

# Cognitive and behavioral modernity in *Homo erectus*: skull globularity and hominin brain evolution

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**ABSTRACT:** In this article we provide evidence that evolutionary pressures altered the cranial base and the mastoid region of the temporal bone more than the calvaria in the transition from *H. erectus* to *H. sapiens*. This process seems to have resulted in the evolution of more globular skull shape – but not as a result of expansion of the brain in the parietal regions but of reduction of the cranial base and the mastoid region relative to the parietals. Consequently, we argue that expansion of the parietals seems to be unrelated to brain evolution, but is more a by-product of reduction in other regions of the skull, reduction that may be related to dietary factors. Additionally, these findings suggest that cognitive and behavioural modernity may not necessarily be dependent on brain shape. Also, it cannot be attributed to the change in brain size because *H. erectus* and modern human cranial capacities overlap substantially. Consequently, we suggest *H. erectus* possessed the full suite of cognitive adaptations characteristic of modern humans without possessing a globular skull with flared parietals. Our results also support the theory that pedomorphic morphogenesis of the skull was important in the transition from *H. erectus* to *H. sapiens* and that such changes may be related to both dietary factors and social evolution.

**KEY WORDS:** Cranial shape, masticatory adaptations, Acheulian industry, cognition, *Homo erectus*

## Introduction

The hominin skull has undergone significant changes since the last common ancestor our lineage shares with chimpanzees and bonobos. Initially, with the

emergence of species such as *Ardipithecus ramidus*, these changes included loss of the large tusk-like canine and reduction of the prognathic face common in other primates, anatomical alterations which have been attributed to changes in mat-

ing and social systems and reduced male on male aggression (Clark and Henneberg 2015; Lovejoy 2009; Suwa et al. 2009). This very distinct configuration of the skull is believed to have evolved as a result of social selection pressures and possible self-domestication evidenced by the paedomorphic skull architecture of *Ar. ramidus* (Clark and Henneberg 2015; Clark and Henneberg 2017) – although a shift in diet in addition to social factors has also contributed to the unique morphology of the early hominin skull (Hylander 2013).

The shift to a hominin skeletal configuration is also central to both locomotion and language ability. For example, hominin upright bipedal gait is associated with a centrally positioned foramen magnum, with the vertically oriented spinal cord entering the centre of the skull (Russo and Kirk 2017) – a feature of human anatomy that has long been recognised as a paedomorphic retention of the infant primate form into adulthood (Bolk 1909). Furthermore, a centrally positioned foramen magnum in addition to reduced facial prognathism, evident at the base of the hominin clade in *Ar. ramidus*, seems to be a prerequisite for the unique hominin vocal tract configuration necessary for the evolution of language (Clark and Henneberg 2017).

The paedomorphic morphogenesis of the skull via the process of self-domestication proposed for early hominins such as *Ar. ramidus*, is believed by numerous researchers to have continued in the *Homo* genus. This model proposes that increasing feminisation and gracilisation of skull morphology, along with associated changes in neurochemical regulation, may have resulted from selection for social tolerance and pro-sociality in the transition from robust to gracile members of the *Homo* genus (Cieri et al. 2014;

Hare 2017). Further, in contrast to chimpanzees the ontogeny of cranial form in *Homo sapiens* results in a highly globular neurocranium, with the face growing less and thus remaining retracted under the anterior cranial base in contrast to the highly prognathic face of chimpanzees (Lieberman et al. 2002).

Other researchers have argued that changes in hominin skull shape are implicated in selection of the brain associated with the unique cognitive and linguistic capacities of modern humans. For example, it has been argued that the evolution of a more gracile and globular skull shape from a more robust ancestral form within the *Homo* genus, was driven by changes in neural architecture implicated in the emergence of behavioural modernity (Neubauer et al. 2018). For example, it has been noted that globular skull form emerges much later than increases in brain size, with increasing globularity becoming evident during the Middle to the Upper Palaeolithic in Europe around 50,000 to 40,000 years ago. Significantly, this is believed to be when evidence of behavioural modernity becomes visible in the archaeological record (Neubauer et al. 2018).

