

Research Article

A 150- Year Conundrum: Cranial Robusticity and Its Bearing on the Origin of Aboriginal Australians

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The origin of Aboriginal Australians has been a central question of palaeoanthropology since its inception during the 19th Century. Moreover, the idea that Australians could trace their ancestry to a non-modern Pleistocene population such as *Homo erectus* in Southeast Asia have existed for more than 100 years, being explicitly linked to cranial robusticity. It is argued here that in order to resolve this issue a new program of research should be embraced, one aiming to test the full range of alternative explanations for robust morphology. Recent developments in the morphological sciences, especially relating to the ontogeny of the cranium indicate that character atomisation, an approach underpinning phylogenetic reconstruction, is fraught with difficulties. This leads to the conclusion that phylogenetic-based explanations for robusticity should be reconsidered and a more parsimonious approach to explaining Aboriginal Australian origins taken. One that takes proper account of the complex processes involved in the growth of the human cranium rather than just assuming natural selection to explain every subtle variation seen in past populations. In doing so, the null hypothesis that robusticity might result from phenotypic plasticity alone cannot be rejected, a position at odds with both reticulate and deep-time continuity models of Australian origins.

1. Introduction

The origin of modern humans remains a core topic of palaeoanthropology. Although four major models are presently being debated, only the out-of-Africa suite has received strong support from interpretations of both the fossil record and DNA [1–6]. Yet, the evolutionary origin of Aboriginal Australians remains controversial owing to the presence of considerable variability in cranial morphology during the Pleistocene and interpretations of its possible phylogenetic importance [1, 2, 7–18]. Moreover, there is sharp disagreement about the possible alternative causes of this variation and its significance to a global understanding of the evolutionary history of modern *Homo sapiens* [1, 2, 11, 12, 17, 18].

Long before a human fossil record was known for Australia, various speculative evolutionary sequences were devised linking nonmodern hominins to Aboriginal Australians. In particular, it was proposed that *Pithecanthropus* (*Homo erectus*) or the late-surviving Ngandong population of this species (sometimes referred to *H. soloensis* [14]) played a role in their origins. This idea has been

an enduring theme of palaeoanthropology for more than 100 years: from Klaatsch [19] through to Westaway and Groves [18]. A recent major review of the question of modern human origins [1] identified three major issues for Australian palaeoanthropology to be resolved: (1) the relationship of the first Australians to later inhabitants of the continent, (2) whether late Pleistocene morphological diversity may have been accentuated by the severity of the last glacial maximum, leading to isolation and the forcing of morphological change in some Australian populations, and (3) if archaic populations such as those known from Ngandong did survive into the late Pleistocene, an analogous situation to that in Europe might have existed, raising the possibility of gene flow with dispersing *H. sapiens*. All three points are clearly interrelated. Regarding the first, the very earliest fossil remains from Australia (e.g., Willandra Lakes Human 3) do seem to fit metrically and morphologically within the range of living Aborigines [8]. Stringer's [1] points 2 and 3 relate to the possible cause(s) of cranial robusticity in some Pleistocene/early Holocene Australians. That is, whether such features arose as a result of natural selection

acting on populations within Australia or were brought here by people who evolved from, or hybridised/admixed with, a nonmodern population in Southeast Asia (i.e., the Solo/Ngandong hominins).

Australian palaeoanthropological theory and method continues to be dominated by adaptationist accounts [20] of robusticity and population history. The assumption that the cranium is optimised part by part and that atomising its form into traits assumed to be heritable units, functionally discrete, to have been shaped by natural selection and, therefore, positively associated with reproductive success, remains the core proposition of the field. In the present contribution, it is argued that the failure to fully consider alternative (nonadaptationist) approaches is a major reason why the interrelated issues of firstly, the cause(s) of cranial robusticity and, secondly, its relevance to reconstructing the origins of Aboriginal Australians remain unresolved. This paper commences with a review of the history of ideas regarding cranial robusticity and the origins of Aboriginal Australians. Then, an alternative to atomisation, herein called the ontogenetic approach, is described and some key concepts underpinning it are introduced. Finally, this approach is applied to some characters used to support the Ngandong ancestry model for Aboriginal Australians.

2. History of an Idea

Ever since Blumenbach's *De Generis Humani Varietate Nativa* of 1795, European scientists have been attempting to understand the affinities and hence origins of Aboriginal Australians. Blumenbach had at hand the skulls of several Australians provided to him by Joseph Banks [21]. However, only with the wider exploration of the continent by Europeans and the beginnings of a global trade in human cranial remains during the 19th Century was a systematic effort made to understand their skeletal morphology [22]. During this period, the deep antiquity of the earth was beginning to be established, including an ancient origin for humankind as presented in Lyell's *Antiquity of Man* [23]. In Lyell's volume, Huxley's (1863) first comparisons of Aboriginal skulls to Neanderthal remains were noted, indicating various morphological resemblances (not exclusive though, or implying ancestry). As the first anthropologist to study human origins from comparative anatomical and fossil sources, and placing his ideas within the Darwinian evolutionary framework, Huxley can reasonably be considered the founder of the discipline of palaeoanthropology. Moreover, as Aboriginal Australians were central to his ideas, as well as to the early development of this scientific field, Huxley ensured their place at the centre of debate surrounding human origins, a position they have held for close to 150 years.

During the early 20th century, many researchers continued to focus on documenting similarities in cranial form between Australians and the Neanderthals [24–26], inspired by Huxley's earlier and highly influential work (see Figure 1). However, following the discovery of fossil human-like remains in Indonesia by Dubois [27], the view eventually emerged that Australians may actually have descended from a local population within Southeast Asia,

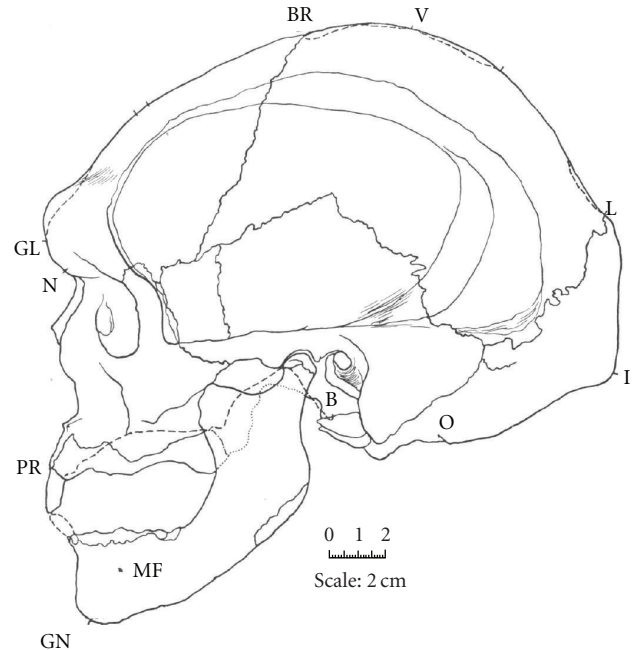


FIGURE 1: Lateral line drawing of an Aboriginal skull described in the early 20th century as “Neanderthaloid” [24].

either *Pithecanthropus* [19] or *Homo soloensis* [28, 29]. Klaatsch [19] found it “impossible to believe that the Australian natives are descended from European palaeolithic man” (page 162) as proposed by Huxley (see other criticisms in [30, 31]). However, the idea of a regional evolutionary sequence between Aboriginal Australians and *Pithecanthropus* in Southeast Asia seems not to have been in the minds of these workers. Instead, they saw Aboriginal Australians as representatives of the most “primitive type” of living *H. sapiens* and had in mind a global evolutionary sequence in which “Solo Man” (Ngandong) and “Rhodesian Man” (Kabwe) were examples of “proto-Australians,” belonging together to living humans in *H. sapiens* [29]. Also, Dubois [28, 29] thought that the Wadjak remains he recovered from Indonesia were “Australoid” although they now seem to be terminal Pleistocene in age and are probably not related to Aboriginal Australians [32].

