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LETTER FROM THE EDITOR

On behalf of my fellow editors and our faculty liaison Professor Jill Shapiro, I am delighted to present to you the third volume of *Sapient*, the Undergraduate Journal of Biological Anthropology.

This journal was created as an opportunity for students in all academic fields to submit works related to four topics: Human Variation and Genetics; Evolutionary Theory and History; Primate Behavior and Ecology; and Paleoarchaeology and Morphology.

This year, the editorial board has focused on fostering the growth of the *Sapient* community in universities across the continent and across the world, as well as increasing the reach of our online presence on social media platforms. We hope to continue building a wide-reaching community which increasingly unites and integrates related fields in academia.

— Rachel Bell

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Asian or Caucasian? The *U.S. v. Cartozian* Naturalization Case of 1925 & the Legal Construction of Armenian Racial Identity

David Momjian, Columbia University

When the Hall of Asian Peoples opened in 1980 at the American Museum of Natural History in New York, a section was reserved for the 3,000-year history of the Armenians. Titled “Armenia: A People of the Caucasus,” the exhibit houses an array of historical items—from the first complete Bible printed in the Armenian language (published in Amsterdam in 1666) to an 18th century ceramic church-ornament from the city of Kutahya. The artifacts were assembled by the Advisory Council for Armenian Studies at Columbia University, under the supervision of anthropologist, Walter A. Fairservis, Jr. (1921-1994), a specialist in Asian cultures.¹ Within steps of the Armenian exhibit are dioramas of Bedouins in their tents, Siberian Yakuts in a shaman healer’s hut, and Lhasan nobles standing before the Tibetan mountains.

While the Armenians are placed within the tradition of Asian cultures, the museum booklet—*Armenia: Crossroads of Cultures*—has a decidedly European bent, noting the Indo-European roots of the Armenian language, as well as Armenia’s contacts with ancient Greece and Rome (Ordjanian, 1980). While highlighting Armenia’s importance as a trade-route connecting China, India and Central Asia with the Mediterranean, the booklet primarily focuses on Armenia’s decision to become the first nation to adopt Christianity as its official religion, its participation in the Crusades, and its Western-influenced art and architecture. If Armenia is situated at a cultural crossroads, the museum booklet has the Armenian people facing due-west.

As a people living in Western Asia (also referred to as Turkey-in-Asia or Asia Minor), Armenians straddled both worlds, with scholars classifying them as an “in-between” people, along with millions of other eastern and southern European immigrants (Barrett and Roediger, 1997; López, 2006). However, American immigration officials were vexed with the question of Armenian race—not knowing whether the Armenians were white-skinned or yellow-skinned, Caucasian or Asian. Many Western observers saw European traits in the Armenians, calling them “the Yankees of the Orient” or “the Swiss of the East” (Carpenter, 1922, p. 271). While the Armenians uniformly self-identified as a “white” race, those who had to decide the racial question for naturalization purposes hotly debated the issue—leading to a string of court cases on the legal construction of race in America.

¹ As the chief scientific consultant for the Hall of Asian Peoples, Fairservis told the *Christian Science Monitor* that the exhibit was needed to combat the “cultural blindness” of Westerners and their “history of ignorance” regarding multicultural Asia. Arguing against the museum’s decision to freeze-frame the dioramas circa 1920, Fairservis wanted the exhibition space to include contemporary depictions, including Communist China. Because the museum refused to install any material deemed “controversial,” Fairservis resigned in protest after the exhibit opened. Christopher Swan, “Hall of Asian People; Orienting the Americans,” *Christian Science Monitor*, November 13, 1980, <http://www.csmonitor.com/1980/1113/111357.htm>

The most significant case involved a wealthy Oriental-rug merchant named Tatos O. Cartozian. *U.S. v. Cartozian* (1925) held that Armenians were “white” and thus entitled to apply for U.S. citizenship. The case unveiled the process by which Armenians became “white”—examining not only skin-color through an anthropological lens, but also the “racialization” of Armenian religious and cultural identity and the degree to which Armenians had successfully assimilated in the U.S. With renowned anthropologist Franz Boas testifying as an expert witness on behalf of the Armenian defendant, the adjudication that Armenians were “white” opened their Americanization-trajectory, but it did little to quell anti-immigration bias against “in-between” peoples. This paper analyzes *Cartozian’s* key holding, which did not rest on a single Armenian’s ability to act “white,” but instead turned on whether an entire group of people could live up to the standards of performing “whiteness” (Gross, 2008). One scholar described this period as one of “provisional or probationary whiteness”—in which Armenians and other immigrant-groups were confronted with cultural and environmental explanations of race, as opposed to purely biological underpinnings (Jacobson, 1998, p. 95). As a result, a “racial grey zone” was created, giving the Armenians the opportunity to prove their “whiteness” through successful acts of assimilation (HoSang, 2012, p. 99).

From the time of the nation’s first naturalization statute passed by Congress in 1790, citizenship in America was limited to “free, white persons”—a statutory requirement that continued until 1952 (López, 1996). Nevertheless, the dream of an all-white America became impractical as a tide of immigrants from Asia, including the Armenians, came to the American shores (Lang, 1981). Although the Armenian presence in America is traced to the establishment of the Jamestown colony in the 17th century, most Armenians immigrated to the U.S. following the Russo-Turkish War of 1878, when American missionaries presented them with educational opportunities (Mirak, 1983). But after more than 300,000 Armenians were massacred in 1894-96 under the authority of the Ottoman Sultan, Abdul Hamid II, Armenians looked to the U.S. as a place of refuge, hoping to escape Turkish persecution (Dadrian, 1995; Walker, 1980).

When the first Armenian naturalization case, *In re Halladjian*, was heard in 1909, most Armenians thought that the question of their “whiteness” was a foregone conclusion. After all, they were a people of the Caucasus, and as Caucasians, the Armenians believed that scientific evidence of their “whiteness” was beyond dispute, and that the fields of anthropology, ethnography and linguistics were unnecessary to resolve the issue (Bakalian, 1993). Physical or cultural distinctions, the Armenians argued, were not important (Atamian, 1955). *Halladjian* involved four

Armenian petitioners from different parts of the Ottoman Empire, all of whom applied for naturalization in Boston. The U.S. attorney determined that four were duly qualified for citizenship, but because they were not “white,” the government opposed their applications. The Armenian community in Massachusetts mounted a strong defense on behalf of their compatriots, and on December 24, 1909, the Commonwealth’s First Circuit Court held that “Armenians have always been reckoned as Caucasians and white persons; that the outlook of their civilization has been toward Europe.”²

In *Halladjian*, the government tried unsuccessfully to group Armenians with “Hindoos or East Indians and other such aliens,” arguing that the words “white persons” should be construed to mean “Europeans and persons of European descent.”³ The government argued, because the Armenians were “an Asiatic or yellow race,” their case should be denied. Rather than using anthropological or ethnographic testimony, the government instead relied on “what the average man in the street understands” the Armenians to be in terms of skin-color. Ultimately, the Circuit Court decided that “Armenians have always been classified in the white or Caucasian race, and not in the yellow or Mongolian,” and because their Christian religion manifested a sympathy with Europe over Asia, many Armenians became “westernized and readily adaptable to European standards.”⁴

Halladjian prompted many Armenians to quickly apply for naturalization. According to the 1920 census (11 years later), of the entire foreign-born Armenian population in the U.S., 29% were naturalized and 13% had received their first papers (Mirak, 1983). However, this trend did not last, since shortly after this census, Armenian racial-identity and therefore, their eligibility for citizenship, once again, came into question (Craver, 2009). In 1925, based on the precedents set in two other immigration cases decided by the federal courts (*Ozawa v. U.S.* in 1922 and *U.S. v. Thind* in 1923), the government renewed its attempts to deny and/or revoke citizenship to “non-whites” (Okoomian, 2002). In 1922, the U.S. Supreme Court held that Takao Ozawa (a native of Japan and graduate of the University of California at Berkeley) was not “white” (despite his very light skin-color) because he was not “Caucasian.” A year later, the same Court held that Bhagat Singh Thind (a high-caste Hindu who was serving in the U.S. military) was not “white”—despite the fact that he was Caucasian (Spickard, 2007).

Thind, in particular, raised new questions as to who was “white,” and therefore eligible for citizenship, using the “common knowledge” test for determining the racial-status of immigrants, a test based on “popular, widely held conceptions of race and racial divisions” (López, 2006, p.5). This new test—which was

rejected previously by the Circuit Court in *Halladjian*—forced Armenians back into an “ambiguous racial status” (Tehrani, 2009, p.2). After its victories in *Ozawa* and *Thind*, the U.S. government sought to revoke the citizenship-status of Tatos O. Cartozian in 1925 on the ground that the Armenian-born applicant was not “white.” By the 1920s, the federal courts regularly challenged citizenship claims using skin-color and racial origins as the primary criteria for deciding the boundary-lines of “whiteness” (Gualtieri, 2009). The *Cartozian* case was viewed by the U.S. Commissioner of Naturalization as the first in a series of test-cases judging the eligibility of citizenship of members of “Asiatic races” (Carver, 2009).

Born in 1877 in Sivas, a city in Central Turkey, Tatos Cartozian arrived at Ellis Island in 1906.⁵ The son of Osgan and Margaret Cartozian, Tatos’ father was killed in 1895 during the massacres organized by the Abdul Hamid II. Through the help of an American missionary, Cartozian settled in the city of Portland, Oregon, where some of his other brothers had established an Oriental-rug business (Lockley, 1928). Literally a rags-to-riches story, the Cartozian brothers became so successful in their business that they opened a second store in Seattle in 1918 and a third the following year in Spokane.⁶ In 1920, in order to provide a sure source of goods, they established an office in Sultanabad, Persia (modern-day Iran), where they operated their own looms for making Persian carpets (Lockley, 1928). Tatos and his brothers were all members of the Portland Chamber of Commerce, and they were also very active in the various Masonic Lodges throughout the state.

As soon as he was eligible, Tatos Cartozian filed his Declaration of Intention to become a U.S. citizen on December 15, 1917—less than a year before the end of World War I. In his filing with the Clerk of the U.S. District Court in Portland, Cartozian lists his skin-color as “white,” but his complexion as “dark.” After waiting the obligatory seven-years under the naturalization statute, Cartozian filed his Petition for Naturalization on January 30, 1923. On May 17, 1923, Cartozian was asked to appear in court with his family so that the judge could see if they met the

⁵Most of the personal history on Tatos Cartozian was retrieved from a membership-only website, Ancestry.com. Cartozian’s census records for 1920 and 1940 were the only decades available for review. The census-taker in both years indicated that Cartozian was “white” in the section asking for his “Color or Race” under “Personal Description.” Cartozian’s World War I draft registration card also lists his race as “white.” Interestingly, Cartozian lists his birth-year as 1877 in most documents, but in his Petition for Naturalization, he lists it as 1879. Without reviewing the court record, which is not available online and must be viewed at the Oregon Historical Society, it is not known whether the prosecutor ever made an issue of this discrepancy. Could he have argued, for instance, that Cartozian was so “un-Western” that he did not even know the year of his birth? In reviewing the records of other Armenian immigrants who passed through Ellis Island in the 1910s and 1920s, I also noticed the surprising number of times the date January 1 was used for a birthday. Presumably, if the immigrant did not know his or her birthday, the American immigration official used “January 1” as a catch-all.

⁶This advertisement for A.O. Cartozian Bros. Co. was found in a 1908 souvenir program for veterans of the Spanish-American War. Printed for a minstrel show at the Helig Theatre in Portland, the Cartozian advertisement epitomizes the “mysteries of the East,” with its depiction of a camel hovering over three Middle Eastern-looking men inspecting an Oriental rug. The Cartozians may have been “Western” in their cultural and religious outlook, but their business was decidedly “Eastern” in the way it presented itself to native Oregonians. The ad can be viewed at http://www.ebay.com/itm/SPANISH-AMERICAN-WAR-VETERANS-MINSTREL-SHOW-Heilig-Theater-1908-Portland-Oregon-/261648618442?pt=LH_DefaultDomain_0&hash=item3ceb7913ca.

