Obituary: Ralph L. Holloway (1935–2025): Scientist, Mentor, and Leader in Paleoneurology

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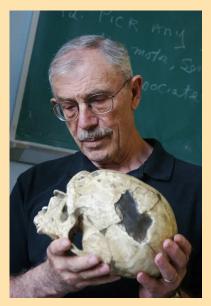
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OBITUARY



Ralph L. Holloway

Dr. Ralph L. Holloway transformed the study of hominin brain evolution and expanded the scope of paleoanthropology through his groundbreaking research on paleoneurology, the analysis of fossil endocasts as direct evidence of our species' neural ancestry. His work laid the empirical and conceptual foundations for much of what we now understand about the evolution of cerebral morphology, hemispheric lateralization, cortical reorganization, and the neurobiological correlates of complex behavior in the hominin lineage.

Holloway was born in Philadelphia in 1935. He began his undergraduate degree at the Drexel Institute of Technology, studying metallurgical engineering. His initial exposure to scientific research came through a cooperative education placement with Armco Stainless Steel in Baltimore, where he experimented with the effects of temperature on metal alloys. Yet it was a general education course in anthropology at the University of New Mexico, where Holloway transferred during his undergraduate years, that eventually sparked a change in his academic interests. During that time, he often worked as a roughneck in the southwest Texas oil fields, before graduating with a degree in geology in 1959.

Holloway briefly worked in geophysics and engineer-



ing, including at Lockheed Aircraft in California. But he found the pull of anthropology undeniable, and he was soon admitted to the Ph.D. program at the University of California, Berkeley. There, he began graduate work under Sherwood Washburn, then a central figure in the new physical anthropology. With his growing interest in the neural basis of behavior, Holloway insisted on enrolling in a neuroanatomy course taught by Marian Diamond, against Washburn's wishes. As a result, Holloway ultimately switched advisors and completed his doctorate under the supervision of Theodore McCown, a supportive mentor who, though not a specialist in the brain, encouraged Holloway to pursue his interests in integrating neuroscience with anthropology. Holloway's 1964 dissertation, "Quantitative Relations in the Primate Brain," was a wide-ranging synthesis of the comparative brain literature.

Immediately after earning his doctorate in 1964, Holloway began as an Assistant Professor of Anthropology at Columbia University and remained there for the rest of his career. During the late 1960s, Holloway persuaded Morton Fried, Chair of Anthropology at Columbia, to approach biologists Cyrus Levinthal and later Nobel prize winner Eric Kandel about working with him on the quantitative histology of the cerebral cortex of various primates, including humans. Their response was, "If we do not know what is happening in the brain of Aplysia [a sea-slug], then how could we possibly learn anything from primate brains? No." Although he was skeptical about the value of endocasts, viewing them as limited proxies that revealed little beyond cranial capacity, a turning point came with a Guggenheim Fellowship that allowed Holloway to travel to Africa and study fossil hominin material firsthand. While working with Phillip Tobias and Alun Hughes at the University of the Witwatersrand in Johannesburg, Holloway became convinced of the scientific potential of endocasts, particularly in assessing cortical asymmetries and structural reorganization. The Taung child (Australopithecus africanus) endocast, previously described by Raymond Dart, captured his fascination. He viewed the lunate sulcus to be in a posterior human-like position, despite the small apelike size of the brain. He resolved to return to the neglected problem of how hominin brains changed not just in size, but in structure.

From that point forward, Holloway became a dedicated paleoneurologist. He refined techniques for producing latex endocasts, documenting sulcal patterns, cerebral asymmetries, and regional morphology. He assembled a vast comparative collection of endocasts made from the skulls of monkeys, apes, fossil hominins, and modern humans. He collaborated with researchers across the world, and many of his specimens have since been digitized and scanned through partnerships with museums and academic colleagues. A representative collection of Holloway's original endocasts are housed at the American Museum of Natural History and can be made available to researchers upon request.