This thesis is based on a putative relationship between globularity and expansion of specific brain regions. For example, the expansion of the parietals, which contributes to globular skull shape, is believed to be associated with evolution of the uniquely human default mode neural network (Neubauer et al. 2018). In modern humans the parietals are expanded laterally relative to the mastoid region and the cranial base. This pattern can be observed in Figure 1 where the relationship between the parietals and the mastoid region in *H. erectus* and *H. sapiens* is graphically illustrated.

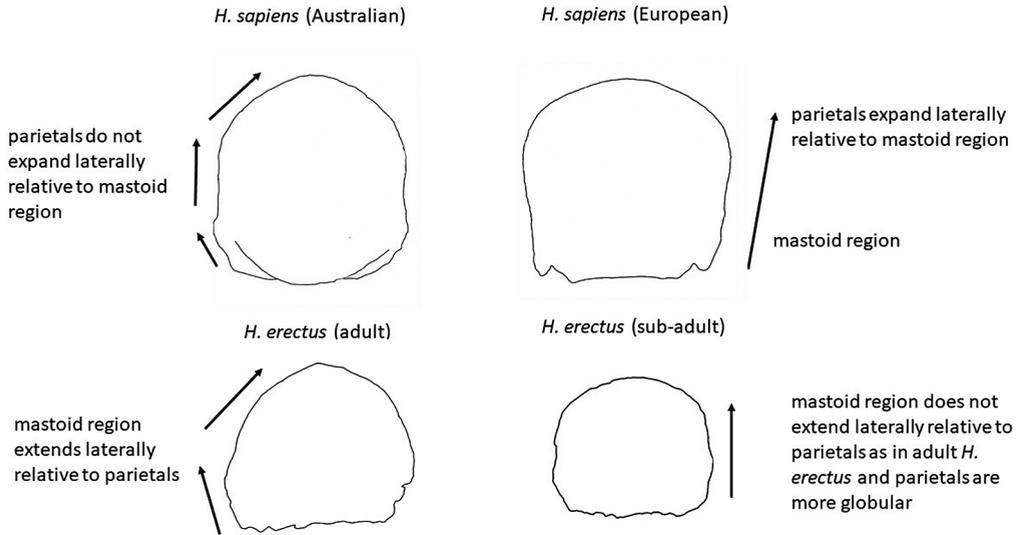


Fig. 1. Globularity in *H. erectus* and *H. sapiens*

Drawn from: *H. erectus* adult (Weidenreich 1943), *H. erectus* subadult (Antón 1997), with both *H. sapiens* from casts. Drawings not to scale but merely designed to provide a rough graphic representation of the argument in this paper. Note that the parietals expand laterally in some *H. sapiens* whereas in *H. erectus* the mastoid region and the base expand laterally. Significantly, the sub-adult Mojokerto fossil shows greater shape affinity with adult *H. sapiens* than it does with adult members of its own species. This has led to the assertion that the transition from *H. erectus* to *H. sapiens* involved paedomorphic skull morphogenesis.

Figure 1 illustrates that adult *H. erectus* lacks the bulging parietals characteristic of European modern humans. As opposed to expanding relative to the mastoid region, the parietals taper medially eventually meeting at the sagittal suture. Further, in modern humans the maximum skull breadth is frequently equivalent to bi-parietal breadth whereas greatest breadth of the skull in *H. erectus* is close to bi-auricular – a difference that results from the different positions of the parietals relative to the cranial base and the mastoid region in each species (Weidenreich 1943, p.22). What is worth noting in Figure 1 is that the subadult Mojokerto child, a fossil of Indonesian *Homo erectus* believed to be approximately 4 years of age (Balzeau et al. 2005), lacks the configuration evident in adult *H. erectus* with virtually no expansion of the

mastoid region relative to the parietals. It should also be noted that the shape of the Mojokerto skull shows greater resemblance to adult *H. sapiens* than adult *H. erectus*.