With the ideas of Weidenreich [33, 34] and Coon [35], the “Pithecanthropoid-Australoid” lineage hypothesis became a major feature of palaeoanthropological theorising. Both these workers believed that modern humans around the world had evolved from regional populations of *Pithecanthropus* (today *H. erectus*). Thus, the regional lineage from this taxon through to Aboriginal Australians was part of a global process, which Howells [36] dubbed the “Candelabra” hypothesis. Parenthetically, it should be noted that this idea was not universally supported; for example, Hrdlička [37] preferred a Neanderthal stage in human evolution and considered Aborigines to belong to an “old race” of “whites,” borrowing heavily from Huxley, while Birdsell's [38] views are strikingly similar to the contemporary out-of-Africa theory.

The increase in the number of fossilised human remains recovered during controlled excavations from the 1960s onwards [39–43], and demonstration of a Pleistocene occupation of the Australian continent [44, 45] encouraged renewed interest in the Pithecanthropoid-Australoid lineage hypothesis [39–43]. Again, it must be stressed that not all researchers accepted this hypothesis, Macintosh in particular reversing his earlier endorsement [46].

During the 1980s and 1990s, this idea was reformulated, initially as the “Regional Continuity” hypothesis [47] and later as the global “Multiregional” model of modern human origins [48, 49]. At its core was the notion of a deep-time Southeast Asian-Australian clade supported by evidence of morphological continuity in the skull and dentition between lower and upper Pleistocene nonmodern hominins in Indonesia through to recent Aboriginal Australians. As Thorne and Wolpoff [47] stated, “in no other region can a specimen (i.e., Sangiran 17) be found that combines so many features that seem unique or at least of high frequency in Pleistocene Australians” (page 345; words in parenthesis added). It is important to note that many proponents of the multiregional model have since the early 1990s regarded *H. erectus* to be a junior synonym of *H. sapiens* [50]; thus, the emergence of modern humans is seen by them as a process occurring within a single, long lasting, and widely distributed evolutionary lineage, or species.

Moreover, Thorne [51–53] proposed that two populations had colonised Australia at different times during the Pleistocene in his “dihybrid” model, the merging of the two giving rise to modern Aborigines. The first population was the “robust” group descended from *H. erectus* and the second a later arriving “gracile” population originating in Pleistocene China and, like modern East Asians, evolving from East Asian *H. erectus*. Although the order of arrivals had to be revised (reversed) once it was established that gracile crania like WLH3 were actually geologically much older than any robust remains recovered from various localities [15, 53].

Three recent variants of the regional continuity model have been published. The first emerged from a test of multiregionalism in Southeast Asia-Australia using the WLH50 calvaria (see Figure 2) [54, 55]. It was found that six of the seven Ngandong calvaria examined were phenetically closer to WLH50 than to any other specimens considered, including early modern humans from Skhul and Qafzeh. In this work, it was concluded that the results implied a “dual ancestry” for Aboriginal Australians because “there is no evidence suggesting WLH-50 can be grouped with either Late Pleistocene Africans or Levantines to the exclusion of the Ngandong sample” [55, page 296]. That is, it was argued that Australians are descended from both an ancient regional population (e.g., Solo/Ngandong) and recent modern humans from Africa through a process of reticulation (admixture/hybridisation). The present author has made similar conclusions employing different fossils and an alternative, multivariate, methodology [2]. However, his findings were argued to be consistent with the “assimilation” model of modern human origins [56, 57], a hypothesis receiving stronger support from genetic studies [2]. Weidenreich in a personal communication to Birdsell [58] changed his mind



FIGURE 2: Willandra Lakes Human 50 calvaria.

late in life and also thought Australians had a dual ancestry. Oppenheimer [59] has also suggested that interbreeding might account for Australian robusticity. The present author has, however, changed his views and no longer considers interbreeding to provide a parsimonious explanation for Aboriginal Australian morphology or the origins of these people [17].

The final recent variant was proposed by Webb [14] and borrows heavily from Birdsell’s “trihybrid” hypothesis [60, 61], as have Thorne’s later ideas [62]. Webb [14] speculated that the first population to colonise Australia was the species *H. soloensis*, an upper Pleistocene descendent of Javan *H. erectus*. He argued that it migrated to the continent as early as 130–150 ka and ultimately adapted to local conditions, founding the robust Australian Pleistocene/early Holocene population. Further, he contended that modern humans entered Australia sometime between 50 ka and 75 ka, tracing their origins back to Africa. These people are argued to have been “Negrito or Negrito-like,” being of small stature, a feature developed “external to Australia” [14, page 239]. The two species (*H. soloensis* and *H. sapiens*) are argued to have gradually formed a single population through “genetic mixing,” but the process was dominated by the modern group, “which had the larger population and constantly, albeit slowly, receives fresh genes through a series of migrations arriving throughout the glacial maximum and after, into the early Holocene” [14, page 269].

3. Some Objections to Continuity

Many objections to Southeast Asian-Australian regional continuity and the related dihybrid origins model have been offered over the last 30 years or so. Some opponents have argued that perceived similarities between robust individuals and *H. erectus* may simply represent the retention of plesiomorphies of later *Homo* by Aboriginal Australians

[11, 63]. Indeed, Larnach [64] found that Aborigines are closest in cranial morphology among living people to *H. erectus* but stressed “their resemblance is never close” (page 159). He also noted that the Solo/Ngandong population exhibits a number of autapomorphies not found among Aboriginal Australians (see also [65, 66]), and “if Australians are descended from Solo Man, then sometime during that descent these unique traits were lost and their sites reverted to a similar state to that obtaining in *Homo erectus*” [64, page 170]. Thus, if regional continuity is correct, *Pithecanthropus* (*H. erectus*) must have given rise to the robust Pleistocene Australian group in a separate event, the Ngandong population (*H. soloensis*) being a late surviving and autapomorphic descendent, and unrelated to Australians. Durband [67] has pointed out that the available data for Javan *H. erectus* especially from the facial skeleton (i.e., $n = 1$ or Sangiran 17) is too inadequate to make reliable phylogenetic inferences.

Moreover, the dihybrid model and by implication regional continuity has been rejected by most Australian workers on the basis of its failure to take adequate account of spatiotemporal variability in cranial and dental morphology, including size, within a single continental population [8–10, 12, 18, 68–75], or at the least its failure to reject this as a null hypothesis. Moreover, some individual features underpinning regional continuity such as vault thickness have been proposed as selected for in response to violence and cranial trauma [8] (see below for a discussion of epigenetic explanations for some robust traits). Finally, the conceptual underpinnings of the dihybrid/migrationist model have been deemed to be founded in a “palaeontological” (i.e., typological) rather than population-based approach [10], as would be demanded by the synthetic evolutionary paradigm.

4. An Alternative Program

As noted above, most studies of Australian robusticity have assumed that the morphological characters under investigation are genetic (or heritable). This concept is used in its broader sense to mean that the phenotype of an individual is a good predictor of the genotype [76]. However, it has become a truism of developmental biology that “the old and compelling idea that there exist specific genes for virtually every structural detail throughout the craniofacial complex is simply not true” [77, page 230]. The more that is learned about the genes and developmental processes forming the cranium, the less tenable the atomisation of complex organs like the cranium has become [78]. Some concepts described in this section indicate powerfully why this is the case and underpin the need for an alternative paradigm in Australian palaeoanthropology.