Over the span of his career, he applied his expert neuroanatomical knowledge to reconstruct the endocranial

morphology of numerous fossil specimens, often from fragmentary remains, including *Australopithecus*, early *Homo, Homo erectus, Homo naledi*, Neandertals, and more. His work took him to Kenya, South Africa, Belgium, and Indonesia, and included early contributions to the study of iconic specimens like KNM-ER 1470 and Sangiran 4. He was among the first to suggest, in published work, that Broca's region could be identified on fossil endocasts, laying the groundwork for making scientific inferences about the evolution of language in the human lineage.

Holloway's views were often ahead of their time. His writings emphasized the significance of brain reorganization over mere increases in brain volume. As early as the 1960s, he argued that selection pressures on social behavior and tool use may have driven changes in parietal and frontal association cortices, and in 1965 at the meeting of the American Association of Anthropologists, he presented his synthesis regarding how early human social adaptations and neural structure had a concomitant effect on one another. Then in 1975 at the James Arthur Lecture for the American Museum of Natural History, he expanded his thesis, arguing that brain evolution in hominins was driven by increasing social complexity and the need for flexible behavioral repertoires, concepts that later found momentum in the "social brain" and "Machiavellian intelligence" hypotheses. Beyond paleoneurology, he authored papers on topics ranging from hemispheric lateralization in apes to sexual dimorphism of corpus callosum morphology in modern human brains. His publications from the 1970s through early 2000s helped shape longstanding discussions about the neural basis of language, cognition, and handedness, and offered a critical analysis of encephalization metrics, such as EQ.

In 2004, Holloway wrote the book "The Human Fossil Record: Brain Endocasts – The Paleoneurological Evidence" (Wiley-Liss), co-authored with his students Douglas C. Broadfield and Michael S. Yuan. This volume brought together decades of empirical work on fossil hominin endocasts and remains a foundational reference for scholars of paleoanthropology.

In 2007, his career was celebrated with a two-day conference titled "The Human Brain Evolving", organized by colleagues under the sponsorship of the Stone Age Institute and Indiana University. The volume of papers stemming from that meeting stands as a testament to his wideranging impact on the study of brain evolution. Holloway was elected as a Fellow of the American Association for the Advancement of Science and the New York Academy of Science and was inducted as a member of the National Academy of Sciences in 2015.

Ralph Holloway was, by all accounts, a complex and charismatic figure. He could be feisty at times, especially when defending empirical rigor, but he was also generous with his ideas. He was known for encouraging trainees at all levels to pursue their own research interests and to resist rigid disciplinary boundaries. Holloway's passion for research was matched by his love of teaching and genuine care for his students. He taught at Columbia for 59 years,

continuing to do so until May 2023, well after his official retirement. A curious undergraduate was as welcome as a grad student to join him for a cup of Earl Grey tea in the lab to discuss their questions or ideas.

His mentorship extended beyond the lab and class-room. A beloved tradition among his graduate students was the weekly lunch. Held at Camille's restaurant on Amsterdam Avenue over plates of pasta, steaks, and fries, these gatherings became informal opportunities to laugh, think, and debate what was happening at Columbia, in anthropology, as well as in the world at large. During these lunches, Ralph was equal parts provocateur and mentor, and the students who took part remember those lunches as a formative part of their intellectual life.

In this way, Holloway trained generations of scientists to value anatomy, comparative analysis, and independent thought. He was also passionate about music—playing trumpet and trombone throughout his life. Impromptu trumpet recitals to students and the endocasts in the Schermerhorn Hall lab were not uncommon. He also enjoyed mystery novels, astronomy, and genealogy. Holloway remained curious and continued to work on research projects until his death. He helped transform paleoneurology from a marginal enterprise into a robust and essential area of anthropological research. He is deeply missed by family, friends, colleagues, students, and the many scholars whose work he shaped and inspired.



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