3-D cranial reconstruction elucidates the evolution of new world monkeys

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Computed tomography scans of fossils from two extinct species point to evolutionary adaptations and kinship with extant howler, spider and woolly monkeys Credit: André Menezes Strauss

Researchers have used computed tomography (CT) scanning to examine and reconstruct cranial fossils belonging to two extinct species of monkey, Caipora bambuiorum and Cartelles coimbrafilhoi. The fossils were found almost 30 years ago in a cave complex in Bahia, Brazil, located in the Caatinga, a semiarid biome that occupies part of Brazil's Northeast Region.

The images were compared with those of craniums from 14 extant Central and South American primate species, enabling the researchers to identify adaptations and infer previously unknown relationships between

the extinct and extant species.

"This is the first-ever study of endocranial morphology involving fossils of New World monkeys, or platyrrhines," said André Menezes Strauss, a professor at the University of São Paulo's Archeology and Ethnology Museum (MAE) and an associate researcher affiliated with the Laboratory of Archeology and Environmental/Evolutionary Anthropology (LAAAE) at the university's Institute of Biosciences (IB-USP) in Brazil.

Using a cast taken from the braincase, paleoanthropologists analyzed endocranial morphology to estimate the shape and size of the brains of the fossil primates.

The results of the study, which was supported by São Paulo Research Foundation—FAPESP, are published in the *American Journal of Physical Anthropology*.

The researchers described cranial and endocranial shape variations in 14 species belonging to the four extant genera in the family Atelidae—Alouatta (howler monkeys), Ateles (spider monkeys), Brachyteles (woolly spider monkeys or muriquis), and Lagothrix(woolly monkeys), as well as the extinct species C. bambuiorum and C. coimbrafilhoi. There are approximately 350 primate species in the world today. More than 200 are platyrrhines.

The study was led by Ivan Perez, an anthropologist at Argentina's La Plata Museum. His collaborators included Brazilian scientists affiliated with the University of São Paulo (USP) and the University of Campinas (UNICAMP), as well as researchers at institutions in Belgium, France, Germany and the United States. Cástor Cartelle, a paleontologist at the Pontifical Catholic University of Minas Gerais state (PUC-MG) for whom Cartelles coimbrafilhoi is named, was also a member of the

research team.

The fossil specimens of C. bambuiorum and C. coimbrafilhoi are deposited at PUC-MG's Natural History Museum in Belo Horizonte, Minas Gerais. The 14 crania of the extant platyrrhines came from collections held by Argentina's La Plata Museum, Brazil's National Museum in Rio de Janeiro, the Argentinian Natural Science Museum in Buenos Aires, and the US National Museum of Natural History in Washington, DC.

"All 16 specimens were digitized using a medical CT scanner. A virtual 3-D model of the endocranium was generated for each sample, and the 3-D models of the cranial surfaces were extracted from the CT scan data," Strauss said.

The fossil specimens were damaged, particularly in the region of the zygomatic arches (cheekbones), so the researchers opted for two strategies to analyze them. According to Strauss, in the case of C. bambuiorum, the right zygomatic arch was absent, but the left arch was intact.

"We reflected the undamaged arch to the damaged side in the 3-D model, taking advantage of bilateral symmetry, and by means of this virtual repair, obtained a complete specimen," he said.

"In C. coimbrafilhoi, both sides were absent, so we used an imputation method to estimate the positions of the missing parts."

Perez digitized 26 anatomical landmarks and 373 semilandmarks along the curves and surfaces of each endocranium, as well as 64 landmarks and 196 semilandmarks on each cranium. In geometrical morphometrics, a landmark is a 2-D or 3-D point of evolutionary significance. Semilandmarks are defined by locations relative to other landmarks, e.g.,

midway between landmarks X and Y.

"The data served as a basis for multivariate analysis to compare all the characteristics of the 16 specimens and to look for similarities and differences that indicated morphological [and hence] adaptive patterns," Strauss said.

In other words, because the specimens of extant species of Atelidae, the largest New World monkeys, included crania of Alouatta, Ateles, Brachyteles and Lagothrix, they were compared with the specimens of the extinct species in order to find out whether the two fossils resembled and might be closely related to any of them.

3-D craniums

Strauss said the data clearly showed that C. bambuiorum should be grouped with Ateles, Brachyteles and Lagothrix, all of which are distant from Alouatta.

This means that the genus Alouatta shares a common ancestor with the other genera of Atelidae and with C. bambuiorum and that it is older than the common ancestor shared by Ateles, Brachyteles and Lagothrix.