Estimates of the heritability for many commonly employed cranial measurements and traits are available (e.g., [79–82]). Although there are some uncertainties surrounding the application of sample-specific heritability estimates to other populations, they nonetheless provide insight into the potential reliability of particular traits/variables as well as a broader understanding of the heritability and integrated nature of cranial ontogeny. Heritabilities vary widely for standard craniometric variables: $h^2 = 0.000 \pm 0.000$ to

0.867 ± 0.156 [81]. Moreover, many variables have been found to exhibit heritability estimates that do not differ from zero (i.e., $h^2 = 0$) [79, 81]. In a recent investigation, only two commonly employed measurements have been found to exhibit high heritability values: palate breadth (MAB) and nasal height (NLH) [81]. Moreover, major length (GOL), breadth (XCB), and height (BBH) dimensions exhibited low to moderate, but statistically significant heritability estimates [81]. However, many important regional measurements such as frontal chord (FRC), bifrontal breadth (FMB), biasterronic breadth (ASB), bizygomatic breadth (ZYB), and nasal breadth (NLB) are characterised by low and nonsignificant heritability estimates [81]. Additionally, these estimates show a spatial pattern whereby lower estimates tend to be associated with the face. In many cases, they are associated with measurements for areas involving attachment sites for the muscles of mastication [81] suggesting an important role for epigenesis in their ontogeny.

Endocranial dimensions show moderate to high heritability estimates including important measures of human basicranial size and angulation [80]. These results highlight the reasonably high heritability and considerable ontogenetic integration (correlation among dimensions) of human endocranial form, but contrast with low-moderate heritability for measurements on the ectocranial surface [81].

In a recent study of the heritability of cranial dimensions employing a 3D approach, Martínez-Abadías et al. [82] found a broadly similar pattern to previous (2D) studies [79–81]. Overall, dimensions showed low-moderate heritability with about 72% being significant (i.e., $h^2 > 0$). Interestingly, they found the face to be the region with the highest number of significantly heritable traits and highest mean heritability, followed by the cranial base and the neurocranium [82]. Within regions they found the orbit, nasal part, neurocranial vault, and basicranium to be characterised by low to moderate heritability, while the masticatory apparatus exhibited low heritability [82], a finding consistent with Carson’s [81] results. Between cranial regions, they also found low-moderate heritability confirming the concept of ontogenetic integration of the cranium. The findings of Martínez-Abadías et al. [82] show that the cranial base, neurocranium, and face are characterised by similar levels of heritability and also strongly point to an important role for epigenesis in ontogeny (see also [80, 81, 83–86]).

Epigenesis is defined as the developmental interactions among cells, tissues, and their environments [84]. It can translate localised developmental alterations into integrated and widespread morphological changes and provide a fundamental mechanism for introducing flexibility into developmental programs including phenotypic plasticity [83–86]. Lieberman et al. [87] have discussed three types of epigenetic interactions during ontogeny: (1) *primary interactions*, occurring at the cellular level, (2) *secondary interactions*, involving those between adjacent tissues during growth, and (3) *tertiary interactions*, in which interactions occur throughout ontogeny between cells within a unit (e.g., via hormones) and the rest of the organism as well as the environment.

One important and widely discussed concept underpinning epigenesis in the ontogeny of the cranium is the

functional matrix hypothesis (FMH) of Moss [88]. He described the FMH in the following way: “The developmental origin of all cranial skeletal elements (e.g., skeletal units) and all their subsequent changes in size and shape (e.g., form) and location, as well as their maintenance in being, are always, without exception, secondary, compensatory, and mechanically obligatory responses to the temporally and operationally prior demands of their related cephalic nonskeletal cells, tissues, organs, and operational volumes (e.g., the functional matrices)” [88, page 9]. The FMH explains many aspects of cranial development and is widely regarded to be an important concept surrounding secondary epigenetic interactions during cranial ontogeny (e.g., [77, 89]).

An important example of tertiary epigenetic interactions is the widely discussed “Wolff’s” law of bone transformation [90]. This “law” is actually a poorly defined and frequently criticised term usually applied as a “catch-all” concept to refer to the adaptation of bone to mechanical stimuli [77, 78, 91, 92]. Put simply, Wolff’s law is, “an extension of the old and trusted idea that form is interrelated with and inseparable from function... that bone grows and develops in such a manner that the composite of physiologic forces exerted on it are accommodated by the bone’s developmental processes” [77, page 233]. Historically, one problem with this concept’s use has been that it was frequently invoked to argue for uniform responses such as bone deposition in the face of biomechanical stress particular from muscle, when very often the opposite response, resorption, had occurred [77, 91]. Thus, while in its general form this law remains valid and useful, it is now widely acknowledged that just how bone responds to mechanical stress is complex and varies according to its location and whether stress is direct or is mediated by other tissue. The reader is referred to some recent and more detailed reviews of this concept [77, 78, 92].

The external environment through tertiary epigenetic interactions has long been argued to be an important determinant of cranial form. For example, the shapes of the neurocranium and nose have long been linked to climatic adaptation [93–100] and facial form to diet or masticatory practices (see [101–104]: see below for a more detailed discussion of this idea). A 3D study of cranial morphology compared to neutral genetic population distances [105] found that the human cranium does preserve a “signal” of population history. However, historical signatures are not equal across cranial regions and seem to be largely concentrated in the temporal bone and neurocranium [105].

The final concepts to be briefly considered here are those of modularity and integration. Modularity is a general property of biological systems, from molecular to ecosystemic levels of interaction [86]. In ontogeny, it represents the observation that morphological features do not vary independently but are integrated with each other, reflecting coordination in development, function, and evolution. They might be thought of as forming modules or “complexes that are highly integrated internally but are relatively independent of each other” [86, page 628]. The morphological characters within modules are characterised by three major properties

[106]: (1) they collectively serve a common functional role, (2) they are tightly integrated by pleiotropic effects of genetic variation, and (3) they are relatively independent of other modules. This independence among structures (modules) allows unrelated components to vary and evolve separately, but the integration within the units maintains functionally necessary relationships among traits [85–87, 106–113]. Morphological integration assumes that developmentally/functionally related traits are coinherited and will produce coordinated responses in evolution [85–87, 106–113].

The cranium is divided along ontogenetic lines into three regions: the cranial base, neurocranium, and face. As the cranial base is in an evolutionary sense the oldest structure, it is phylogenetically highly conserved [112] and believed to be subject to stronger genetic influence in ontogeny than the neurocranium and face [77, 113–116]. Moreover, it widely is assumed that the face is the most sensitive region to epigenetic factors as it stops growing later in ontogeny than either the cranial base or neurocranium [77, 114, 115]. Thus, it is subject to greater influence from mechanical loading during mastication and from various environmental factors during ontogeny [116–119]. There is, however, considerable evidence that the face and neurocranium are characterised by both integration between regions and considerable modularity, or region-specific integration [77, 80–83, 85, 87, 115, 120–123]. Moreover, this pattern seems to characterise humans, chimpanzees, and gorillas [106, 120, 124, 125] and is known to be phylogenetically conserved in mammals [107, 126]. Cranial shape patterns appear early in ontogeny and remain from early childhood until adulthood [127], including in depository and resorptive cranial growth fields [115, 128]. Although this is somewhat simplistic as endocranial shape continues to change in humans through adolescence, well after brain growth it has ceased [129].