²The Circuit Court further held that all of the Armenian petitioners “were white persons in appearance, not darker in complexion than some persons of north European descent traceable for generations. Their complexion was lighter than that of many south Italians and Portuguese.”

³*In re Halladjian*, 174 F.3d 834, 837 (Mass. Cir. Ct. 1909).

⁴In the same opinion, however, the Circuit Court ruled that Finns and Hungarians belong to the “Mongolian or yellow race”! Unlike the Armenians, these races had neither sought a modern education nor were they aligned with the “prevailing ideals, standards, and aspirations of the people of Europe.” *In re Halladjian*, 174 F.3d 834, 840-41 (Mass. Cir. Ct. 1909).

visual test of “whiteness.” The judge stated that he was doubtful of the right of an Armenian to be naturalized, but that he would admit Cartozian so that the Government could bring a “cancellation suit” from which either side could appeal (Carver, 2009). After taking the oath of allegiance, Cartozian was granted U.S. citizenship by the U.S. District Court.

Two years later, Cartozian’s citizenship was “cancelled” by the U.S. government. Here he was—a Horatio Alger success-story in the country’s Pacific Northwest—whose own government now revoked his “true faith and allegiance” to the U.S. by claiming he was ineligible for citizenship—all due to his skin-color. The prosecuting lawyer argued that “it makes no difference whether a man is a Caucasian or not or what the racial and language history of the people may be if the man on the street does not recognize him as white.”⁷ Cartozian’s legal team countered by arguing that both science and common-knowledge identified Armenians as “white.” Scientific testimony was given by anthropologists Franz Boas and Roland Burrage Dixon and scholar Paul Rohrbach, founder of the German-Armenian Society, in support of Cartozian’s case. In support of the claim that the Armenians were commonly known to be “white,” the defense team drew testimony from leaders of racially-restrictive fraternal organizations, such as the Loyal Order of the Moose and the Masonic Grand Lodge of Oregon, who attested to the common interpretation of Armenians as “racially white.” Otherwise, how could an Armenian immigrant have been admitted to these organizations?

Just like in *Halladjian*, the U.S. government lost its case to Cartozian in 1925. In its opinion, the U.S. District Court in Oregon ruled “that the Armenians are of the Alpine stock” and therefore must be considered “white” by law.⁸ To establish this fact, Cartozian’s legal team had called upon Boas to explain away the Asian-ness of a people whose origins resided squarely within the Asian territory of the Ottoman Empire. Boas testified that:

“The weight of the authority has been such, that their conclusions have been accepted without hesitation, particularly the evidence in regard to the European origin of the Armenians and their migration into Asia Minor. The evidence is so overwhelming that nobody doubts any more their early migration from Thrace across the Hellespont into Asia Minor. Although the Armenian province is within the confines of the Turkish Empire, being in Asia Minor, the people thereof have always held themselves aloof from the Turks ... on account of their religion, though color may have had something to do with it.”⁹

Boas also stated that the Christianity of the Armenians in a predominantly Muslim area of the world was further proof of their European ways. But the judge hearing the case did not believe that there was a dispositive test to determine a person’s race. The inquiry, according to the District Court, was not one to be determined by purely ethnological and scientific research. The test must also consider the “common understanding” of race, in a bow to the government’s lawyers. Even after considering both methods of inquiry, the result was the same, with the judge holding that “Armenians are white persons, and moreover

that they readily amalgamate with the Europeans and white races.”¹⁰

Whether the judge hearing the *Cartozian* case was surprised by the expert fire-power of the defendant’s case is not known. But a close reading of the opinion suggests otherwise. Indeed, the judge very early on in the decision rejects the notion that a visual inspection of a party’s skin-color is “practical” in determining “whiteness.” And while proper attention is paid to the scholarly “authorities” on racial classifications, most of *Cartozian* is about the willingness of Armenians to assimilate in America. One witness, James Barton, Foreign Secretary of the American Board of Commissioners of Foreign Missions, testified that the Armenians readily assimilate with Europeans and Americans, and that he personally knows of “ten or fifteen Armenians in Boston who have married American wives.”¹¹ Another witness, M. Vartan Malcolm—a successful Armenian lawyer and a graduate of Amherst College and Harvard Law School—testified on the number of Armenian men who had married “girls of Irish, German, Swiss, or French parentage.”¹² Even Boas discussed the importance of inter-marriage and assimilation when he cited statistics showing that 10% of first-generation Armenians married outside of their nationality. Furthermore, another key witness, Mrs. Otis Floyd Lamson (born Amenoush Tashjian in Erzerum, Turkey) exemplified the trend that the Armenians were presenting to the court. Lamson—daughter of an Armenian-Congregational minister and educated at the American College for Girls in Smyrna, Turkey, the University of Berlin and the Johns Hopkins School of Medicine—was married to Seattle orthopedic surgeon, Dr. Otis Lamson, a former University of Pennsylvania football star (Craver, 2009). According to the court’s opinion, Lamson testified that “the Armenians here very readily assimilate the American home life, provided they speak English.”¹³

The *Cartozian* case, just like the *Ozawa* and *Thind* cases before it, put on trial the petitioner’s potential for assimilation within the mainstream white, Anglo-Saxon culture of America (Tehrani, 2000). Their “Caucasian” identity and eligibility for citizenship were no longer based solely on scientific or geographic standards or even on how they were identified by the average man on the street. Instead, American courts would base the decision on the ability of an immigrant to pass as “white” in a cultural sense (Bakalian and Bozorgmehr, 2009). In order to prove “whiteness,” a precondition to naturalization, all three petitioners from these seminal cases presented evidence of their ability to live their lives as “white men” (Gross, 2008). Their legal teams presented evidence of not only their fluency in the English language, but also their usage of English at home, their education, their family’s education and social standing—and in Tatos Cartozian’s case, religious belief—which the court held was an essential factor for integration into the “white culture.” In *Cartozian*, Christianity, not skin-color, becomes a deciding factor in the eyes of the court of the petitioner’s ability to act sufficiently “white” (Tehrani 2000). However, performance of “whiteness” was not limited to religious belief. One of the determining

¹⁰*U.S. v. Cartozian*, 6 F.2d 922 (D. Oregon 1925).

¹¹*U.S. v. Cartozian*, 6 F.2d 921 (D. Oregon 1925).

¹²*U.S. v. Cartozian*, 6 F.2d 921 (D. Oregon 1925).

¹³*U.S. v. Cartozian*, 6 F.2d 922 (D. Oregon 1925).

⁷*U.S. v. Cartozian*, 6 F.2d 919 (Oregon Dist. Ct. 1925).

⁸*U.S. v. Cartozian*, 6 F.2d 920 (Oregon Dist. Ct. 1925).

⁹*U.S. v. Cartozian*, 6 F.2d 919-20 (D. Oregon 1925).

factors in *Cartozian* was the evidence submitted to the court proving a history of Armenian inter-marriage with Americans and Europeans—what is referred as an immigrant’s ability to “amalgamate readily” with native-born Americans.¹⁴

Throughout American legal and cultural history, the battle waged over “whiteness”—its definition, boundaries and proper contenders—has been a “fairly untidy affair” (Jacobson, 1998, p.5). The massive wave of immigration in the 19th century brought to America a diversity of peoples who considered themselves “free white persons” and therefore challenged the “monolithic quality of whiteness” that had reigned since the days of the Early Republic (Jacobson, 1998, p.38). As a result, it eventually fell to the American courts to define “whiteness.” Even if a favorable adjudication had allowed certain immigrant groups to become American citizens, anti-immigration bias flourished in the country between the 1920s and the beginning of World War II.

In 1930, Stanford researcher Richard Tracey LaPiere conducted a survey of close to 500 non-Armenian residents in Fresno, California concerning their impressions of Armenians. His results were discouraging. Most of the respondents listed derogatory traits as principal characteristics of the Armenians, including “dishonesty,” “undependability,” and “arrogance” (HoSang, 2012, p.99; Jendian, 2008, p. 67). For at least half of the respondents, the Armenians reminded them of Jews, and over 90% refused to accept marriage between Armenians and members of their families. Even the fact that the Armenians were Christians was of no importance, as more than 40% of the respondents refused to accept the Armenians as members of their local church (Jendian, 2008). Tatos Cartozian may have won his court case in 1925, but his “whiteness” was apparently of a different color in the eyes of those who still racialized boundaries in the decades that followed.

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¹⁴ *U.S. v. Cartozian*, 6 F.2d 922 (D. Oregon 1925).

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A Timeless Inquiry: The Quest to Understand Wormian Bones

Sarah Ricklan, Columbia University



The occurrence of Wormian bones, or bones that form between sutures in human skulls, has fascinated scientists and anthropologists for centuries. In fact, people have been writing about Wormian bones from the seventeenth century and continue to write about them today. With such extensive literature on the subject, a progression in understanding over the course of history would be expected. However, upon examining the literature, this progression is hardly present. Granted, there exist some minor differences in understanding, including a shift towards a more scientific and less anthropological outlook. For the most part, however, the same major themes of analysis are found in scholarly assessment old and new. Indeed, Wormian bones remain mysterious despite centuries of study.

Several major themes have been found to run through the scholarly analysis in articles and books ranging in publication date from 1888 (“Stillborn Children And Wormian Bones,” 1888) to 2013 (Bellary *et al.*, 2013), with one letter from 1643 (Jeanty, Silva, and Turner, 2000). First, many scholars take interest in describing Wormian bone development. In that vein, many take care to differentiate between Wormian bones and other sutural bones such as Inca bones. Second, scholars tend to discuss which factors cause Wormian bones to form. Finally, scholars wonder what, if anything, Wormian bones indicate about a person who has such bones. This paper seeks to address each of these three major common themes individually and in order. Each of these themes will be addressed by examining scholarly consensus and debate. Through this discussion, a historical understanding should emerge. At the end of the paper, the arguments will be synthesized and a historical overview will be presented.

Wormian Bone Development

The first major theme scholars discuss throughout

historical time relates to Wormian bone development. One of the most exhaustive authorities on the subject is Parker. Parker begins his analysis by speaking historically, explaining that Wormian bones were first documented by Olaus Worm (Parker, 1905). Interestingly, Worm does not actually discuss their development. Instead, he describes a case in which he sees various small bones in the skull, and documents their anatomical location and their general appearance (Jeanty *et al.*, 2000). Instead of defining Wormian bones by their appearance, Parker defines Wormian bones in terms of their development. Parker says that Wormian bones develop from independent centers of ossification, separate from the regular centers. Usually, says Parker, Wormian bones can be seen on both the exterior and interior of the skull, and are variable in size. However, Parker acknowledges that it is difficult to distinguish Wormian bones purely by sight unless the scholar knows how they developed (Parker, 1905).

