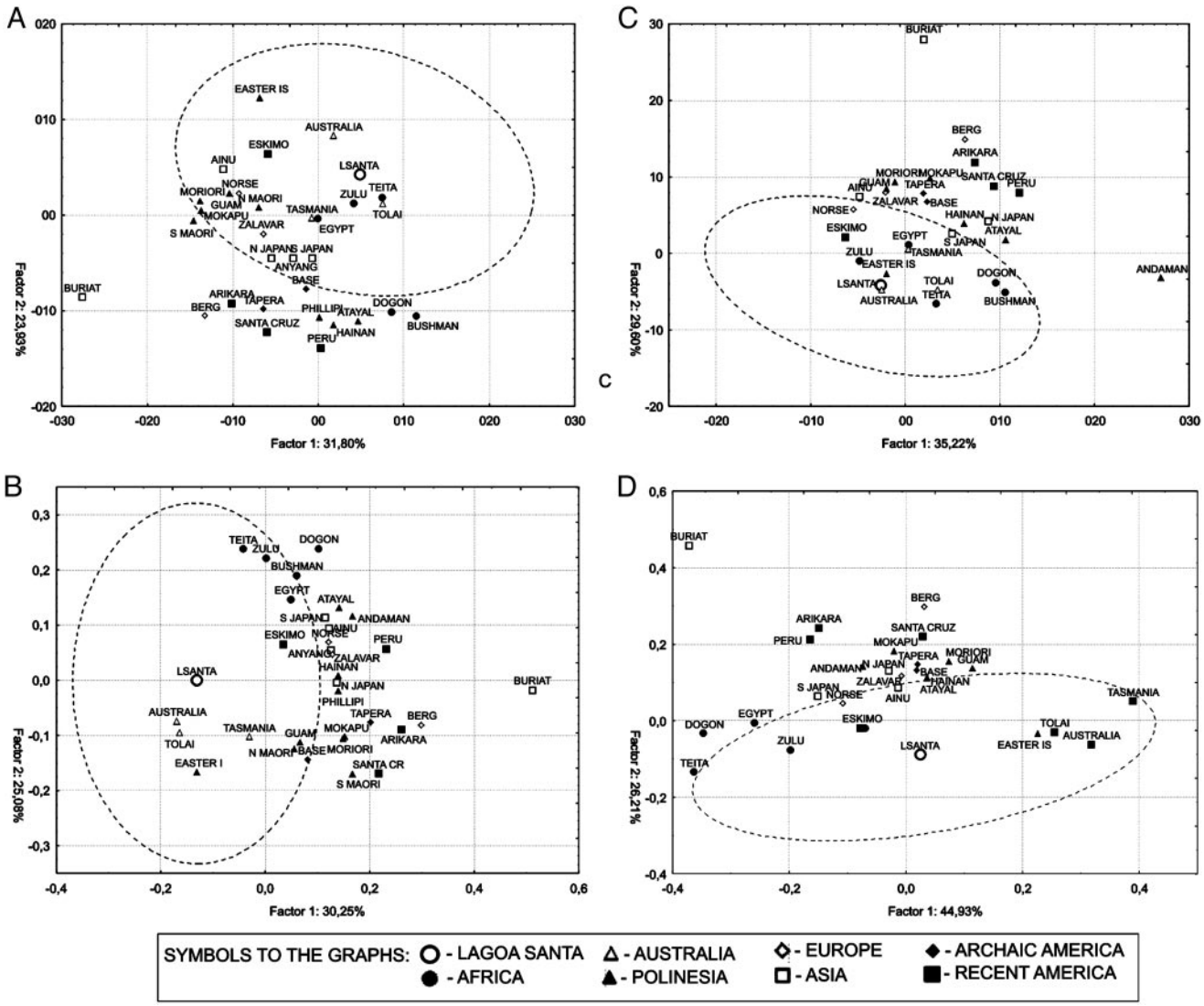

Fig. 3. Graphs showing the 95% confidence interval dispersion of the Lagoa Santa individual skulls as seen through the first two principal components. (*A*) Analysis of males, with size and shape considered. (*B*) Analysis of males with size effect corrected. (*C*) Analysis of females, with size and shape considered. (*D*) Analysis of females with size effect corrected. Only the 55 best preserved skulls were included.