A range of studies aiming to test and develop Enlow’s ideas about facial and cranial growth [77, 115, 130] have been published over the past two decades and employed a range of techniques including 3D morphometrics [119, 122, 123, 130–144]. Many studies have focussed on interactions between the cranial base, neurocranium, and facial form, and some major findings include that larger relative brain size is associated with a larger basicranial angle, while large faces may produce the opposite situation, although the influence of facial size seems to be weaker than for brain size [140]. Lieberman et al. [122, 123] also found that cranial proportions (neurocranial shape, or degree of brachycephaly versus dolichocephaly) depend on interactions between cranial base width and brain volume. This has been confirmed by 3D studies showing that changes in cranial base width play an important role in cranial shape variation, including facial width [127]. Moreover, studies of the heritability of cranial regions confirm strong covariation between the breadth measures of major developmental regions of the skull [82]. Additionally, independent of age and size, an important proportion of cranial shape variability seems to be traceable to differences in the position and orientation of the face and masticatory system relative to the braincase [127].

Experimental research using mice suggests that integration in the mammalian skull is highly structured following a hierarchical scheme dominated by covariation between the widths of the neurocranium and the basicranium and, to a lesser extent, also the face [85]. Thus, the cranial base can be thought of as the “skull’s central integrator” [122, 123]. It strongly influences overall cranial shape, constraining facial breadth, height, and length, and neurocranial breadth and length, helping prevent the “different regions from evolving independently and would preserve the functional and architectural requirements of the skull” [82, page 29].

5. Nonadaptationist Explanations and Australian Robusticity

The above review of some ontogenetic concepts and recent research findings provide the context for a reconsideration of the possible causes of cranial robusticity among Australians. There have been very few synthetic attempts to explain it using nonphylogenetic or nonadaptationist approaches. One important, but overlooked, example is that of Howells [145] who proposed that robusticity may have been “a phenotypic plastic response to some regional and transient environmental stimulus. That is, the phenomenon would be, not adaptation and selection, resulting in genetic change in the post-Mungo population, but a reversible phenotypic shift, on an unchanged genetic basis, toward larger size and related allometric effects on the face and mandible particularly, producing in some relatively smaller-brained individuals the special flattened and narrow frontal which is so striking in Cohuna and some of the Kow Swamp skulls” (pages 646-647). This explanation is broadly consistent with the ontogenetic approach outlined above, being in large part a putative example of tertiary epigenetic interactions.

The cultural practice of artificial deformation, another example of tertiary interactions, has been argued to have produced or exaggerated the acute angle of the frontal squama, angulation of the parietals, and aspects of occipital squama morphology in a small number of robust Australian crania such as Kow Swamp 5, Cohuna, some Coobool Creek crania and Nacurrie 1 [9, 146–151]. Other epigenetic factors have been proposed to explain vault thickness, including, increased levels of growth hormone [8], nutritional phosphorous deficiency [8], and inherited anaemia [13, 14, 152, 153]. The latter (pathology) hypothesis has been examined to some extent by Stuart-Macadam [154], Curnoe and Thorne [16], Westaway [155], and Curnoe [16] but requires further scrutiny (see below).

Lahr and Wright [156] using multivariate statistics considered spatial (or architectural) aspects of cranial form and proposed that the “superstructures” (see below) characteristic of cranial robusticity may be integrated and covary allometrically. For Australian Aborigines, they concluded that like other human populations the expression of robust characters was likely a response to some functional complex, possibly mastication. They also suggested that the “distinctive anatomical combination present in Australian crania of a very narrow vault and pronounced robusticity, does not represent a plesiomorphic state” inherited from either

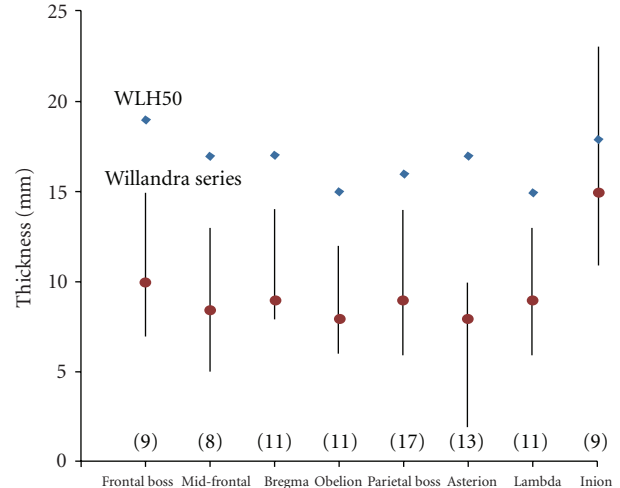


FIGURE 3: Thickness in Willandra Lakes Human (WLH) 50 compared with the sample median and range for the remaining Willandra Lakes series (NB: numbers in parenthesis are sample size).

early modern humans or the Solo/Ngandong population [156, page 184]. Moreover, they proposed that allometry in combination with this regional morphology might explain extreme robusticity seen in the Pleistocene of Australia. However, in attempting to explain the origins of this cranial morphology, they turned again to an explanation involving natural selection during the settlement of Australia.

In recent research by the present author [17], the ontogenetic framework was adopted in an attempt to explore nonphylogenetic explanations for cranial robusticity among Pleistocene/early Holocene Australians. It was concluded that robusticity among these individuals may have been the result of the complex developmental and functional interplay between (1) a large neurocranium, (2) narrow cranial base, (3) large viscerocranium with considerable high midfacial projection, and (4) large dentition, especially the posterior teeth, with their resultant large jaws (mandible and maxilla) and high volume of masticatory muscles. While it was suggested that these features were probably heritable to some extent, other factors such as body size, advanced physiological age, environmental effects from the physical demands of a hunter-gatherer lifestyle in an arid zone, dietary factors including food abrasiveness and limited preparation of food, and the use of teeth as tools may all have been factors affecting (exaggerating) the expression of robusticity in the Australian context.

5.1. Cranial Thickening as Pathology in WLH50. As noted above, pathological processes are suggested to have greatly enlarged the already thick vault bones of WLH50 (Figure 2). Webb [13, 14, 152, 153] has listed three indicators of pathology in this individual: (1) uniform vault thickness, (2) identification of the “hair-on-end” sign on lateral radiographs of the calvaria, and (3) a thin vault cortex.

Figure 3 compares vault thickness at eight locations in WLH50 with the median and range for the remaining Willandra Lakes series, as measured by Webb [13]. The large absolute thickness of the WLH50 vault is striking

although thickness at one landmark (*inion*) does lie well within the range of the remaining Willandra Lakes sample. It is also very clear that vault thickness in WLH50 is far from uniform, as it varies between locations in a similar magnitude to the medians for the Willandra Lakes series (Figure 3). The magnitude of change (difference) between each of eight locations was calculated for WLH50 and the rest of the Willandra Lakes series, and the median value is actually larger in this individual (2 mm versus 1 mm). Moreover, a nonparametric Mann-Whitney *U*-test showed that the sample medians are statistical indistinguishable ($n = 7/54$, $U = 187.5$, $P = .98$; Monte Carlo $P = .98$). Thus, WLH50 does not possess a vault of uniform thickness when compared to the rest of the Willandra Lakes Human sample.

Figure 4 is a lateral radiograph of WLH50 taken in 2006 by the author and A. Thorne. After careful inspection, no indication of the hair-on-end sign can be seen. Figure 5 is a lateral slice of a CT-scan of WLH50 also taken by the author and A. Thorne in 2006. Again, in this and every slice inspected by the present author (245 slices in three planes, or 735 images), no evidence of the hair-on-end sign can be found. There is, however, evidence for abrasion on the external cortex around bregma (Figure 5), which may have been mistaken by Webb for the vertical spiculations sometimes associated with porotic hyperostosis.