Histologically, scholarly consensus seems to indicate that Wormian bones are membranous in origin and form from independent centers of ossification. Parker develops this idea, further explaining that Wormian centers of ossification either branch off from the normal centers of ossification or alternatively begin and remain entirely separate centers. Parker further explains that they grow from the inside to the outside, as normal bones grow (Parker, 1905). Hess argues that while most Wormian bones are membranous, some “wormian-like” (Hess, 1946, p. 61) bones might be cartilaginous. He also confirms Parker’s suggestion that Wormian bones are either independent from the beginning or separate at some point in development (Hess, 1946). The debate over this matter continues through history. Pryles and Khan, as well as Bellary *et al.* say that Wormian bones emerge from separate centers of ossification (Bellary *et al.*, 2013; Pryles and Khan, 1979). On the other hand, Cremin *et al.* maintain that they are formed from ossification centers that separate from the primary ossification centers (Cremin, Goodman, Spranger, and Beighton, 1982). Other scholars, such as Stotland *et al.* suggest several possibilities, thus implicitly acknowledging the uncertainty (Stotland, Do, and Knapik, 2012). While the general thrust of scholarship seems to side with the independent centers argument, it is interesting to note that so much debate has occurred, and that there is some doubt on the matter. However, Parker makes a fair point when he argues that

“The origin of Wormian bones by supernumerary centres [sic] or by division of primary centres [sic] is axiomatic, since they must either arise by separate centres [sic] and remain distinct, or develop as a part of the regular centres [sic] and in some manner

later be severed from their origin" (Parker, 1905, p. 17-18).

In other words, they start out either one way or another, but ultimately, Wormian bones develop as independent bones.

Parker seems to be at the forefront of understanding the timeline of Wormian bones' development. In his assessment, Parker discusses several authorities who suggest that Wormian bones only form at a late stage of development. He even notes that some authorities think Wormian bones do not develop until months after birth (Parker, 1905). Decades later, Hess furthers the idea that Wormian bones develop after birth (Hess, 1946). However, Parker does not hold this position to be necessarily true, as he notes that some evidence suggests otherwise (Parker, 1905). Indeed, today's scholarship argues that Wormian bones can and do develop in utero. For example, Rosignoli and Tonni discuss using 3D sonography to find Wormian bones in a fetus in its second trimester of development (Rosignoli and Tonni, 2013). This clearly proves that Wormian bone development does not happen exclusively after birth.

It is also clear from the literature that Wormian bones are not the same as other sutural bones. As early as 1888, the *British Medical Journal* understood that the Inca bone, also called the interparietal bone, epactal bone, or lambdoid bone, forms specifically out of the occipital, when the top and bottom portions of the occipital fail to unite ("Stillborn Children And Wormian Bones," 1888). Parker agrees that the Inca bone is formed from the membranous part of the squamous portion of the occipital. However, he emphatically expresses that people have been too loose with terminology. Parker explains other scholars' assessments; these scholars say that Inca bones are the same as epactal bones, but distinct from interparietal bones. To them, interparietal bones are simply bones that do not develop from independent centers of ossification. To Parker, however, this assessment does not show a correct understanding of the bones' development. Instead, Parker believes that interparietal bones and Inca bones are one and the same thing, referring only to bones formed in the membranous squamous portion of the occipital. While Parker is not clear about how he defines the epactal bone, he seems frustrated with the discussion and dismisses the debate (Parker, 1905). Parker's rant about terminology and his scathing comments about previous scholars give the reader a flavor of the scholarly debate in the early twentieth century. These features make reading his work both entertaining and immediate.

The literature continues Parker's legacy of distinguishing Inca bones and other bones. Almost one hundred years later, Fujita *et al.* discuss Inca bones as forming from the membranous squamous occipital while "suture bone[s]" (Fujita *et al.*, 2002, p. 199)—possibly Wormian bones, although the authors are not clear—develop from independent centers of ossification. Fujita *et al.* do, however, note that it is difficult to differentiate the types of bones (Fujita *et al.*, 2002). Other confirmations of Parker's analysis are given by Udipi and Srinivasan as well as Kumud (Kumud, 2011; Udipi and Srinivasan, 2011).

Indeed, many if not most articles from the mid-1940s on discuss the biological development of Wormian bones or other sutural bones. This seems to indicate an apparent historical shift as scholars move towards discussing biological and histological

issues instead of anthropological ideas further expounded upon later in this paper. This obsession with development certainly seems odd, since Wormian bone development seems well-established and undisputed. A skeptic might argue that this repetitive analysis comes from a lack of certainty about anything else related to Wormian bones combined with a need to publish research papers; development is one of the only concepts scholars can confidently discuss in papers. Alternatively, perhaps the matter of development would not be solidified if not for the concurrence of so many scholars through time.

The Causes of the Bones

Now that the development of Wormian bones and its scholarly analysis over time has been discussed, the second theme can be addressed. Scholars throughout the ages have asked a relatively simple question: what factors cause Wormian bones to form at all? On a general level, Parker suggests that Wormian bones form when the bones in the skull do not fuse in the normal way; Wormian bones come as a supplement to help the skull close (Parker, 1905). Soon after Parker writes, Barclay-Smith presents a case study in which Wormian bones were found in the bregmatic fontanelle of a fetus. He observes that the Wormian bones form before synostosis begins, and suggests that Wormian bones might be a way for the skull to fuse earlier in development than normal (Barclay-Smith, 1910). In this way, he corroborates Parker's position. Indeed, this suggestion is prevalent even in modern discourse. Tonni *et al.* explain that the chance of having a Wormian bone is 3.5 times greater if the patient's cranial bones fuse earlier (Tonni, Lituania, and Rosignoli, 2013).

Following neatly from this idea, Parker asserts that Wormian bones correlate with skull size. He records that patients with hydrocephalus, and thus a severely enlarged skull, have a high number of Wormian bones. Apes, with smaller skulls than humans, have few Wormian bones by contrast (Parker, 1905). Barclay-Smith also suggests such a correlation (Barclay-Smith, 1909). To summarize this theory, the larger the brain, or the more exposed a brain is, the larger the surface area that needs covering by bone. In order to help cover the surface area, Wormian bones form. This general theory fits well with discussions about pathological associations with Wormian bones discussed later in this paper.

While this idea makes logical sense, it does not have any real predictive power. Indeed, the explanation discusses the circumstances under which Wormian bones might arise and the purpose they would serve in those circumstances, but it does not predict when Wormian bones will form in other circumstances and why they form in such situations. In order to analyze this question, scholars debate environmental factors as compared to genetic factors. First, environmental effects will be examined. In a landmark article, Dorsey examined artificially deformed Kwakiutl skulls for the presence of Wormian bones. He divided the deformed skulls into two general categories. In one category, the bandage used to deform the skull did not leave an indentation on the skull. In these skulls, Dorsey found fewer Wormian bones. The second category consisted of skulls in which the bandage did leave an indentation on the skull. In

these skulls, Dorsey found many more Wormian bones. Further, Dorsey writes that more Wormian bones were present in longer skulls than in shorter ones. These findings seem to suggest that Wormian bones are associated with artificial deformation. Further, Dorsey proposes a mechanism behind these findings: Wormian bones supplement normal bone growth as normal bones are lengthened and intense pressure is applied to them (Dorsey, 1897).

Dorsey remains the authority on the matter for decades, but in 1977, El-Najjar and Dawson reexamine these findings. They looked at skulls with two different types of deformation in a Pueblo Indian population, as well as fetal skulls. While they found that symmetrically deformed skulls had the greatest frequency of Wormian bones, they did not confirm Dorsey's findings. Instead, they found that there was no significant difference between the occurrence of Wormian bones in undeformed skulls and the occurrence in deformed skulls. This implies, then, that environmental stress does not directly result in Wormian bone formation. One of El-Najjar and Dawson's stronger points argues that since the fetal skulls they examined also had Wormian bones, environmental stress cannot be the cause, since fetal skulls are not artificially deformed (El Najjar and Dawson, 1977). This approach holds up in light of the Wormian bones found in fetal cases discussed by the British Medical Journal, Barclay-Smith, and Rosignoli and Tonni (Barclay-Smith, 1910; Rosignoli and Tonni, 2013; "Stillborn Children And Wormian Bones," 1888). However, El-Najjar and Dawson do acknowledge that pressure does seem to have some effect on Wormian bone presence, as more Wormian bones were found on the deformed sides of asymmetrically deformed skulls than were found on the unaffected sides (El Najjar and Dawson, 1977).

A medium between the two opinions seems to be reached in 2010, when Van Arsdale and Clark take up the matter once again. They looked at skulls from the Philippines, and found three different types of skulls. Some were not deformed, some had frontal and occipital flattening, and some had only occipital flattening. Their findings show a higher frequency of Wormian bones in deformed skulls than what one would predict in a null case. Further, areas of the skull that were most likely to be affected by the deformation had more Wormian bones than other areas. However, Van Arsdale and Clark do not wholeheartedly agree with Dorsey, as they note that many normal skulls also had Wormian bones (Van Arsdale and Clark, 2012). Van Arsdale and Clark conclude that artificial deformation probably has some—but not an absolute—effect on Wormian bone formation, perhaps by increasing the "tendency towards extra-sutural bone formation" (Van Arsdale and Clark, 2012, p. 124).

Since environmental factors cannot fully account for Wormian bone formation, it is time to turn to the second argument: genetics. One major hint towards Wormian bones' heritability lies in Kellogg's work. He studied the hereditary nature of osteogenesis imperfecta, a disease affecting bone formation that, as will be discussed at length later in this paper, might be associated with Wormian bones (Kellogg, 1947). The fact that this disease seems to be heritable suggests a

genetic component, albeit secondarily, to the presence of Wormian bones. But one of the landmark arguments for genetic inheritance of Wormian bones comes from Torgerson. Bennett summarizes his articles.¹ Torgerson found that the trait was not only inherited, but also a dominant trait (Torgerson, 1951, 1952, 1954). However, Bennett rejects the notion that Wormian bones are directly inherited. Instead, he argues that genetics might influence bone development, which in turn would affect Wormian bone presence or absence (Bennett, 1965).

Major work towards understanding the genetic component of Wormian bones was undertaken by Berry and Berry in the 1960s. Berry and Berry studied normal variations in the skull, including Wormian bones, in several geographically distinct populations. Their results suggest that these variations are indeed heritable. However, Berry and Berry explain that Wormian bones have genetic undertones that are regulated during development by epigenetic factors. They emphasize that although variations might be heritable, the expression of the inherited genes is controlled by epigenetic factors. In other words, Wormian bone development is not directly caused by the genes (Berry and Berry, 1967).

Later work, however, has produced evidence that associate specific genes with Wormian bones. In their case study, Stotland *et al.* discuss an association between Wormian bones and cleidocranial dysplasia that has a mutation in the RUNX2 gene (Stotland *et al.*, 2012). By singling out this specific gene, they suggest a concrete genetic factor affecting Wormian bones. Similarly, Piagkou *et al.* find an association between Wormian bones and large parietal foramina. They suggest that the two phenomena are genetically linked (Piagkou, Skotsimara, Repousi, Paraskevas, and Natsis, 2013). They also cite Roybal *et al.*, who suggest that Wormian bones are associated with the MSX1/2 gene (Roybal *et al.*, 2010). Given these findings, the argument for genetic causes of Wormian bones seems convincing. However, there is still room to argue that these findings only explain Wormian bones secondarily, either by causing disease or by affecting development, and thus Wormian bones might not be directly heritable. Given advances in genetic technology, further genetic and molecular research might produce a more conclusive understanding of Wormian bones' formation.

The Effects of the Bones

It is now appropriate to transition to the third and final theme that runs through scholarly debate. Having surveyed the mechanistic aspects of how and why Wormian bones form, the question arises: what does it mean if someone has Wormian bones? There are three main ways in which scholars try to answer this question. First, scholars wonder if Wormian bones indicate that a person has a disease. Second, scholars associate Wormian bones with race. Third, scholars see Wormian bones as an indication of criminality. Each of the three lines of thought will be addressed separately.

¹Torgerson's article is unavailable through Columbia Libraries or online. His 1951 article is cited by Bennett, Stotland *et al.*, Rosignoli and Tonni, and Tonni *et al.*, his 1952 article is cited by Bennett and Berry and Berry, and his 1954 article is cited by Bennett, El-Najjar and Dawson, and Stotland *et al.* The citations to his articles are based on Bennett's citations of Torgerson's work.