"However, when the position of C. bambuiorum is analyzed solely in relation to Ateles, Brachyteles and Lagothrix, the conclusion is that the fossil is clearly closest to Brachyteles," Strauss said.

"The hypothesis that C. bambuiorum was similar to a giant spider monkey (Ateles), initially posited by Cástor Cartelle 20 years ago, was refuted by our data, which showed that the extinct monkey was actually much more similar to a 'giant' muriqui (Brachyteles)."

In the case of C. coimbrafilhoi, the multivariate analysis produced some

surprises. The first was that the data did not clearly group it with any of the four extant genera of Atelidae but consistently filled the previously empty morphospace between Alouatta and the other three genera.

"With regard to the fossil species, we show that C. bambuiorum is positioned within the range of variation observed for Brachyteles, whereas C. coimbrafilhoi presents an endocranial shape that does not overlap with the range of variation observed for any of the extant Atelidae. Of the four genera, C. coimbrafilhoi is closest to Alouatta in endocranial morphospace but closest to Lagothrix in cranial terms," Strauss said.

"We found that when the size factor was removed, the characteristics of C. coimbrafilhoi were intermediate between Alouatta on one side, and Ateles, Brachyteles and Lagothrix on the other," Strauss said.

"Our results suggest that within the atelid clade, the extinction of C. bambuiorum and C. coimbrafilhoi led to a significant loss of biological variation that could not have been imagined with the discovery of these fossils," the article concludes.

The entire lineage of New World primates, distributed from northern Argentina to Central America, the Caribbean and Mexico, descends from a single band of founders comprising small African monkeys believed to have crossed the former South Atlantic (then a third of its current size) some 45 million years ago on rafts of floating vegetation.

Research on monkey fossils in the Americas began in Brazil 183 years ago in 1836, when Danish naturalist Peter Wilhelm Lund discovered the remains of a much larger primate than all extant platyrrhines in a cave in the Lagoa Santa area of Minas Gerais.

Lund named this monkey Protopithecus brasiliensis, which means

"Brazilian ancestral monkey". It became extinct over 10,000 years ago and is a close relative of Brachyteles, the largest extant platyrrhine.

Fossils found since then (mostly single teeth and fragments of mandibles, plus a few craniums) belonged to very ancient platyrrhines that became extinct millions or tens of millions of years ago in Argentinian Patagonia, high up in the Chilean Andes and Bolivian Altiplano, in the Amazon rainforest of Peru, and on several Caribbean islands.

Although more than 30 extinct platyrrhine species have now been described, P. brasiliensis has never lost its status as a giant much larger than the rest, with two exceptions.

Almost complete skeletons of two other giant platyrrhines were found in 1992 in an inner chamber of Toca da Boa Vista, Brazil's largest cave complex (in Bahia). They lived at the end of the Ice Age over 10,000 years ago.

Both fossils were studied at PUC-MG by Cartelle, who described one of the specimens as a giant spider monkey belonging to a new species he called Caipora bambuiorum. He identified the second specimen as a member of the species described by Lund (P. brasiliensis).

C. bambuiorum and P. brasiliensis belong to the family Atelidae. The largest atelid genus is Brachyteles, whose members can reach 15 kg, followed by Alouatta, which are typically 10 kg or less. C. bambuiorum and P. brasiliensis were 60% larger. When alive, they must have weighed over 25 kg, about as much as an African baboon.

In 2013, thanks to American anthropologists, the fossil found in Toca da Boa Vista and initially thought to be a Protopithecus was found to be an exemplar of a new species named Cartelles coimbrafilhoi in homage to

Cástor Cartelle.

The research group led by Perez concluded that C. coimbrafilhoi is related to Alouatta and not, as Cartelle thought, to Brachyteles.

New scientific techniques have now supplied a novel interpretation of these two fossils, especially C. coimbrafilhoi.

The 3-D model of C. coimbrafilhoi's cranium constructed by the researchers showed that its morphological adaptations were different from those of any other New World primate, extant or extinct.

"Computed tomography enabled us to produce a new analysis of C. coimbrafilhoi, with novel conclusions. We now believe this giant monkey from the Pleistocene found in Bahia was neither Alouatta nor Brachyteles. Its unique cranial characteristics are no longer seen in any other New World primate," Strauss said.

The Protopithecus described by Lund was not included the study by Perez, Aristide, Strauss and colleagues, for lack of a cranium that could be scanned. The fossils found so far are highly fragmented.

More information: Leandro Aristide et al, Cranial and endocranial diversity in extant and fossil atelids (Platyrrhini: Atelidae): A geometric morphometric study, *American Journal of Physical Anthropology* (2019). DOI: 10.1002/ajpa.23837

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