It is also clear in Figures 4 and 5 that the external table of WLH50 is far from thin. To assess this quantitatively, the ratio of diploë to external table thickness was calculated from thickness measurements made on CT-scans just lateral to the median sagittal plane by the author. External table thickness was chosen because along with the diploë this vault component is altered in cases of porotic hyperostosis [157]. The median of this ratio for WLH50 measured at nine locations shows the diploë to be 1.4 times as thick as the external table, while in WLH3 the median shows it to be 0.9 times as thick. While WLH50 certainly does exhibit relatively thinner external table, it is far from thin. Finally, the results of a Mann-Whitney *U*-test showed the median difference between WLH3 and WLH50 to be statistically nonsignificant ($n = 9/23$, $U = 74$, $P = .22$; Monte Carlo $P = .23$).

5.2. Ontogenetic Examination of Some Phylogenetic Characters. Table 1 lists 16 morphological traits for WLH50 used to support a role for the Solo/Ngandong population in the evolution of Aboriginal Australians (i.e., a reticulate or dual ancestry model) [54, 55]. These “nonmetric” traits were originally selected in order to avoid “duplicating features that seemed to reflect the consequences of the same anatomical variation” [55, page 294]. While somewhat ambiguous, this statement is understood by the present author to imply that traits were employed that were believed to be developmentally and functionally nonintegrated and, therefore, to be characterised by weak or absent covariation. This assumption is crucial to an evaluation of the phyletic valency of cranial robusticity in the Australian context and the implicit assumption that characters shared by Australian and Solo/Ngandong crania are homologous. (The reader is referred also to Bräuer et al. [158] who provided a critical



FIGURE 4: Lateral plain film X-ray of Willandra Lakes Human 50.

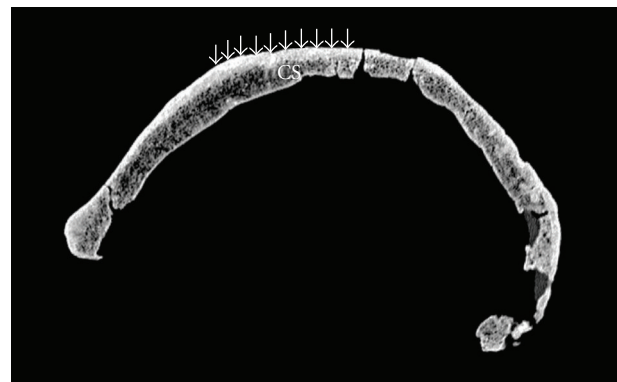


FIGURE 5: Sagittal CT-scan of Willandra Lakes Human 50 (lateral to the MSP). Arrows indicate surface abrasion; “CS” denotes coronal suture.

evaluation of the character coding and statistical methods employed by Hawks et al. [54] and Wolpoff et al. [55].)

All of the characters shown in Table 1 belong to a single cranial (developmental) unit, namely, the neurocranium. A small part of the lateral cranial base is preserved while the facial skeleton is missing save a fragment of zygomatic bone. Moreover, these traits represent two subunits of the neurocranium most of them belong to the cranial vault (14), with the remaining (2) belonging to the orbit subunit (Table 1). Given the now well-established finding of ontogenetic modularity and integration of the neurocranium (e.g., [77, 80–83, 85–89, 106–144]), there are good reasons to be suspicious about the use of the atomisation in this instance.

According to the functional matrix hypothesis [88], the cranium comprises various functional cranial components (FCC), which are ontogenetically integrated. One FCC contains the brain, cerebellum, and ocular globe, sharing a common embryological origin in the neural tube [77]. This FCC

TABLE 1: Cranial traits used in phenetic studies of WLH50 (characters from [55]).

Character	Developmental subunit*
(1) Angular torus	Vault
(2) Coronal keel	Vault
(3) Sagittal keel on frontal	Vault
(4) Lateral frontal trigone	Vault
(5) <i>Linea obliquus</i> strongly developed	Vault
(6) Mastoid crest	Vault
(7) Sagittal keel on parietal	Vault
(8) Postlambdoidal eminence	Vault
(9) Prebregmatic eminence	Vault
(10) Projecting inion	Vault
(11) Sulcus dividing the medial and lateral elements of the supraorbital torus or superciliary arches	Orbit
(12) Superior margin of the orbit blunt (as opposed to sharp)	Orbit
(13) Suprainiac fossa	Vault
(14) Supramastoid crest	Vault
(15) Temporal line forms a ridge	Vault
(16) Transversely extensive nuchal torus	Vault

* After Ackermann and Cheverud [120].

develops in an integrated way being subjected to common heritable and epigenetic factors. The neurocranium largely develops as a result of the passive displacement of the vault bones, occurring within a connective tissue stroma, which is enlarged by the growing brain [77]. As a result, all three parts of this FCC follow a common growth trajectory, reaching 90–96% of their adult size by about age 6–7 [77, 89, 115, 129]. However, the neurocranium also forms an integrated unit with the cranial base, the “neurobasicranial complex,” and its form is strongly influenced by factors such as basicranial flexion, while the developing face also epigenetically “fine-tunes” basicranial morphology, indirectly altering the form of the cranial vault [122, 123, 131, 132, 136, 138–144].

Additionally, all 16 characters are cranial “superstructures” as originally defined by Weidenreich [159]. He suggested that superstructures develop in response to tension (“pull”) from muscles, a hypothesis subsequently verified experimentally with respect to some cranial crests [77, 78, 91, 92, 115, 160, 161], implying that they “belong to, or sit only upon, the outer bony table” [91, page 208]. However, this situation is not universal for superstructures and their development is complex.

As Enlow has shown [77, 91, 115, 161], the external surface of a bone is frequently shifted from an endosteal position. This means that developmental changes within the endocranium as well as epigenetic factors acting on the external table determine the morphology of the vault. Moreover, different processes may be involved in remodelling the neurocranium in spatially adjacent regions, and different regions of the cranium may exert influence over the growth of a single structure at different ontogenetic

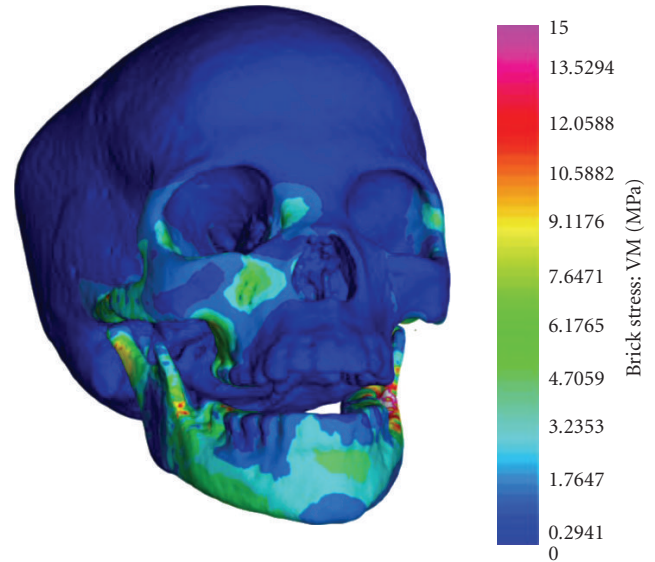


FIGURE 6: Stress (von Mises) distributions in a high-resolution three-dimensional computer simulation of cranial mechanics in a Holocene San skull (modified from [166]).

stages. For example, about midway up the frontal squama is a reversal line from resorptive (inferiorly) to depositional (superiorly) remodelling [77]. Once the frontal lobes have largely completed their enlargement, the internal table stops growing, while the outer table continues to remodel, progressively separating the inner and outer tables, and replacing through resorption cancellous bone to form the frontal sinus. However, this continued growth now results directly from the anterior remodelling of the upper face or nasomaxillary complex [77]. Further, the orbit (subunit) is contained within this region, and the inner table of its roof (endocranial side) is resorptive while the external (orbital plate) is depository [77]. As the orbital roof continues to remodel inferiorly along with the growth of the frontal lobes of the brain, the orbit must grow anteriorly to provide sufficient room for the growing eye; it is displaced outwards with other bones of the orbit which form part of the face according to the V principle [77].