troids. Multiple quantitative techniques were used as a precaution, taking into account that multivariate tests can produce slightly different results. The first test is based on principal coordinate analyses, extracted from distance matrices corrected for heritability. The second test explores the individual dispersion of Lagoa Santa when compared to worldwide population centroids. The third test is based on sample centroids, which allowed us to include all of the 81 skulls available for Lagoa Santa and to avoid replacement of missing values.

Results

The morphological affinities of Lagoa Santa skulls were first analyzed through principal coordinate analysis, with an assumed heritability of 0.55 [calculated by using RMET 5.0 (written by John H. Relethford and available on request)], applied to "size and shape" and on "shape" information alone. Males and females were analyzed separately. The influence of size was corrected by dividing the values of each craniometric variable by the geometric mean of all variables measured in one individual (17). The heritability value expresses the average amount of the variation in the skull morphology that is estimated to be due to genetic contribution (18). Only the 55 best preserved skulls from Lagoa Santa were used in this analysis to minimize the replacement of missing values and to maximize the number of variables. When necessary, missing values replacement was done through multiple regressions of the means of each variable across all populations included in the analyses. After the screening, only 25 variables could be used in the case of males, and only 17 variables, in the case of females.

Fig. 2 presents the positions of all series included in the analysis when plotted in two-dimensional graphs defined by principal coordinates 1 and 2 (PCo1 and PCo2). The amount of information contained in each axis is also presented in the figure. In Fig. 2*A* (males, size and shape), the sample from Lagoa Santa shows its strongest morphological affinity with Tolai (a Melanesian sample from New Britain), followed by the remaining Australian series. Fig. 2*B* (males, shape alone) shows a similar topology, with Lagoa Santa again close to Tolai. Fig. 2*C* (females, size and shape) places the early Americans very close to Tolai. Both series occupy the region of the graph dominated by Australo-Melanesians. This pattern repeats itself in Fig. 2*D* (females, shape alone). In the four graphs the reference samples taken from Howells' database are, in general, grouped in accordance with geography, as found by him in his seminal studies (3, 15). The two Brazilian late archaic samples show a very different cranial morphology when compared with the early South Americans. The samples occupy a position in the multivariate space close to East Asians and/or late Amerindians.

To consider the individual variability of the Lagoa Santa sample, principal components analyses were applied to the same set of 55 best preserved skulls used in the principal coordinate analyses, and to the centroids of Howells and late archaic Brazilian series. By doing this, we were able to assess the morphological dispersion of the individual skulls of Lagoa Santa in relation to the central tendencies of the world comparative populations. The results (Fig. 3) show a tendency for late Americans and Asian centroids to remain outside of the 95% confidence ellipses of the individual dispersion of Lagoa Santa. Fig. 3*A* (males, size and shape) shows that, whereas most of the world series fall within the dispersion of Lagoa Santa, none of the five late American samples used are part of the Paleoindian dispersion. When size effect is corrected (Fig. 3*B*), fewer series can be found within the Paleoindian dispersion. These are mainly Australian and African samples, although some Polynesian (Guam and North Maori) and American series (Eskimo and Base) can be found in the extremity of Lagoa Santa's 95% confidence dispersion. Fig. 3*C* (females, size and shape) shows that the majority of the series within the Paleoindian dispersion

Fig. 4. Geographical location of other early human skeletal remains in the Americas showing Paleoamerican morphology and their respective chronological range.

are Australo-Melanesians and Africans. With the exception of Eskimo, no other late American series are found within Lagoa Santa's female dispersion. The same can be said when size is corrected (Fig. 3*D*).