First, Wormian bones may have pathological significance. In this vein, there are three main categories of diseases that appear in the literature. The first is vague, in that it acknowledges that Wormian bones are associated with some disease or condition that might cause death, but the exact problem and association is unclear. For example, the British Medical Journal discusses Dr. Grace Peckham's findings of stillborn children with Wormian bones. Dr. Peckham suggests that brain damage might have been caused during labor as the Wormian bones prevented the other cranial bones from being able to move and thus relieve the increased pressure on the brain during birth ("Stillborn Children And Wormian Bones," 1888). It is not clear, though, why these infants experienced more pressure than other viable infants born with Wormian bones; perhaps some unknown underlying condition caused the problem. Another example of uncertainty is found in a case study by Barclay-Smith, in which he examines Wormian bones in fetal skulls (Barclay-Smith, 1910). While Barclay-Smith does not ask or address this question, the reader wonders whether the Wormian bones had anything to do with the fact that the fetuses were not brought to term.

The second possible set of pathological conditions associated with Wormian bones includes diseases that affect metabolism and thus bone formation. Once again, Parker comes as an early source to shed light on this idea. He prefaces his discussion of the bones' pathological implications by saying that Wormian bones and pathologies are likely not directly related. Instead, Wormian bones' "occasional association with definite pathological processes may be secondary or incidental" (Parker, 1905, p. 29). Still, Parker analyzes a number of pathologies that have been suggested to be associated with Wormian bones. He finally concludes that osteogenesis imperfecta seems to be the most likely associated pathology, as it inhibits normal bone development, thus making extra bones useful (Parker, 1905).

Hess also discusses metabolic and developmental pathologies associated with Wormian bones. He notes that Wormian bones are often found in patients with dysostosis cleidocranialis, a disease that causes widespread bone malformation. Hess also discusses other diseases with which Wormian bones are associated. He notes that despite these findings, there are some diseases in which bones fuse early and patients do not present with Wormian bones. Further, many people without pathologies do have Wormian bones. In other words, while Wormian bones may be associated with pathologies, they do not tell the physician what the disease is and if a disease is even present (Hess, 1946). Even so, Pryles and Khan confirm both Hess' and Parker's suggestions of associated diseases, saying that Wormian bones are often found in patients with osteogenesis imperfecta or cleidocranial dysostosis (Pryles and Khan, 1974). Similarly, in their case study, Stotland *et al.* discuss a Wormian bone found in a young girl with metopic craniosynostosis who was later diagnosed with Turner syndrome. They repeat the sentiment that while Wormian bones are associated with metabolic disorders affecting ossification, Wormian bones themselves are not pathological (Stotland *et al.*, 2012).

Most extensively and rigorously, the question of osteogenesis imperfecta is taken up and studied by Cremin, *et*

al. Almost all osteogenesis imperfecta patients in their study had Wormian bones. Cremin *et al.* conclude that although Wormian bones are also found alongside other diseases such as cleidocranial dysostosis, physicians should still use Wormian bones to identify whether someone might have osteogenesis imperfecta (Cremin *et al.*, 1982). While these results are interesting, the real appeal of this study is its meticulous methodology that reflects a shift in the science. Cremin *et al.* do not consider every occurrence of Wormian bones significant. Instead, only Wormian bones more than six millimeters by four millimeters in diameter and arranged in a mosaic pattern were considered significant. Further, only patients with at least ten of these Wormian bones were assessed (Cremin *et al.*, 1982). With this tight methodology, the association with osteogenesis imperfecta becomes even more compelling. Marti *et al.* wanted to see if they could use this suggestion for a practical purpose: to determine whether pediatric patients with fractures should be screened as victims of abuse or rather patients with osteogenesis imperfecta. However, Wormian bones were not found to correlate with osteogenesis imperfecta in their study, and seem more random than indicative of pathology (Marti, Sirinelli, Maurin, and Carpentier, 2013).

The third set of pathologies that might be associated with Wormian bones includes disorders of the Central Nervous System and mental retardation. One of the earlier accounts of Wormian bones associated with such pathologies is discussed in an 1897 article by Paterson. Paterson presents a case study of cretinism, a disease that affects mental and nervous function. The affected child in this study had a Wormian bone (Paterson, 1897). While Paterson does not discuss the association of the disease with the Wormian bone, its presence provides an early foundation for the analysis of the association. Another hint in this direction comes from Lombroso, who, while he does not discuss the biological mechanisms or any particular evidence, mentions that people with epilepsy have Wormian bones (Lombroso, 1911). A more rigorous discussion of Wormian bones associated with Central Nervous System disorders appears in the literature much later. Hess lists many diseases that might be associated with Wormian bones; among these, he notes that Wormian bones are often found in patients with Central Nervous System disorders (Hess, 1946). While it is not their primary focus, El-Najjar and Dawson also bring up this possible association (El Najjar and Dawson, 1977).

However, it is Pryles and Khan that undertake extensive research on the matter, advancing the theory through clinical research. They found an association between mental retardation and Wormian bones. In fact, they found that patients with mental retardation had Wormian bones with a frequency four times higher than that of unaffected patients (Pryles and Khan, 1974). In a later paper, they looked at hundreds of randomly selected roentgenograms from children admitted to hospital. Of 515 patients examined, 91 had Wormian bones. Of those 91, 87 had Central Nervous System issues (Pryles and Khan, 1979). This high percentage suggests that there is some association between the two phenomena. Historically, though, this is one of the last times the issue of correlation between Central Nervous System disorders and Wormian bones is analyzed. The theory

seems to lose its popularity, with scholars preferring to discuss instead pathologies associated with metabolic disorders.

The second major feature with which scholars associate Wormian bones is more traditionally anthropological in nature: Wormian bones associate differently with different races. Deniker writes a book on race, with information ranging from cultural customs to physical characteristics. One distinct physical characteristic Deniker discusses is the occurrence of Wormian bones. Deniker finds Wormian bones and Inca bones in the people he studies, but he finds fewer in "Negro crania" (Deniker, 1900, p. 67), and even fewer in Europeans. Deniker concludes that these bones are more commonly found in American peoples (Deniker, 1900). El-Najjar and Dawson, however, say that, while people used to think such bones were found only in American Indian populations, this is not actually the case (El Najjar and Dawson, 1977).

Many other scholars address regional and racial correlation indirectly. In contrast to Deniker, Parker found that Parisians had more Wormian bones than Negroes, and Incas even fewer (Parker, 1905). Unlike Deniker, though, Parker's assessment is only secondarily related to race; to Parker, as discussed above, frequency of Wormian bones has to do with skull size, and it just happens that different races have different cranial capacities and thus different skull sizes. While the racial correlation is not necessarily corroborated, Bellary *et al.* do note that Wormian bones might be more common in Chinese populations, where parents place their children on their backs to sleep, thus causing deformation (Bellary *et al.*, 2013). As discussed above, deformation might cause Wormian bones to form. Again, this view does not say anything about the race correlation itself, but rather involves itself with cultural practices that happen to fall within racial lines. Finally, Berry and Berry discuss variations that occur within different populations of people. However, like the scholars that have already been mentioned, Berry and Berry do not focus on race qua race. Instead, they discuss heritability of physical variations; since distinct populations share a gene pool, these physical variations occur with different frequencies in different populations (Berry and Berry, 1967).

Third, some scholars see Wormian bones as indications of criminality. In his 1899 article, Brower discusses the causes of the crime he sees in the communities around him. Many causes are sociological, stemming from urbanization and drunkenness. Brower discusses at length the physiognomical aspects of criminality. He asserts that, among a whole slew of physical characteristics, criminals are prognathic, pale-skinned, and have wrinkles around the nose and mouth. Importantly, he says that they have many Wormian bones in the fontanelles (Brower, 1899). In fact, Brower considers criminals' brains backward and even a "reversion to the carnivorous type" (Brower, 1899, p. 1285). The association of Wormian bones with criminality is not unique. In 1911, Lombroso writes a book about crime, in which he says that criminals have Wormian bones (Lombroso, 1911). Furthermore, criminals also have "characteristics presented by savage races" (Lombroso, 1911, p. 365).

To the modern reader, Lombroso's locution is highly disturbing. With this sentence, Lombroso associates Wormian bones with criminals and inferior—savage—races. By saying that criminals share this trait, Lombroso advances a view that

certain races are dangerous. Obviously, such arguments relating to racial and social inferiority based on physical characteristics are no longer remotely valid in modern discourse, scientific or otherwise. In fact, one of the starkest contrasts between the discussions of Wormian bones before the 1940s and since then is the emphatic nature of the arguments. Many nineteenth-century and early twentieth-century writers make strong claims, frequently without much evidence. From the mid-1940s and on, scientists seem more cautious in their statements. They are careful to present many sides of the debate, even though they have access to larger pools of evidence and scientific advancements that can produce more definitive results. Perhaps this shift came in the wake of World War II, a war in which people saw the dangers of race science and strong, unsubstantiated claims about others.

In that vein, Parker's landmark 1905 work deserves special commendation. As one of the first major authors on the subject, Parker seems to be a pioneer and ahead of his time. While moments in his book seem archaic, Parker lays out the scholarly debate and presents many different answers to each issue in a way that seems modern and familiar to the twenty-first century reader. Further, in terms of content, his assessments of Wormian bones' relationship to osteogenesis imperfecta and to increased skull size in general remain popular lines of thought to this day. In sum, Parker's work seems to stand the test of time, and can easily be put into conversation with authors who wrote more than a century after he wrote.

That being said, it is notable and indeed surprising that for the most part, nothing has changed since Parker wrote in 1905. Scientists nowadays can discuss advanced genetic markers and can have a bit more to say about genetic versus environmental factors. But scientists still do not know how these two factors interact to cause Wormian bones to form. The major thrust of research, however, has been in examining what Wormian bones indicate. With the advancement of imaging technology, scientists today can look at live patients with Wormian bones instead of almost exclusively studying skulls from deceased patients. But scientists still do not know, and do not extensively discuss, whether there is a causal relationship between certain diseases and Wormian bones, or just an association. Their discussion of metabolic disorders and Wormian bones is logical, but the association with other pathologies, such as Central Nervous System disorders, remains largely unresolved. Additionally, scientists have yet to account for the presence of Wormian bones in healthy patients. Further, they have yet to decide whether Wormian bones can be used as a diagnostic tool or are merely just an interesting feature that is sometime indicative of certain diseases.

Ultimately, the major themes that run throughout historical treatment of Wormian bones leave the scientific community with a diluted understanding. First, Wormian bones are understood developmentally as intramembranous bones most likely coming from independent centers of ossification. Second, they seem to develop in order to supplement normal skull formation and fusion. Third, Wormian bones are a result of some unknown interaction between genetic factors and environmental influences. Finally, there may be some association with certain pathologies, but this relationship is not entirely

understood and does not exist in a one-to-one correlation. It seems, then, that despite intensive historical treatment of Wormian bones, the scientific community is not much further in its understanding of these small bones. Indeed, Wormian bones remain a mystery. Perhaps as scientific discourse moves forward, future researchers will be able to answer this centuries-old question that has amazed dozens of scholars through time.

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Neandertal Cranial Morphology: Diagnostic Features and Theories of Explanation

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Introduction

Human beings are, in a certain way, rather self-absorbed. We have a great interest in understanding ourselves – in understanding what makes us ‘human’. But to fully understand our present we must also understand our past, and it is that which makes the study of our evolutionary history so intriguing.

As the hominins most chronologically close to anatomically modern humans, Neandertals are of particular interest when studying the human evolutionary lineage. There is much we can learn from the archaeological and fossil records they have left us. But in order to study Neandertals, we have to be able to identify them. To that end, I will outline some of the generally accepted distinctive features of Neandertal crania, as well as some of the advantages and disadvantages of using these traits as diagnostic criteria. Then, I will examine the effect that intraspecies variation has on the use of these criteria. I will conclude by evaluating some of the more popular explanations for Neandertal cranial characteristics.