In the case of the supraorbital torus, also considered to be a superstructure by Weidenreich [159], there is now abundant evidence that this feature develops epigenetically as a result of the spatial relationships among the face, neurocranium, and cranial base rather than biomechanical stresses during mastication [77, 115, 162–167], contra [168]. For example, Figure 6 is a Holocene San skull indicating stress gradients from masticatory stress as analysed with the finite element method [166]. The supraorbital region is unaffected by strain in this homogenous 3D model (but see similar results using a heterogeneous model [165]).

Thus, while 14 characters might be regarded as superstructures of the cranial vault, developing to provide muscle attachments and remodelling in response to mechanical stress, research into the supraorbital torus makes clear that the two orbital roof features lack epigenetic influences from the muscles of mastication. The supraorbital develops as

a result of a complex interplay between the shape of the neurocranium and breadth of the basicranium, growth of the frontal lobes of the brain, development of the frontal sinus, remodelling of the orbit to accommodate the growing eye, and growth of the nasal region, which develops in response to lung enlargement and in particular affects the superior orbital rim, and the anteroposterior length of the face seems also to be a determinant of its position relative to the frontal squama and, therefore, the degree of frontal recession seen [77, 115, 122, 123, 137, 162–171]. Moreover, crania with high midfacial projection exhibit a long anterior sphenoid resulting in a viscerocranium positioned anterior to the neurocranium [133, 134, 170, 171] and in a prominent supraorbital. Finally, the development of the supraorbital region may even be epigenetically influenced by exercise through the effects of hormones seemingly independently from (but commonly with) other structures such as thickened vault bones (see [172, 173]; see also [8]).

As noted above, Mitteroecker and Bookstein [106] have found four common cranial factors or trajectories across a range of primates including humans, which are integrated through genetic effects such as pleiotropy and linkage, as well as epigenetic processes.

Factor 1. An enlarged and prognathic maxilla, relatively small cranial capsule, cranial crests, and enlarged zygomatic arches are features epigenetically associated in primates mainly as a result of masticatory muscle action. These are all characteristics of cranial robusticity and while they can be observed as a package in better-preserved crania (e.g., Cohuna, Kow Swamp 1), some of them are observable in incomplete remains such as WLH50 (Table 1, Figures 2 and 7) [2, 8–14, 16–18, 41–43, 46–52, 54, 55, 64, 72, 151].

Factor 2. This pattern contrasts broad and short crania with narrow and long crania (brachycephalic versus dolichocephalic crania), including both the face and the neurocranium, and also involves changes in the overall size of the face relative to the neurocranium. All robust Australians (e.g., Cohuna, KS1, WLH50) exhibit narrow and long crania (Figures 2 and 7) [2, 8–14, 16–18, 41–43, 46–52, 64, 72, 151]. Overall neurocranial length, breadth, and height are characterised by moderate but significant levels of heritability, suggesting a large amount of variation in these features determined by epigenetic forces [79, 81, 82]. Moreover, while their faces are absolutely long and consistent with this factor (e.g., KS1, KS5, Cohuna), they differ in exhibiting absolutely and relatively broad faces [2, 8, 9, 11–14, 17, 18, 41–43, 47–49, 51, 52, 151]. However, facial shape has been found to exhibit weaker correlations with neurocranial and basicranial shape than these regions have with each other, perhaps explaining why the face is the most variable part of the skull in humans [85]. Additionally, the dimensions of facial length, breadth, and height are characterised by moderate heritability indicating that additive genetic variation accounts for approximately 30% of the phenotypic variation [79, 81, 82]. Further, facial breadth is well known to be under strong ontogenetic influence from the muscles of mastication [171, 174–178]. A positive correlation between total masticatory

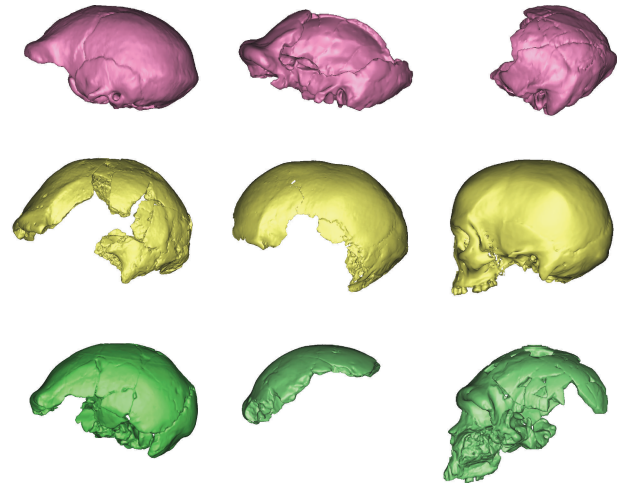


FIGURE 7: Three-dimensional models of various fossil crania made from CT-scans, left lateral view: (top to bottom, left to right) *H. erectus* Sangiran 2, OH9, and Sangiran 4; Pleistocene Australians WLH50 and WLH3; African Holocene San; premodern Middle Pleistocene Africans LH18, Florisbad, and Bodo. Models scaled to approximately the same A-P length.

muscle size (cross-sectional area) and body size (stature and weight) has also been found [171, 174–178]. The body size of the WLH50 individual, like other Pleistocene Aboriginal Australians, would have been large by later Holocene and contemporary standards [8, 17]. In fact, metrical dimensions of size and endocranial volume reveal it to be one of the largest Pleistocene modern humans found anywhere in the world and comparable in size to early African crania such as from Herto, and larger than many nonmodern individuals (compare with data in White et al. [179]), including *H. erectus calvarii* [17].

Factor 3. Encompassing relative size of the midface and neurocranial globularity, two characteristics that are tightly associated during postnatal ontogeny. While sample size disallows a proper comparison, robust Australian individuals such as KS1 are certainly characterised by a relatively narrow midface (ZMB/NPH = c66%) compared with the gracile Keilor cranium (c76%) (data from [151]). Moreover, these and other crania are strongly contrasted in their degree of neurocranial globularity; robust crania exhibiting highly angulated vaults, with receding frontal squamae (Table 1, Figure 2) [2, 8, 9, 11–14, 17, 18, 41–43, 47–49, 51, 52, 151]. In contrast, individuals such as WLH1, WLH3, and Keilor possess more globular crania (see Figure 7) [2, 9, 13, 14, 17, 41, 42, 51–53, 71, 72, 151].