Noting the similarity between the subadult skull shape of *H. erectus* and adult *H. sapiens*, researchers have argued that modern human skull shape evolved through the process of paedomorphism (Antón 1997; Balzeau et al. 2005). For example, in the sub adult *H. erectus* fossil, the frontal region is anteriorly rounded and the parietal region is relatively more developed than in adult *H. erectus*, with the specimen sharing relative development of the cerebral region comparable with modern human adults (Balzeau et al. 2005). While some authors have questioned the notion that certain aspects of human skull architecture are

neotenus or paedomorphic (Dean and Wood 1984), the above observations do provide some support for the theory proposed by Gould that the retention of subadult ancestral features in the adults of descendant populations was an important component of phylogenesis in the hominin lineage (Antón 1997; Gould 1977).

It has been proposed that important factors influencing skull shape are the different growth trajectories of the neurocranium, the cranial base and the face (Lieberman et al. 2000). This model proposes that the neurocranium and the cranial base are on a rapid neural growth trajectory, with most of the growth in these regions being achieved by 6 years of age, while facial growth continues throughout ontogeny as part of the skeletal growth trajectory, not being complete until approximately 16–18 years of age. Additionally, the ontogenetically coupled growth of the neurocranium and the cranial base, is believed to result in the cranial base constraining the lateral growth of the neurocranium, while vertical and posterior growth of the cranium is not constrained by the dimensions of the base. As the authors write: ‘...given a large brain and a narrow cranial base, the cranial vault is likely to grow backward and upward to accommodate the brain’ (Lieberman et al. 2000, p. 297).

While there is merit to the above model, as it explicates the different growth trajectories of the skull associated with growth of the brain and the cranial base, and the face and the rest of the skeleton, it fails to consider different growth trajectories associated with different parts of the cranial base itself. For example, it has been observed that the central section of the cranial base associated with growth of the brain does achieve adult

size during childhood, while growth of the lateral sections of the base associated with the jaw and mastication continue to grow throughout adolescence and into adulthood (Sejrsen et al. 1997). This suggests a more nuanced conception of the ontogeny of skull morphogenesis – one we suggest that has significant implications for both the ontogenesis and phylogenesis in hominin evolution.

One of the unresolved issues in palaeoanthropology is the cognitive capacities of archaic hominins such as *H. erectus*. While some authors have argued that the cognitive, behavioural and technological capacities characteristic of modern humans were already in place in *H. erectus* (Bednarik 2013, 2015; Sterelny 2012; Webb 2006) others have argued that behavioural modernity and cognition evolved in tandem with changes in brain/skull shape within the *H. sapiens* lineage (Benítez-Burraco and Kempe 2018; Boeckx and Benítez-Burraco 2014; Neubauer et al. 2018; Niego and Benítez-Burraco 2019; Progovac and Benítez-Burraco 2019). In this article we attempt to falsify the hypothesis that modern human skull shape resulted from selection for altered neural architecture, cognitive adaptations and behavioural modernity.

## Materials and methods

We collected data from the literature to determine the relationship between the calvaria and the cranial base. This involved comparing the amount of variation that exists between various populations of modern humans and *H. erectus*. Data were collected for *Homo erectus* (Rightmire 2013), medieval Polish (Wokroj 1953), contemporary Aboriginal Australians (Milicerowa 1955), Ugandans (Górny 1957) as well as Australian

fossils (Webb 2018a). In order to determine the size of the calvaria we used maximum length from glabella to opisthocranium, maximum breadth from euryon to euryon, maximum height either as basibregmatic diameter or porion-vertex height (auricular height) and additionally, the maximum width of the frontal bone (co-co). In order to represent variation of the cranial base we used distance from nasion to basion, biauricular width and width from asterion to asterion. Face size, in relation to skull size was represented by the basion-prosthion diameter and face protrusion (prognathism) was expressed as an index =  $100 \times (\text{ba-pr}) / (\text{ba-n})$ .

Globularity of skulls can be quantified in a number of ways. When seen from above (*norma verticalis*) the cranial index ( $100 \times \text{maximum skull breadth} / \text{maximum skull length}$ ) is useful to ascertain globularity, while in the lateral view (*norma lateralis*) it is the height index expressing skull height as a percentage of the maximum length. We decided to combine the two expressions of globularity – horizontal and vertical – by expressing the sum of skull height and skull breadth as a percentage of maximum skull length. Since for some samples the skull height was reported as the auricular height (porion-vertex) and for others as the basibregmatic height, there is a slight difference between values of the indices calculated for different samples used here. We correct for this taking into account the fact that the basibregmatic height is about 20 mm greater than auricular height (Fox et al. 1996).