Diagnostic Features of Neandertal Cranial Morphology The Neurocranium

When examining the cranial morphology of fossil hominins, there are several characteristics traditionally considered to be indicative of a Neandertal. The first and most basic is the general shape of the skull. Upon visual inspection it is clearly longer and wider, with a lower vault and a maximum width lying just above the squamosal suture (Cartmill and Smith, 2009). The anterior portion of the neurocranium is expanded, resulting in a lesser degree of postorbital constriction (Cartmill and Smith). Measurements of maximum cranial length and breadth presented in Cartmill and Smith support this general conclusion. The cranial shape can also be quantified by calculating the vault-height index. The generally lower index values of Neandertals reflect their distinct cranial profile (Cartmill and Smith). When viewed from the rear, the Neandertal skull presents a rounded, oval silhouette known as “en bombe” (Tattersall and Schwartz, 2006; Cartmill and Smith, 2009).

The occipital bone of the Neandertal cranium is particularly distinctive. For example, of the four diagnostic features identified by Santa Luca (1978), three (a large occipitomastoid crest, a distinct occipital torus, and the presence of a suprainiac fossa) are located on the occipital bone. In Neandertals the occipitomastoid crest often equals the mastoid process in length or even extends below it (Santa Luca, 1978; Cartmill and Smith, 2009). Santa Luca refers to the

occipitomastoid crest as being “larger” (p. 628) than the mastoid process; Cartmill and Smith clarify that the occipitomastoid crest is displaced downwards, so that the mastoid process does not protrude so far below the cranial base. The reason for this downward displacement is unclear, but may relate to the expansion of the occipital lobe of the brain (Cartmill and Smith). The occipital torus (or nuchal torus) is horizontal, of uniform vertical thickness, and has no external occipital protuberance or only a slight protuberance (Santa Luca).

The last of Santa Luca’s Neandertal autapomorphies is the suprainiac fossa, an elliptical depression located above the occipital torus. It is delineated inferiorly by the superior nuchal line, but its upper boundary is more nebulous (Tattersall and Schwartz, 2006; Cartmill and Smith 2009). Its surface is often pitted, giving the appearance of rugosity (Tattersall and Schwartz; Cartmill and Smith). This pitting is also found by the external occipital protuberance in anatomically modern humans, at the attachment point of the nuchal ligament (Cartmill and Smith). This has led to speculation that the nuchal ligament in Neandertals was broader and fan-shaped, attaching over the suprainiac fossa (Cartmill and Smith). The pitting may also reflect resorption of bone in that area (Balzeau and Rougier, 2010). Many consider the suprainiac fossa to be an important defining trait of Neandertals (Santa Luca, 1978; Balzeau and Rougier, 2010; Nowaczewska, 2011), despite other researchers (Haile-Selassie *et al.*, 2004; Trinkaus, 2007) describing similar fossae on anatomically modern human skulls. A study examining the gross anatomy and internal bone structure of fossae in Neandertals and anatomically modern humans found that the suprainiac fossa is systematically present in Neandertals at all developmental stages and has a distinctive internal composition, different from the internal composition of equivalent fossae on anatomically modern human skulls (Balzeau and Rougier, 2010). A subsequent paper by Nowaczewska (2011) examined the etiology of these fossae and concluded that they were convergent traits, lending support to the claim that the suprainiac fossa is a trait unique to Neandertals, and that similar fossae in modern humans are convergent rather than homologous.

These are not the only distinctive characteristics of the occipital. Neandertals exhibit an occipital plane longer than the nuchal plane (Cartmill and Smith, 2009). As the shape of the occipital bone is roughly that of the posterior part of the brain, the Neandertal occipital structure reflects enlargement of the occipital cortex (Cartmill and Smith). However, as Neandertal crania are usually wider than those of anatomically

modern humans, the total area of their nuchal plane (and thus the surface for neck muscle attachment) is therefore larger (Cartmill and Smith). Rak *et al.* (1994) cite an elongated, oval foramen magnum as a distinctive Neandertal trait in their examination of a Neandertal infant (Amud 7), which would be consistent with the elongation of the cranium in general. However, Cartmill and Smith (2009) contend that an elongated foramen magnum can be found in other human populations and thus cannot be considered a Neandertal autapomorphy. In a response to criticism from Creed-Miles *et al.*, Rak *et al.* (1996) reexamined the foramina magna of several Neandertals, arriving at the conclusion that while oval-shaped foramina magna may be found in modern humans, the length of Neandertal foramina magna is still statistically significant and can serve as a distinguishing trait.

Perhaps the most visually striking feature of the Neandertal neurocranium is the occipital bun, or “chignon”, although its function remains unclear. It has been suggested that the occipital bun serves to direct the nuchal plane downward, increasing the horizontal surface available for muscle attachment; it may also be the result of a surge in posterior brain growth late in development, causing the bone to bulge outward (Cartmill and Smith, 2009). This structure is most often described as a posterior projection of the occipital bone, but in fact it involves many aspects of the posterior cranial morphology (Gunz and Harvati, 2007). Cartmill and Smith (2009), for example, define the occipital bun as a posterior protuberance at the back of the vault produced by a combination of lamdoidal flattening (flattening of the parietal and occipital bones around the lambda), a relatively vertical lower occipital plane, and a downward directed nuchal shelf. The most visible aspect of the occipital bun, the convex midsagittal profile of the occipital squama, is not singularly sufficient to distinguish Neandertals (Gunz and Harvati). Only when a full suite of occipital, parietal, and temporal landmarks is considered can a full separation between Neandertals and modern humans be obtained; this indicates that the morphology of the occipital is closely integrated with the morphology of the rest of the braincase and cannot be considered a distinguishing trait on its own (Gunz and Harvati). This leads to difficulties in the practical evaluation of fossil hominids, as the presence of a true occipital bun cannot be conclusively determined unless the majority of the neurocranium remains intact.

Some anatomically modern humans exhibit a similar feature, which is alternatively termed a “hemibun” and a true occipital bun, depending on whether the observers consider it to be an analogous or homologous feature (Nowaczewska and Kuźmiński, 2009). There is also disagreement regarding which anatomically modern specimens exhibit this feature, likely as a result of different methods of defining an “occipital bun” (Nowaczewska and Kuźmiński). In most cases, the shape of the midline occipital profile is examined (Nowaczewska and Kuźmiński), but as just demonstrated this is not sufficient to successfully define an occipital bun. Supporters of the multiregional evolution model often point to the hemibun as an indication of gene flow between Neandertals and early European populations of anatomically modern humans, but Nowaczewska and Kuźmiński’s analyses suggest that the development of the occipital plane is different

in Neandertals and anatomically modern humans. They suggest that the similarities between modern humans and Neandertals are by-products of similar relationships between occipital convexity, relative height of the cranial vault, and the parietal mid-sagittal profile, which is not sufficient to conclusively prove the features are homologous (Nowaczewska and Kuźmiński).

The other bones of the neurocranium provide their own diagnostic features. While much of the morphology of the frontal bone is archaic, such as the flat, sharply sloping squama and larger frontal angle, the morphology of their frontal sinuses is distinct from that of modern humans (Cartmill and Smith, 2009). Although generally restricted to the supraorbital region, Neandertal frontal sinuses are more voluminous than those of modern humans (Cartmill and Smith). On occasion this expansion is so pronounced that the walls of the supraorbital torus near the midline are extremely thin (Cartmill and Smith). On the temporal bone, a mandibular fossa with well-developed medial walls and a thick, projecting postglenoid fossa is often observed. The articular eminence, which forms the anterior wall, is contrastingly less pronounced than in modern humans (Cartmill and Smith). This morphology has been linked to heavy use of anterior dentition (Hinton, 1981) and is often used to support the Anterior Dental Loading Hypothesis, which will shortly be discussed in depth.

More recently, CT scans of the temporal region have revealed that the form of the bony labyrinth varies between Neandertals and modern humans (Tattersall and Schwartz, 2006). In Neandertals, the anterior and posterior semicircular canals are smaller, the posterior canal is lower relative to the lateral canal, and a line through the ampullae of the anterior and posterior canals makes a larger angle with the plane of the lateral canal (Spoor *et al.*, 2003). These differences in form may be related to differences in locomotor behavior (namely, decreased agility and less running) and kinematic properties of the head and neck (relating to the more robust nature of Neandertals) (Spoor *et al.*).

The Splanchnocranium

Neandertal faces are just as distinctive as their braincases—broad and long, with large features (Cartmill and Smith, 2009). While the size of the orbits is comparable to contemporaneous anatomically modern humans, they are larger than those of modern humans (Cartmill and Smith), and Tattersall and Schwartz call the nasal aperture “very large” (2006, p. 12). The teeth are also large, necessitating a large alveolar process to house them, and the infraorbital foramen is increased in size (Cartmill and Smith). This last feature might constitute a cold adaptation – a larger infraorbital foramen would allow greater blood flow to the face, which would be advantageous in a colder climate. However, it is also possible that a large infraorbital foramen is simply a consequence of the increase in general facial size (Cartmill and Smith). The apparent size of the face is only increased by its “puffy” shape (Tattersall and Schwartz, 2006, p. 12), reflecting inflated maxillary sinuses. This inflation results in a flat or convex infraorbital plate, thereby eliminating the canine fossa (Cartmill and Smith). However, despite the general increase in facial size compared to modern humans, it is necessary to remember that the Neandertal face is not uniformly robust (Cartmill and

Smith). Rather, some areas are reinforced or buttressed such as around the nose and between the orbital and facial plates of the zygoma, while other areas are more gracile (Cartmill and Smith).

The supraorbital torus is to the splanchnocranium what the occipital bun is to the neurocranium—a prominent trait clearly visible to casual inspection. The presence of a supraorbital torus is in fact an archaic feature, but in Neandertals it is arched over each orbit (Tattersall and Schwartz, 2006) whereas in earlier forms such as *H. erectus* and Heidelbergers it is more bar-like (Cartmill and Smith, 2009). Between the eyes it is depressed by a supraglabellar fossa (Smith and Ranyard, 1980). It is thickest over the midpoint of the eye, and thins laterally (Smith and Ranyard). Compared to modern humans, the torus is thicker both anteroposteriorly and superiorinferiorly, and is separated from the forehead by a supratatorial sulcus, or flattening (Smith and Ranyard). Internally, the expansive frontal sinus of Neandertals occupies the glabellar region, extending out into the orbital region of the torus (Smith and Ranyard). Supraorbital tori were heavier in early Neandertals and lighter in later fossils, although the difference is not large (Howell, 1951).

There are many proposed theories to explain the presence of such a large brow ridge. Oyen *et al.* (1979) found patterns of deposition and remodeling of fine, cancellous bone in non-human primate, Neanderthal and AMH crania, suggesting that supraorbital tori were formed by processes closely related to masticatory activity. Thus, the supraorbital torus could exist to strengthen that area of the skull against the stresses placed on the bone by vigorous chewing (Oyen *et al.*, 1979). A complementary explanation involves masticatory stresses as well as expansion of the brain and orbital region of the skull (Oyen *et al.*). Finally, a contrasting hypothesis posits that the supraorbital torus is an adaptive response to the need for protection from heavy blows landing above the eyes (Oyen *et al.*). The results of Oyen *et al.*'s study ultimately favor masticatory stress to explain the structure of the Neanderthal brow ridge.