Factor 4. A roundish and relatively short and high neurocranium to elongated, ellipsoidal crania. Exaggeration of the latter generates an occipital bun and lambdoid flattening along with large browridges. Robust Australian crania all exhibit ellipsoidal crania (superior outline); many have an occipital bun and lambdoid flattening, and all exhibit prominent browridges by modern human standards (see Figures 2 and 7) [2, 8, 9, 11–14, 17, 18, 41–43, 47–49, 51, 52,

151]. Although the WLH50 calvaria is actually relatively tall in addition to being very long, this probably results from the combination of large endocranial volume and very narrow cranial base (see [17, 156]; see also [180, 181]). A range of other factors interacting in a complex manner are also known to influence the development of the supraorbital part, cranial shape being one of them (see above).

It is interesting also to note that Mitteroecker and Bookstein [106] found that their Factors 1 and 2 were the most highly conserved among humans, chimpanzees, and gorillas, with all three sharing a single ontogenetic trajectory owing to the presence of tight integration during development. Many of the traits listed in Table 1 can be explained by variation within these two highly constrained modules. Trajectories for Factors 3 and 4 were found to deviate considerably in humans compared to chimpanzees and gorillas suggesting that certain human cranial features have decoupled during evolution [106]. They opined that this difference was best explained by local developmental factors unique to humans such as relative brain size, posture, and locomotion (Factor 3), and facial shape, mainly involving the browridge (Factor 4). In the end, this research indicates that selection does not act on individual features, but instead cranial traits form part of an integrated and heritable set of factors or trajectories. Australian cranial robusticity lies on the trajectory for all four factors but is never as extreme in its expression as seen among nonmodern hominins.

Figure 7 presents 3D models (scaled to the same length) constructed by the author from CT-scans of WLH3 and WLH50, a Holocene African hunter-gatherer and various Pleistocene (nonmodern) hominins. Compared to WLH3 and the Holocene San individual, WLH50 does exhibit a receding frontal squama, prominent browridge, and some projection of the occipital. However, compared to all nonmodern, middle Pleistocene calvarii, WLH50 is tall, has a more upright frontal squama, which bulges anteriorly (prebregmatic eminence), and has relatively rounded parietal and occipital profiles and mild lambdoidal flattening. In fact, it closely resembles WLH3 in all these respects. Moreover, it lacks the strongly projecting browridge and a posttoral shelf so evident in all middle Pleistocene remains, whether belonging to *H. erectus*, *H. heidelbergensis/rhodesiensis*, or archaic *H. sapiens/H. helmei*. Its profile including the frontal squama is quite rounded (globular) compared to nonmodern crania. Thus, the purported similarities between WLH50 and *H. erectus* seem to have been greatly exaggerated, particularly when a comparison involving Middle Pleistocene African crania, the putative ancestors of all modern humans [1], is made. Instead, WLH50 simply presents as a more rugged version of the WLH3 morphology, the two resembling each other in their angle of the posterior part of the frontal squama and profile of the parietals and occipital; when compared with the San cranium, and indicating regional-specific features for Australian crania. Moreover, the comparatively modest differences in shape between WLH3 and WLH50 seem to be explicable in terms of the ontogenetic trajectories described by Mitteroecker and Bookstein [106].

Another important recent study of cranial robusticity with strong bearing on the morphology of WLH50 and other

Pleistocene/early Holocene Australians is that of Baab et al. [182]. They tested for integration/correlation among various robusticity traits in a global sample of humans including recent Aboriginal Australians. Overall, they found that crania with more prognathic faces, expanded glabellar and occipital regions, and longer skulls were more robust than those with rounder vaults and more orthognathic faces. This supports the findings of Lahr and Wright [156] and, more broadly, the results of Mitteroecker and Bookstein [106].

Baab et al. [182] also found evidence for significant positive but weak coexpression among all robust traits (frontal trigone, sagittal keel, infraglabellar notch, supraorbital torus, zygomaxillary tubercle, and prebregmatic eminence) with the exception of the occipital torus. They did, however, find that the supraorbital torus is strongly and significantly correlated with an infraglabellar notch and moderately and significantly correlated with a zygomaxillary tubercle and a zygomatic trigone. Moreover, moderate and significant correlations were found between the zygomaxillary tubercle and bregmatic eminence, inferolateral rounding of the orbit, infraglabellar notch, and zygomatic trigone; between a bregmatic eminence and inferolateral rounding of the orbit; infraglabellar notch and zygomatic trigone. They concluded that epigenesis through masticatory function was the most likely cause of the development of these traits.

One feature studied by Baab et al. [182] failed to show correlation with the other robust traits they examined, namely, the occipital torus. Again this seems to be explicable in terms of epigenetic forces during ontogeny. For example, Perez et al. [183] have described a positive association between occipital muscle attachment areas and head shape (dolichocephaly) among males in a sample of South American hunter-gatherer crania. Thus, it may simply be an epigenetic consequence of an elongated cranium, in-line with other changes such as a protruding occipital and formation of an occipital bun [106, 122, 123, 180, 181]. A related character is the suprainiac fossa in WLH50 (Table 1). Functionally, this feature is suggested to provide attachment for nuchal ligament [184] or to represent an area of resorptive bone developing in response to bending forces along the nuchal torus [185]. Irrespective of its cause, this feature is actually found in both WLH3 and WLH50 (personal observation) and cannot, therefore, be considered a defining trait of Australian robusticity nor evidence bearing on their phylogenetic history.

The issue of vault ridges (or keeling) has not been explicitly addressed in most ontogenetic studies of the human cranium. Although Baab et al. [182] did find statistically significant moderate correlations between a sagittal keel and bregmatic eminence, both features are associated with cranial vault sutures. Their development may, therefore, be part of the integrated process of ontogeny and result from epigenetic factors relating to cranial shape and mechanical forces.

The research of Baab et al. [182] also highlights that while integration and modularity are fundamental to understanding cranial ontogeny, certain features sometimes show lower than expected correlation and covariation than expected. Similar findings have been made with respect to the endocranium [186–188].

A number of researchers have specifically addressed the issue of the mechanical effects of mastication on cranial sutures experimentally. *In vivo* studies [188] found that strain (tension or compression) along sutures was not the result of torsion but rather the localised effects of masticatory actions. Strain was found to be significant along all of the major vault sutures, and its effects varied depending upon the muscle involved. For example, while masseter contraction tensed the coronal suture, the temporal caused compression at this region. Moreover, an earlier study [189] found that even a relatively small bite force was sufficient to cause separation of the sagittal suture in juvenile monkeys, from which they concluded that “such separation might act as a major factor in the local control of osteogenesis of the sutures” [189, page 907]. Additionally, Sun et al. [190] confirmed earlier findings of significant masticatory strain along vault sutures and further found that synostosis (normal fusion) resulted in increased suture strain and enhanced bone growth on the ectocranial surface leading to thicker bones in adults. Finally, the sutures have also been suggested to play a role in dissipating masticatory strain [191], while the diploë may also play a similar role [165]; although these hypotheses require further testing.

Clinical interest in cranial ridges along the major vault sutures stems from understanding the causes and treatment of abnormal head shape as result of congenital or acquired conditions (such as birth injuries) or pathophysiological processes leading to clinical craniosynostosis (premature suture closure). Midline ridges are found within the clinical spectrum of such cranial deformities [192]. However, in the absence of changes to vault or facial shape, they are considered normal variants [193]. The metopic ridge can arise in an infant (before two years of age) from premature closure of the metopic suture, while a midline bony ridge over vertex from front to back may develop following premature fusion of the sagittal suture in adults prior to 40 years of age [192]. Coronal bony ridges can also form in cases of premature craniosynostosis, again arising any time before normal closure of the coronal suture (typically around 40 years of age [192]).