To take into account the information provided by all 81 Lagoa Santa skulls and not only the 55 best preserved specimens, the centroids (averages) of all series were analyzed by using a conventional principal component analysis applied to the raw database (50 variables, uncorrected for heritability). The graphs based on the first two principal components are shown in Fig. 5, which is published as supporting information on the PNAS web site. These analyses did not significantly change the topologies generated by the principal coordinate analyses.

Discussion and Conclusions

The three different quantitative analyses undertaken in this study demonstrate that the first South Americans exhibit a cranial morphology that is very different from late and modern Northeastern Asians and Amerindians (short and wide neurocrania; high, orthognatic faces; and relatively high and narrow orbits and noses) but very similar to present Australians/Melanesians and Africans, especially with the former (narrow and long neurocrania; prognatic, low faces; and relatively low and broad orbits and noses). Taking into account the large number of early specimens used in this study, this trend is unlikely to be a result of sample bias. The phenomenon cannot, as well, be said to represent the result of microevolutionary processes restricted to Lagoa Santa because the same cranial pattern has already been described in places as distant and as ecologically different as Southern Chile [Magellan's Strait (19)], Colombia [Sabana de Bogotá (20, 21)], Mexico [Mexico Basin (22) and Baja California (23)], United States [Florida (24)], and elsewhere in Brazil [Bahia (25) and São Paulo (26)] (Fig. 4).

Two different hypotheses can be proposed to explain the morphological differences observed between early and late

Native South Americans (27). One is a local microevolutionary process that transformed, *in situ*, the Paleoamerican morphology into that prevailing today among Native Americans. The other is that the Americas were successively occupied by two morphologically differentiated human stocks, with the Paleoamerican morphology entering first.

We believe the second hypothesis is more plausible for three reasons: first, it would be very unlikely that the same evolutionary event (directional morphological change) happened in the Americas and in East Asia in parallel at approximately the same time (the parsimony principle) (28); second, because in South America, at least, the transition between the two morphological patterns was, as far as we know, abrupt (29); and third, cranial morphology has recently been shown to respond adaptatively only to extreme environmental conditions, being therefore much less plastic than originally thought (30). No transoceanic migration is necessary to explain our findings, because Paleoamerican-like humans were also present in East Asia during the final Pleistocene (31–35) and could perfectly well have entered the New World across the Bering Strait. A final solution to this dilemma will depend of course on a better understanding of what was happening in North America at the same time.

Recent archaeological data can be used to support a dual occupation of the New World, either directly or indirectly. Dixon (36), for example, analyzed the diversity of the projectile points found in the earliest sites of North America and concluded that two different and independent cultural traditions (or cultures) entered the continent in the final Pleistocene. According to Dixon, bow-and-arrow technology was brought to the Americas only by the second tradition, because the atlatl was the primary hunting weapon of the first.

A pre-Clovis occupation of the New World, as strongly suggested by recent findings in South America (37, 38), would not strictly be requisite to accommodate our findings. However, it would make them more plausible. The deeper the chronology of the settlement of the Americas, the more plausible the entrance of humans exhibiting a more generalized cranial morphology in the New World.

Our results and interpretation are more difficult to reconcile with information coming from molecular biology. As recently summarized by several leading scholars in the field (39, 40), DNA analyses (mainly mtDNA and Y chromosome) have generated very different scenarios for the occupation of the Americas. As to the number of migrations, the proposals have oscillated from one to four. As to time of entrance, figures as distant in time as 12.0 to 35.0 kyr ago have been proposed. There is, however, a recent trend toward a small number of migrations (one to two) and time depths more compatible with the archaeological findings (*ca*. 15 kyr). The lack of a perfect match between morphological and molecular information can be easily explained by a very frequent event in molecular evolution: loss of DNA lineages throughout time. An example of this loss is the X mitochondrial haplogroup. Nowadays it is completely absent among the Indians of South America (41), whereas a couple of millennia ago it could still be found in the subcontinent (42). More light on this subject will be certainly shed when Paleoindian DNA fragments are recovered and analyzed.

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