Another characteristic feature of the Neanderthal splanchnocranium is the sharply retreating midface (Schwartz and Tattersall, 2006). In archaic species of *Homo*, the entire splanchnocranium—including the jaw—is projected forward from the braincase. In anatomically modern humans, the entire face is brought below the braincase. Neandertals exhibit a peculiar prow-like profile in which the nasal or midface skeleton projects forward from the neurocranium, while the lateral parts of the face (the cheekbones) are swept back (Cartmill and Smith). Two possible scenarios explain this distinct morphology, and each imply a different taxonomic relationship between Neandertals and modern humans. Neandertals may represent an intermediate stage between archaic *Homo* and modern humans, in which the lower part of the face began to move under the brain case while the nasal area remained projecting forward. This would place them as ancestors to modern humans. It is also possible that some time after the splanchnocranium began to move under the neurocranium, the midface of Neandertals moved back out to project further – an autapomorphy that would suggest Neandertals had already diverged from the ancestral line of modern humans (Cartmill and Smith).

One area of Neanderthal cranial morphology that has

engendered a surprising amount of debate is the internal structure of the nose. The debate began with the claim of three unique Neanderthal features of the internal nose: an internal nasal margin with a well-developed vertical crest, the swelling of the lateral nasal cavity wall into the cavity itself, and the lack of an ossified roof over the lacrimal groove (Schwartz and Tattersall, 1996). Schwartz and Tattersall (1996) defined the internal nasal margin as a rim of raised bone projecting from either side of the anterior nasal, which expands to become a vertical crest protruding medially into the nasal cavity. They hold that this structure is not the same as the conchal crest, as it arises farther forward and is oriented more vertically (Schwartz and Tattersall, 2006). While they call these three traits autapomorphic and suggest they are unique among hominids and perhaps terrestrial mammals, Schwartz and Tattersall admit that this is not proof that Neandertals and modern humans are separate species. However, they believe it is supportive of that theory (Schwartz and Tattersall, 1996). Franciscus (1999) responded to Schwartz and Tattersall's claims, countering that the so-called "internal nasal margin" is actually the structure known as the crista turbinalis, and that there is considerable variation in how this crest (and other internal nasal crests) presents. He suggested that the crest is simply more visible in Neandertals as a result of their nasal aperture being wider, particularly at the top. He also stated that the crista turbinalis is not unique to Neandertals, but is present in high frequencies both in recent humans and in fossil *Homo* (Franciscus, 1999). Franciscus also refuted Schwartz and Tattersall's other two supposed autapomorphies. Measuring the internal nasal breadth of several specimens he found that Neandertals actually have wider posterior nasal apertures, which is inconsistent with swelling of the lateral wall (Franciscus, 1999). Finally, he cited a study which found both open and closed lacrimal grooves in recent human skulls, again eliminating the possibility of the trait being an autapomorphy (Franciscus, 1999).

Schwartz and Tattersall returned yet again (this time with one more co-author) to the question of the internal nasal margin some years later. In 2008, Schwartz *et al.* set out to answer two primary objections from Franciscus and other contrary reports: first, that the feature they identified as the internal nasal margin is homologous to the mammalian maxilloturbinal (or inferior nasal concha), and second that the internal nasal margin is a separate feature, but one also present in modern humans. Upon reviewing a large sample of Neanderthal, modern human, and primate remains, they concluded that the vertically oriented medial swelling they had previously identified was not the same structure of the maxilloturbinal, which is also present in some Neanderthal specimens, and that only Neandertals and one Heidelberg possessed this feature, confirming its autapomorphic status (Schwartz *et al.*, 2008). It is worth noting that the first objection Schwartz *et al.* refer to is somewhat inaccurate – Franciscus did not maintain that the unidentified structure was a maxilloturbinal, but rather a crista turbinalis, or oblique ridge articulating with the maxilloturbinal (Franciscus, 1999).

Which contention is correct? That is difficult to determine without a strong grasp of the internal structure of the nose in primates and modern humans, but this is difficult to achieve

considering the variable nature of the expression of many of the interior crests, as well as the simple fact that internal nasal structures are delicate and unlikely to be well-preserved (Franciscus, 1999).

The Mandible

While fossil mandibles may not be the most glamorous of finds, they are very common. In fact, they are the most commonly found skull remnant after teeth (Cartmill and Smith, 2009), and so it is imperative to consider what distinctive Neandertal traits might be visible in the mandible. The most obvious is the lack of a true bony chin (Cartmill and Smith). Later specimens exhibit a concavity which gives the impression of some forward projection of the base of the mandible, but these fossils lack the mental trigone that characterizes the modern human chin (Cartmill and Smith). The receding cheekbones of many Neandertal fossils shift the temporal fossa backwards relative to their dentition, and with them the mandibular ramus (Cartmill and Smith). This results in a narrowing of the ramus and a retromolar space, or gap between the last molar and the ascending ramus of the mandible (Tattersall and Schwartz, 2006; Cartmill and Smith). Some suggest this as a distinctive Neandertal trait (Ahern, 2006; Tattersall and Schwartz), but while Franciscus and Trinkaus (1995) found retromolar spaces in about 75% of the Neandertal fossils they examined, they also found retromolar spaces in about 60% of the Qafzeh-Skhul sample and around 30% of the European modern human sample. In addition, Nicholson and Harvati (2006) found the retromolar space to be associated with increased mandibular size in modern humans, casting some doubt on its classification as an autapomorphic trait. Finally, there is the horizontal-oval (H-O) pattern of the ramus (Ahern, Cartmill and Smith), which is defined by the presence of a broad band of bone incorporating the mandibular lingula and extending horizontally across the entrance of the mandibular nerve into the mandible (Cartmill and Smith). This feature can be interpreted to provide an expanded, reinforced attachment area for the sphenomandibular ligament, increasing mandible stability (Cartmill and Smith).

Frequencies of Diagnostic Traits

The above features are generally considered to be characteristic of Neandertal skulls—but how useful are they as diagnostic traits? In order to determine which features are most significant in distinguishing Neandertals from other taxa, it is necessary to examine the frequencies at which they occur. A table from Ahern (2006) lists frequencies of some of the more distinctive traits, both in Neandertals and in Upper Paleolithic modern humans. Although the sample size considered is rather small (a necessary evil, as there are few Neandertal remains and some of them are not sufficiently well-preserved to identify some of these traits), the chart gives a helpful overview of the frequency and relative significance of Neandertal cranial traits. Where there is debate over the definition of a trait, both a liberal and conservative version are included (e.g., for the occipital bun the “liberal” definition would likely include hemibuns and the “conservative” definition would not; the liberal definition of suprainiac fossa includes fossae in anatomically modern humans).

An examination of this table clearly demonstrates that the best traits for identifying Neandertals are the suprainiac fossa (in particular the conservative definition) and the large occipitomastoid crest, rather than the more visually striking traits such as the occipital bun (although with the possible exception of the anterior mastoid tubercle, all the traits listed give a decent separation between Neandertals and Upper Paleolithic modern humans. It would be interesting to consider a more thorough chart, listing more diagnostic criteria (in particular some from the splanchnocranium, which is not represented in the table discussed) and with a larger sample size if possible.

The Problem of Intraspecific Variation

The traditional diagnostic features of Neandertals (e.g. occipital buns, prominent supraorbital tori, suprainiac fossae, weakly projecting mastoid processes) are most often found in the “classic” Neandertal specimens (Cartmill and Smith, 2009). The core group of fossils belonging to this group includes Neander valley, Spy, Chapelle-aux-Saints, La Ferrassie, La Quina, Le Moustier, and el Sidrón – all western European finds (Howell, 1951; Cartmill and Smith, 2009). However, there is a great deal of geographic variation among Neandertals (Howell, 1951), and fossils from the near Middle East/Levant and Eastern Europe often do not exhibit the same cranial morphology (Cartmill and Smith).

Levantine specimens tend to have less emphatically Neandertal morphology. For example, the remains from Tishik Tash display a Neandertal-like cranial vault with a suprainiac fossa, but a less exaggerated supraorbital torus (Cartmill and Smith, 2009). Shanidar Neandertals exhibit many typical Neandertal-like features in their postcranial anatomy, but lack any trace of occipital bunning (Cartmill and Smith). Fossils from sites such as Amud, Kebara, Tabun and Dederiyeh have widely varying cranial capacities, more rounded vaults, and no occipital buns, but do possess an elongated foramen magnum (Cartmill and Smith). The Tabun C2 mandible provides a clear mosaic of Neandertal traits such as a retromolar space, H-O patterned mandibular foramen, and large anterior dentition, as well as modern human traits such as a true chin (Cartmill and Smith).

This apparent dilution of unique Neandertal traits can be used to argue that human populations of Levant were transitional between Neandertals and anatomically modern humans, in line with the multiregionalism hypothesis of modern human origins, or that interbreeding occurred between Neandertals and anatomically modern humans (Cartmill and Smith, 2009). It has also been interpreted as a result of the less extreme climate following from the climatic adaptation hypothesis: if the distinctive features of classic Neandertals arose as adaptations to cold stress, then Neandertals living in less frigid environments would possess those traits to a lesser degree (Cartmill and Smith).

Evaluation of Central and Eastern European Neandertals reveals that in many cases they also exhibit more ‘modern’ and less ‘classic Neandertal’ morphology (Jelinek *et al.*). Fossil jaws from Ochoz and Sipka lack mental spines (true chins), but the Sipka jaw is thicker at the base than at the alveolar process, which is a more modern feature (Jelinek *et al.*, 1969). A frontal bone from Sala displays a supraorbital torus, but one that is less

pronounced, like the tori of Levantine finds rather than those of classic specimens (Jelinek *et al.*). This variation from the classic form is less easily explained, as there is less geographic separation from the Western European populations and the climate was more similar to that of the classic Neandertals (Cartmill and Smith, 2009).

Distinguishing Neandertals from Other Hominins

Can we say, based on the fossil record, that Neandertals were a separate species? First, it would be necessary to establish them as separate from Heidelbergers or transitionals. Considering the nebulous nature of "Heidelberg" as a taxonomic classification, this is a challenging endeavor beyond the scope of this paper. The taxonomic status of anatomically modern humans being somewhat clearer, it should be possible to quantify the level of difference between Neandertals and modern humans, and thus determine whether they are indeed separate species.

On the other end of the Neandertal range, "transitional" or "progressive" forms with features characteristic of both Neandertals and anatomically modern humans can be found (Cartmill and Smith, 2009). For example, the Saint-Césaire Neandertal displays typical infraorbital and mandibular morphology and midface projection, but has a reduced torus, reduced anterior teeth, and narrow nose (Cartmill and Smith). Fossils from Vindija are generally considered to be Neandertal but possess supraorbital tori which are commonly thinner and differently shaped, as well as higher foreheads, narrower noses, and possible chins (Cartmill and Smith). In order to fully explain the Neandertal fossil record and clarify the relationship between that taxon and ours, we must determine whether these remains represent a gradual transition from Neandertals to humans, which would imply an evolutionary relationship, or whether their features result from convergent evolution and the two taxa consist of separate lineages.

The strongest evidence indicating that Neandertals and modern humans were a separate species comes from geometric morphometric analyses systematically carried out a wide range of crania, including Late Pleistocene fossil hominins, two comparative samples of modern humans, and one comparative sample of chimpanzees (*Pan paniscus* and *Pan troglodytes*) (Harvati, 2003). Detailed measurements were taken of every skull, and statistical analyses of those measurements indicated that the level of variation between modern humans and Neandertals is greater than that between different populations of modern humans, and greater even than the differences between the two chimpanzee species (Harvati, 2003). A follow up study (Harvati *et al.*, 2004) examined variation in modern human skulls, Neandertal skulls, and twelve species of non-human primates. Once again, the data indicated that differences in the configurations of cranial landmarks between Neandertals and modern humans were significantly greater than those found between subspecies of other primate populations (Harvati *et al.*, 2004).