Premature synostosis of one or more sutures is accompanied by compensatory growth, both in other sutures, and by remodelling (appositional growth) of other parts of the skull [194]. Premature closure of sutures prevents separation of the bones and affects skull growth in a direction perpendicular to the affected suture, leading to skull deformations [194, 195]. Much later in life (i.e., around 40 years of age), premature craniosynostosis of the sagittal and coronal sutures can occur and leads in mild cases to the development of sagittal and coronal ridges. Among robust Australian crania, the parietals are relatively long and the lower occipital scale (nuchal plane) is unusually relatively short [151]. Moreover, premature craniosynostosis of the sagittal suture at around 40 years of age can result in dolicocephaly, accompanied by a narrow head with bitemporal widening, sometimes frontal and occipital bossing, and a midline bony ridge over the vertex from front to back [192].

The current clinical incidence of synostosis is 1 in 2,000–3,000 newborns although syndromic craniofacial

malformations involving more than one suture occur in about 15% of cases [192]. Sagittal craniosynostosis is rarer, with an incidence of about 1 in 5,000 adults [192]. The aetiology of craniosynostosis is heterogeneous: hereditary, mechanical, teratogenic, and idiopathic [195]. Multiple genetic and environmental causes have been identified. Among the latter are rickets caused by vitamin D deficiency or resistance, chronic renal failure, hypothyroidism and hypophosphatasia, and multiple causes of abnormal fetal positioning *in utero* leading to constraint of the fetal skull [192]. Rickets is documented among human remains from the Willandra Lakes [153]. Moreover, synostosis may have been more common in the past among some populations. For example, White [196] found an incidence of 3% in a sample of normal Mayan skulls, rising to 31% among those from the precontact period; and in 41% of them premature synostosis was apparently explained by artificial deformation. This lends support to suggestions that artificial deformation may be an exaggerating influence in the robusticity of Pleistocene/Holocene Australians [9, 146–150].

6. Conclusions

The idea that Aboriginal Australians possess an unusual and phylogenetically informative pattern of cranial robusticity has been important in palaeoanthropology for about 150 years. There has, however, been a wide range of views about specific aspects of their evolutionary history. Particularly, whether or not Pleistocene nonmodern populations in Southeast Asia (i.e., *Pithecanthropus*, *H. soloensis*, or *H. erectus*) played a role in their evolutionary history. Irrespective of whether the multiregional, assimilation, or Out-of-Africa model has been supported, most investigations have taken the human cranium to be optimised part by part, and atomised its morphology into traits assumed to be heritable units, functionally discrete, shaped by natural selection and, therefore, to be positively associated with reproductive success in order to make phylogenetic inferences. Yet, a large body of research from the morphological sciences, including anatomy and embryology, pathology, genetics, and evolutionary biology makes it clear that these assumptions may be unrealistic and that atomisation should be used with great care in phylogenetic reconstruction.

The human (vertebrate) cranium is characterised by ontogenetic and functional modularity, with much integration/covariation among the elements within each module, as well as between them. Moreover, epigenesis is a powerful, pervasive, and very complex force, its influences being felt in all levels of organisation during ontogeny, from cellular interactions to those among adjacent tissues to interactions with the external environment of an organism. Additionally, while many aspects of cranial size and shape are heritable, epigenesis may determine 70% or more of variation seen within populations with well-established pedigrees [79–82]. Finally, many of the traits designated “robust” are also characterised by some ontogenetic integration and are likely to derive from a set of common epigenetic factors, which includes the spatial effects/constraints of size and shape, for

example, central integrating features such as the cranial base and mechanical effects from the muscles of mastication.

While there is clearly a strong message in this research for palaeoanthropology in general, its implications for studies of Australian Aboriginal robusticity are particularly acute. Phylogenetic reconstruction across all organisms and employing all methods involves a set of important assumptions about the traits used. For example, Lieberman [197] lists seven such assumptions, the first four being relatively uncontroversial, with the remaining three particularly relevant here although hardest to satisfy; (5) characters should reflect independent units of information about phylogenetic relationships, (6) they must be heritable if they are to provide reliable information on ancestry and descent, and (7) they should be equivalent units or homologous structures. The ontogenetic approach outlined here suggests that these assumptions probably cannot be met in the case of phylogenetic reconstructions involving robust Australian crania when using atomised traits. Most characters are unlikely to be independent units, being integrated in their development and influenced by a complicated set of epigenetic interactions [77, 83–89, 106–144, 160–167, 169–178, 180–183, 188–197]. They also show mostly low to moderate heritability [79–82] and are in some instances clearly not homologous in modern humans and nonmodern hominins.

For example, a character used widely in studies of the evolutionary origins of Aboriginal Australians is the possession of a flat frontal squama among robust individuals [2, 8, 9, 11–14, 16–18, 39–43, 47–49, 51, 52, 63, 72, 151]. Putting aside epigenetic explanations involving pseudopathology [17, 146–150], this trait fails to satisfy all three assumptions of phylogenetic reconstruction. The size and shape of the growing brain in accordance with the functional matrix hypothesis [77, 88, 114, 115] and its epigenetic interactions with the developing cranial base largely determine the size and shape of the vault. Moreover, there are also influences from the growing face although, they are more subtle than those of the basicranium [122, 123, 131, 132, 136, 138–144]. The anteroposterior length of the face seems also to be a determinant of its position relative to the frontal squama and, therefore, the degree of frontal recession present; crania with high midfacial projection exhibit a long anterior sphenoid, resulting in a viscerocranium positioned anterior to the neurocranium [122, 123, 131–134].

In nonmodern hominins like *H. erectus*, a flat frontal squama results from a complex combination of a small frontal brain lobe, broad cranial base, combined high midfacial projection and long anterior sphenoid. However, in anatomically modern humans with our large brains, including relatively broad and steep frontal lobe [198], angulation of the frontal squama results from the brain being epigenetically forced to grow excessively posteriorly by a narrow cranial base resulting in a long and tall cranium [17, 156, 180, 181]. Moreover, a flat frontal squama is associated with a browridge, the orbital roof being forced to grow forward to accommodate the growing eye, and an occipital bun, the result of the posterior growth of the brain within a narrow vault. Additionally, because the brain and its frontal lobe are relatively broader and more globular (taller)

in modern humans and our face characterised by significant retraction [137, 170], the brow is never as prominent in modern humans as it is in nonmodern hominins including in WLH50 (see Figure 7) [122, 123, 181, 199]. As noted above, WLH50 is among the largest modern humans found in the fossil record globally and is comparable in size to the earliest modern remains such as from Herto (see data in [179]), and larger than many nonmodern crania including *H. erectus*. While large cranial size and a narrow cranial base, as seen in WLH50, are certainly plesiomorphic traits, they are not shared with *H. erectus* or other nonmodern hominins but are plesiomorphies of anatomically modern *H. sapiens* [17, 122, 123]. Moreover, they seem to have been important influences on the form of this calvaria and other Australian remains.

To conclude, there is now ample evidence that the atomisation of cranial robusticity has provided a misleading picture of the evolutionary history of Aboriginal Australians. Moreover, models suggesting that living Australians as demonstrated by their robust cranial morphology can trace their origins to the nonmodern hominins of Pleistocene Southeast Asia should be reconsidered in light of major developments in the morphological sciences. In 1976, Howells [145] issued a challenge to Australian palaeoanthropology to reject a null hypothesis that differences between gracile and robust crania can be explained by phenotypic plasticity alone. So far, this challenge has been ignored. It is time to reconsider the adaptationist program and to take a more parsimonious approach to explaining Aboriginal Australian origins, one that takes account of the complex processes involved in the ontogeny of the human cranium rather than just assuming that natural selection explains every subtle variation seen in past populations.

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