These conclusions are greatly supported by the findings of Ponce de Leon and Zollikofer (2001), who, through computerized fossil reconstruction and geometric morphometrics, demonstrated that characteristic differences in the cranial and mandibular shapes of Neandertals and humans, such as a

broadened temporal region, elongated foramen magnum, or retromolar space, arose very early in development (possibly prenatally) and were maintained throughout later ontogeny. This is a strong indication of species-level separation between the two taxa.

Explanations for Cranial Morphology

It seems fairly certain that Neandertals had different craniofacial morphologies from modern humans, possibly to the point of a species-level distinction. What, then, is the cause of these differences? There exists a theory (and often more than one) to explain every individual aspect of the Neandertal cranium, but here I will focus on four of the more popular theories of explanation: climatic adaptation, anterior dental loading, genetic drift, and movement of the sphenoid.

Cold Adaptation

One of the earliest theories proposed to explain the peculiarities of the Neandertal face was the climatic adaptation theory (Cartmill and Smith). Brose and Wolpoff (1971) suggest that anterior displacement of the face would increase separation between the nose and the brain. This separation, along with a particularly large nasal aperture, would be valuable in the cold for regulating the temperature and humidity of inhaled air (Brose and Wolpoff, 1971). Similar logic can be used to explain enlarged frontal and maxillary sinuses as cold-adaptations. However, the cold-adaptation hypothesis faces many challenges. Much of its supporting evidence comes from ecogeographic patterning of modern humans – but ecogeographical patterning of the nasal aperture, for example, correlates narrower noses with colder climates, and wider noses in warmer climates where they could be used to dissipate more heat (Holton and Franciscus, 2008).

Likewise, the maxillary sinus has been shown to shrink with a decrease in temperature, rather than grow (Rae *et al.* 2006; Rae *et al.* 2011). Rats raised in cold temperatures exhibit smaller maxillary sinuses and nasal apertures than rats raised at warmer temperatures (Rae *et al.* 2006), directly contradicting the climatic adaptation hypothesis. This data is consistent with comparative studies of temperate primates, suggesting that hominin crania would respond similarly to cold stress (Rae *et al.*, 2006). A later paper by Rae *et al.* (2011) expanded on this result by investigating the assumption that Neandertal maxillary sinuses are hyperpneumatized at all, and found that not only would pneumatization not be expected to increase in the cold, but the relative level of inflation of the maxillary sinuses in Neandertals is corresponds to the overall size of the cranium (Rae *et al.*, 2011).

Other aspects of the cranium, however, might be influenced by adaptation to a cold climate. Nowaczewska *et al.* (2011) used linear regression and correlation analysis to show that the correlation between basicranial breadth and ambient temperature is stronger than that between temperature and other neurocranial variables (maximum neurocranial length and breadth, endocranial volume). They also found that this correlation remained strong even when controlling for other variables such as overall neurocranial size (Nowaczewska *et al.*, 2011). So while the low ambient temperature of the Neandertal range does not seem to affect the splanchnocranium, it may be influencing the shape of other aspects of the skull.

Anterior Dental Loading (“Teeth as Tools”)

Another hypothesis, the anterior dental loading hypothesis (ADLH), explains the Neandertal facial anatomy as an adaptive response to high-magnitude forces generated by mastication and paramasticatory activity (such as using the teeth as tools) (O'Connor *et al.*, 2005). The buttressing of the Neandertal face along with the lack of articular eminence, H-O configuration of the mandible, degeneration of the temporomandibular joint, and large, heavily worn anterior dentition all seem to support this hypothesis (Cartmill and Smith, 2009).

O'Connor *et al.* (2005) measured points on the Neandertal and modern human cranium and mandible, then calculated from these values the force-production capability and force-production efficiency of each. Contrary to what would be expected according to the ADLH, the primary dichotomy found was not between Neandertals and anatomically modern humans but rather between gracile forms and robust forms, regardless of taxon (O'Connor *et al.*). The results indicate that Neandertals were not able to generate significantly larger dental loads than modern humans, nor were they considerably more or less efficient at doing so (O'Connor *et al.*).

Challenges to the ADLH do not end there. Wang *et al.* (2010) studied the relationship between facial length and biomechanical stress in macaques, and their results indicated that comparable muscular force generates less stress on a shorter face. As selective pressure would be highly unlikely to result in a face simultaneously better at distributing high loads and worse at generating them, this seems to be a blow to the ADLH. They add, however, that the selective pressure for a shorter face might have been counterbalanced by a tough diet requiring large grinding molars, and thus a slightly longer jaw (Wang *et al.*).

Genetic Drift

It is possible that variation in cranial form between Neandertals and humans is not a result of adaptation due to natural selection at all, but rather the result of random genetic drift, where geographic or reproductive isolation led to the accumulation of trait differences (Weaver *et al.*, 2007). This is not necessarily to say that natural selection did not act on cranial morphology at all, but rather that selective pressures were acting more or less in the same way on Neandertals and other hominids (Weaver *et al.*). Of course, this assumes that there was geographic or reproductive isolation, a point on which there is great debate in the scientific community.

Assuming that there was isolation of some kind between the two taxa, a comparison between the level of variation seen and the level of variation predicted based on neutral evolution should indicate whether selective pressure is operating on the cranium. Weaver *et al.* performed this sort of comparison using four different statistical tests. Their results indicate that the mean morphological differences between humans and Neandertals are not outside the range expected under neutral evolution. If anything, their results indicate that natural selection played a larger role in the diversification of modern human crania rather than the differentiation of Neandertals and anatomically modern humans (Weaver *et al.*).

Smith (2011) reached a similar conclusion using microevolutionary modeling and examining patterns of variance/covariance (V/CV). Her results indicate that V/CV patterns in the basicranium, temporal bone, and face are consistent with the hypothesis of neutral genetic evolution, although the V/CV pattern of the mandible deviated from the expected pattern (Smith, 2011). Therefore it is possible that natural selection is acting only on certain aspects of the cranium.

Sphenoid Position

As the other theories considered in this paper involve complex processes acting on multiple areas of the cranial anatomy at once, Lieberman's (1998) proposal that the shortening of the sphenoid produced the modern cranial shape provides an interesting contrast. It seems unlikely that the movement of a single bone could produce such drastic changes in craniofacial morphology – until one considers the central position of the sphenoid in the skull. Shortening of the sphenoid affects spatial relationships between the face, neurocranium, and cranial base, which all together determine the degree of facial prognathism or projection (Lieberman, 1998). This, in turn, has significant effects on brow ridge size, frontal angulation, and overall roundness of the skull (Lieberman). Lieberman thus suggests that many of the distinct features of the modern human face arose from a single, developmentally early shift in the position and length of the sphenoid bone.

Conclusions

There are unquestionably many challenges in analyzing Neandertal cranial morphology, as traditional diagnostic features appear only in a subset of the group, and even then are often of only limited value. Classic defining traits such as the occipital bun suffer from discrepancies in definition and possible homologous features in other hominid taxa. Still, the weight of the evidence suggests that Neandertals are significantly different from modern humans, and have certain morphological traits which are distinct enough to use as diagnostic features, though the best option might be to take a holistic approach, considering as many individual traits as possible as well as the relationships between them. This would also minimize the effect of differences in morphology due to intraspecific variation, as non-classic Neandertals, while missing some of the traditionally key diagnostic features, are still overall Neandertal-like in their morphology.

Considering the evidence examined above, climatic variation seems an unlikely explanation for Neandertal cranial morphology. The evidence regarding anterior dental loading is sufficiently contradictory that I believe we must default to genetic drift as the null hypothesis, until such time as alternative explanations can be more conclusively proved or disproved. Shortening of the sphenoid may have brought about the modern human face, but the reason for the ontogenetic shift remains unknown.

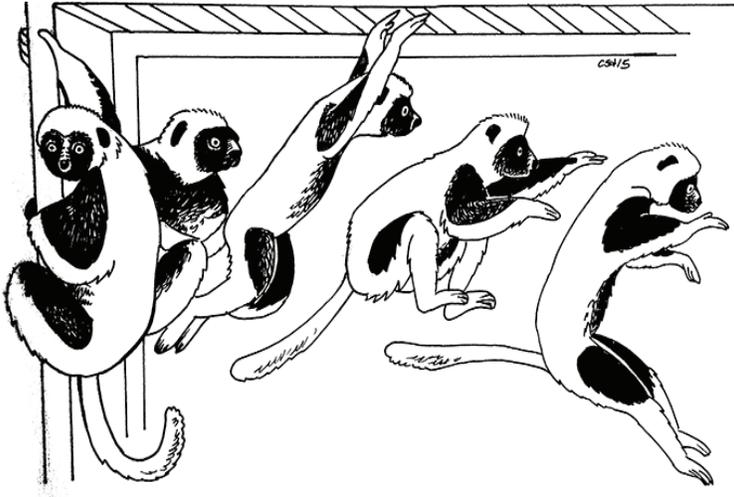
In sum, we can only hope—unlikely as it may be—that as more fossils are discovered, and new evidence emerges from sources other than skeletal remains, relationships between hominins become clearer rather than more complex.

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Caging Effects on Locomotion and Posture: Are Captive *Propithecus coquereli* (Coquerel's Sifaka) Well-Served by Current Cage Structure?

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Abstract

When *Propithecus coquereli* are in captivity, they live in an environment that is not an accurate representation of their natural habitat. The goal of this study was to determine whether or not the captive *P. coquereli* participate in locomotor and postural states on structures that reflect their natural habitat. These results will allow zoos and research institutions to design appropriate enclosures in the future. To determine if the structures were sufficient, we used scan sampling to record what locomotor and postural states four *P. coquereli* participated in, and we noted what structures they were on during the scans. We found that the subjects used horizontal structures during 65 +/- 23% of the scans and used vertical structures during 35 +/- 25% of the scans. Their main forms of locomotion and posture were crouching, sit-cling, and vertical clinging (19 +/- 2%, 46 +/- 4%, and 17 +/- 3%). It was determined that these *P. coquereli* subjects do not have the appropriate structure to reflect their natural environment, and that their cages should be redesigned to include appropriate structures.

Introduction

Appropriate caging for captive species is essential for their wellbeing (Chang, 1999). When animals have very specialized morphology, managers of captive facilities need to be careful to include structures in their cages that allow them to act naturally (Chang, 1999). Here we look at how a species with a specialized morphology for vertical clinging and leaping, *Propithecus coquereli*, changes its locomotion, posture, and structure choices in a captive setting. By observing the behavior of the subjects in captivity, the information collected will help inform zookeepers how to redesign captivity cages.

When discussing caging, morphology should be taken into

consideration. The Intermembral Index (IMI) is a numerical value that is used to represent the proportion of limbs in primates and is an indicator of their primary form of locomotion (Ankel-Simons, 2007). An IMI value is calculated by summing the length of the humerus and radius, dividing that by the length of the femur and tibia, and multiplying the ratio by 100 (Crompton, 2003). If a primate has an IMI value less than 75 this means that they have longer legs than arms, which can sometimes suggest adaptations for vertical clinging and leaping (Defler, 1999). If the primate is a vertical climber and leaper, their enclosure should contain a variety of structures for them to leap onto to encourage natural locomotion. If a primate has an IMI value between 75 and 100, their arms and legs are about the same length, so they are likely quadrupedal (Defler, 1999). If a primate is quadrupedal, its enclosure should be large with enough horizontal space for the primate to move around. An IMI value greater than 100 means a primate has longer arms than it does legs, which may suggest adaptations for brachiating (Defler, 1999). Brachiators should have many horizontal poles in their enclosures so they can use their arms to move freely within it. *P. coquereli* has an IMI value of 62, which indicates along with other morphological traits that the species uses vertical clinging and leaping (Glander, 1993).

Vertical clingers and leapers are primates who rest on and move between vertical structures (Warshaw, 2007). Before conducting the study, I predicted that the *P. coquereli* will spend the majority of scans in a vertical posture or locomotive state. It was also predicted that they will spend the majority of scans on vertical structures. In the wild, vertical clingers and leapers spend the majority of their time in vertical postures while on vertical structures (Garber, 1992). *Saguinus fuscicollis*, also vertical clingers and leapers, are in vertical clinging postures on vertical tree trunks during 79% of scans in the wild (Garber, 1992). *S. fuscicollis* have the same primary locomotor type as *P. coquereli*; thus they should have similar locomotor and postural use. *Callimico goeldii* are not vertical clingers and leapers, but leaping accounts for 23% of their total travel (Garber, 2009). When leaping, *C. goeldii* leaps from vertical tree structure to vertical structure 55% of the time. Although they are not vertical clingers and leapers, leaping does constitute nearly a quarter of their locomotion, which is significant.

P. coquereli need cages that have a variety of vertical structures that are similar to what the subjects would face in the wild. These primates usually rest and sit-cling while holding onto to a vertical structure (Garber, 1992). Cages would need a variety of vertical structures for the subjects to leap onto and off of, and on which to rest and sit-cling. Based on this information, it is predicted that the *P. coquereli* will spend the majority of the

scans on vertical structures, and the majority of their time in a vertical locomotor or postural state. To test this hypothesis, we will observe semi-free ranging *P. coquereli* subjects at the Duke Lemur Center.

Methods

Study Site and Subjects

The study was conducted over two days at the Duke Lemur Center in Durham, North Carolina. Subjects included four *P. coquereli* ranging in age from juvenile to adult. The individuals were identified using collars, tail shaves, and natural markings such as fur color.

The lemurs were housed in 1-5 cages: the number of cages available varied from day to day depending on husbandry needs. The indoor cages contained at least one chainlink fence, one vertical pole that was made of smooth hardwood, a plastic bucket, one horizontal structure made of plywood shelves, and three horizontal structures made of cinderblock wall space. The vertical pole was in the center of the cage and the bucket was in the upper right hand corner of each cage. The plywood horizontal structure as attached to the chainlink wall, and there was one cinderblock horizontal structure per cinderblock wall. The vinyl floor was also considered a structure in this study. Animals were provisioned with chow and browse on the floor that was placed in their cage daily by Lemur Center employees. The outdoor cages contained three chainlink walls, one cement wall, and one cement floor per cage. Those cages also had ropes hanging from the ceiling and branches attached to the chainlink walls.

Protocol

Scan sampling was conducted for a total of 130 minutes with samples occurring at two minute intervals between 9:02 am and 9:34 am on February 20, 2014 and 8:43 am and 10:21 am on February 25, 2014. The locomotion and structure use for each subject were recorded. Two researchers scanned for locomotion, posture, and structure usage and reported that data to the third researcher who recorded the information using a Psion Workabout event recorder loaded with The Observer software (Noldus, 2002). Two major categories of locomotion and posture were used in this study: vertical locomotion/posture and horizontal locomotion/posture. Vertical locomotion/posture specifically includes scaling, leaping, vertical clinging, and hanging. Horizontal locomotion/posture specifically includes hopping, crouching, running, and sit clinging. Within these enclosures three separate structure categories were defined: vertical structures, horizontal structures, and angled structures. Vertical structures included the chain-link wall, the wooden pole located in the middle of each cage, and the ropes hanging from the chain-link ceilings. Horizontal structures included the plywood shelf taking up ½ of the width of the chain-link wall, the single cinderblock shelf cut into each of the cinderblock walls, the floor which makes up the entire bottom of the cage, either made of vinyl (indoor enclosures) or cement (outdoor enclosures), and the hard plastic buckets with perforated holes on all sides.

Data Analysis

The data, consisting of 67 scans, were downloaded from the Psion Workabout onto a computer. To test the prediction that the subjects would be seen on vertical structures more than horizontal structures, I first sorted the data across all four subjects by structure. I calculated the average amount of scans in which each structure was used, and created a bar graph to plot this information. I then found the standard deviation for each structure and included that on the bar graph, using error bars. A black line separates the vertical and horizontal structures within the bar graph.

This process was repeated to test my prediction that the subjects will spend the most amount of scans in vertical postures and locomotive states, so the data were sorted by postures and locomotion. Again, the bar graph represented the average amount of scans across all individuals in which each posture and locomotive state was seen, and the standard deviations were illustrated by error bars. The bar graph was divided by black lines that separate the locomotor and postures by whether they were vertical or horizontal.

Results

Structures

Contrary to what was expected, the subjects spent the most amount of scans on horizontal structures rather than vertical structures (65 +/- 23% vs 35 +/- 25%; Fig. 1). Due to the IMI value of *P. coquereli*, I predicted that the subjects would spend the greatest amount of time on vertical structures, but they did the opposite. The bucket, horizontal pole, and horizontal shelves were the most used structures (15 +/- 3%, 23 +/- 10%, 27 +/- 6%). The ground and ceiling were the least used structures (.5 +/- 1% and 5.5 +/- 4% respectively). Figure 1 summarizes these observations.

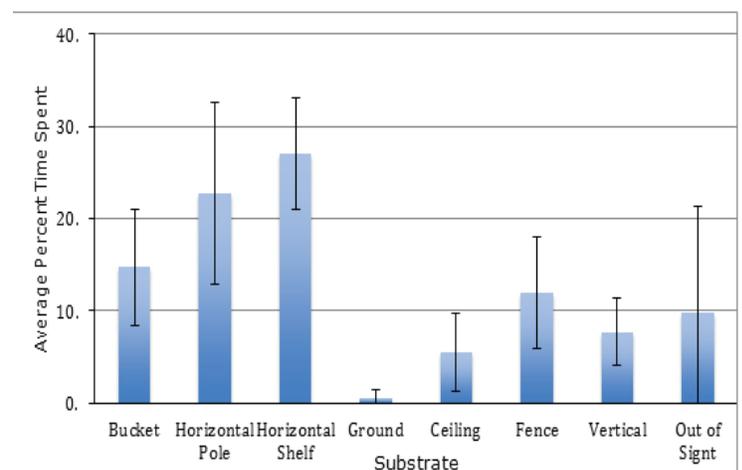


Figure 1: The average time spent on different structures during the scans. N=4 individuals over 130 minutes at the Duke Lemur Center. Error bars = Standard Deviation.

Locomotion and Postures

Contrary to our predictions, the *P. coquereli* subjects spent the most time in crouching, sit clinging, and vertical clinging postures (19 +/- 2%, 46 +/- 4%, and 17 +/- 3% respectively; Fig.

2). During the scans, hopping, leaping, hanging, and scaling combined for a total of 11 +/- 1.6% of recorded locomotive states. These distributions indicate that during the scans, the subjects spent a greater percent of their time at rest in a posture state than they spent being active (82 +/- 9% vs 11 +/- 1.6%). The subjects were seen leaping 4 +/- 0.6% of the time. They spent the most amount of scans sit clinging and the least amount of time scaling (46 +/- 0.4% vs .3 +/- 0%). Figure 2 clearly highlights these results.

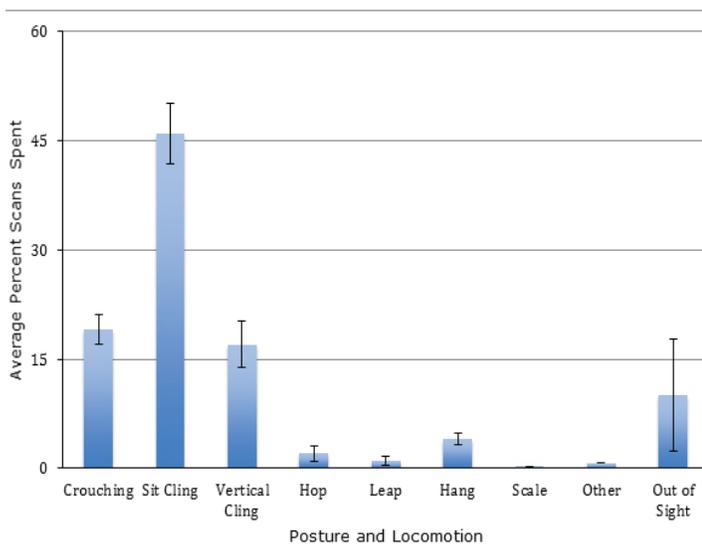


Figure 2: The time spent in different postures and locomotive categories during the scans. N=4 individuals over 130 minutes at the Duke Lemur Center. Error bars = Standard Deviation.

Locomotion and Posture on Structures Not Seen In The Wild

Buckets are not found in the wild, but the subjects used them during 15 +/- 3% of the scans. While in the bucket, the subjects rested, interacted with the other subjects, and sat (15 +/- 0%, 22 +/- 1%, and 63 +/- 2%). There are few, if any, completely horizontal structures in the wild other than the ground, and the subjects were on horizontal poles and shelves during 50 +/- 16% of the scans that included horizontal structures. While on the horizontal structures, the subjects sat, groomed one another, played, and ate during 87 +/- 5%, 5 +/- 0%, 5 +/- 0%, and 3 +/- 0% of the scans, respectively.

Discussion

The data from the scans suggest that *P. coquereli* in captivity spend the majority of their time on horizontal structures rather than vertical structures (65 +/- 23% vs 35 +/- 25%). They also spent the majority of the scans in horizontal locomotors and postures rather than vertical ones (82 +/- 3% vs 7.3 +/- 7%). The data does not support my predictions, though it is important to note that the data was collected using scan sampling, so other structures and postures/locomotors occurred but were not recorded because they did not happen on the scan.

Cages are designed to benefit both people and the captive animals (Hosey, 2013) Enclosures may include structures that are not necessarily beneficial to the subject but they are

easier for the zookeeper to clean (Hosey, 2013). People are often considered over the captive animals when zoo visitors are taken into consideration (Hosey, 2013). People visit zoos with the hopes of seeing as much interaction between species as possible, and some captivity centers design enclosures with that in mind (Cole, 1985). Zookeepers can therefore manipulate structures to allow visitors to see as many subjects as possible (Cole, 1985). Although a larger cage may be beneficial to certain species, zookeepers may keep them in a smaller one so the visitors feel that they have optimized their experience and seen a variety of animals. Rather than designing enclosures for the benefit of zookeepers and visitors, enclosures should be designed solely for the benefit of the animals inside them.

When cages are designed for the subjects rather than the observers the behavior of the subjects change, which can be seen in *Mandrillus sphinx* (Chang, 1999). In this study subjects became more active and their behavior reflected that of their species in the wild (Chang, 1999). A similar study found that "77.8% of naturalistic enclosures provided a suitable environment for the resident animals versus 39.7% of non-naturalistic enclosures" (Hosey, 2013). If captive animals have enclosures that accurately represent their natural habitats, their behavior and substrate use will likely be similar to how they naturally behave in the wild.

In order to ensure that captive animals have enclosures that are an accurate copy of their natural habitat, enclosures should be redesigned. For *P. coquereli*, cages should be large enough that the subjects have an abundance of room to hop on the floor of the enclosure. The cages also require more vertical substrates since in the wild, *P. coquereli* rests and sit-clings on trees. There should be some representation of that in their enclosures. Some of the vertical substrates should have angled substrates attached to them to reflect branches coming off trees. Fewer horizontal substrates could be included in enclosures because in the wild, there are few, if any, completely horizontal substrates other than the ground. Substrates that are not found naturally in the wild, such as buckets, should be removed so *P. coquereli* can live in an enclosure that reflects their natural habitat.

This study should be repeated in the future, but should use focal sampling rather than scan sampling. Scan sampling allows for some behaviors and substrates to not be recorded because they were not performed or used on the scan. If a focal sample is used, all behaviors and substrates can be recorded and provide a more accurate depiction of the subject's actions.

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