## Results

Our results indicate that the calvaria of modern humans and *H. erectus* differs less

than does the cranial base. For example, Figure 2 illustrates variation in both the length and breadth of calvaria morphology in *H. erectus*, modern Aboriginal Australians, fossil Australians and Poles. As can be seen our measure of cranial size in *H. erectus* – that is width and length – falls within the range of the Aboriginal and Polish sample. By contrast, our measure of cranial base morphology in Figure 3 shows greater difference between modern humans and *H. erectus* than that evident in our measure of calvaria morphology in Figure 2, with the vast majority of *H. erectus* measures outside the range of modern human variation. This result suggests that in the transition from *H. erectus* to *H. sapiens* selection on the cranial base and mastoid region was greater than selection on the calvaria. Data in Table 1 confirm this suggestion: not all calvarial dimensions differ significantly when comparing *H. erectus* and modern samples, while basicranial width dimensions and jaw length differ significantly, being notably smaller in moderns. Modern/*erectus* ratios of calvarial dimensions oscillate around 1 while basicranial and gnathic ratios are below 1.

If selective pressure did affect the evolution of the cranial base more than the calvaria then the question arises as to why this may have occurred? If changes in diet and mastication resulted in reduction of the mechanical supports for mastication on the cranial base, then we would also expect to see an increase in globularity accompany the reduction of the facial apparatus necessary for mastication. In other words, *H. erectus* should have both a larger face and larger cranial base than *H. sapiens*, with the consequent lateral expansion of the mastoid region relative to the parietals resulting in a non-globular form. Conversely, if the base and mas-

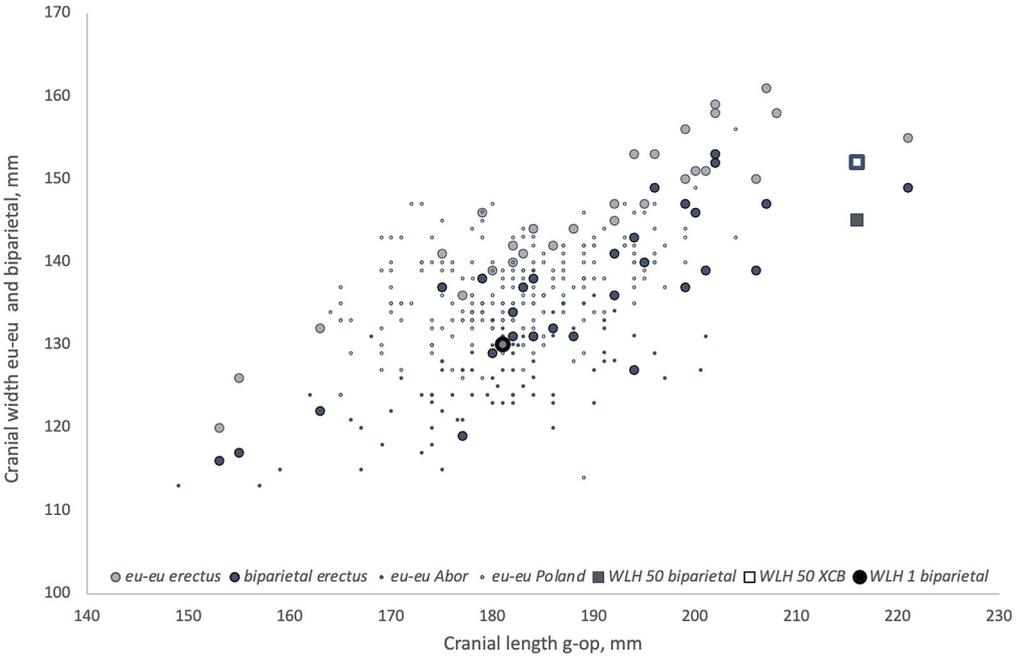


Fig. 2. Measures of the size of the calvaria in *Homo erectus* and modern humans

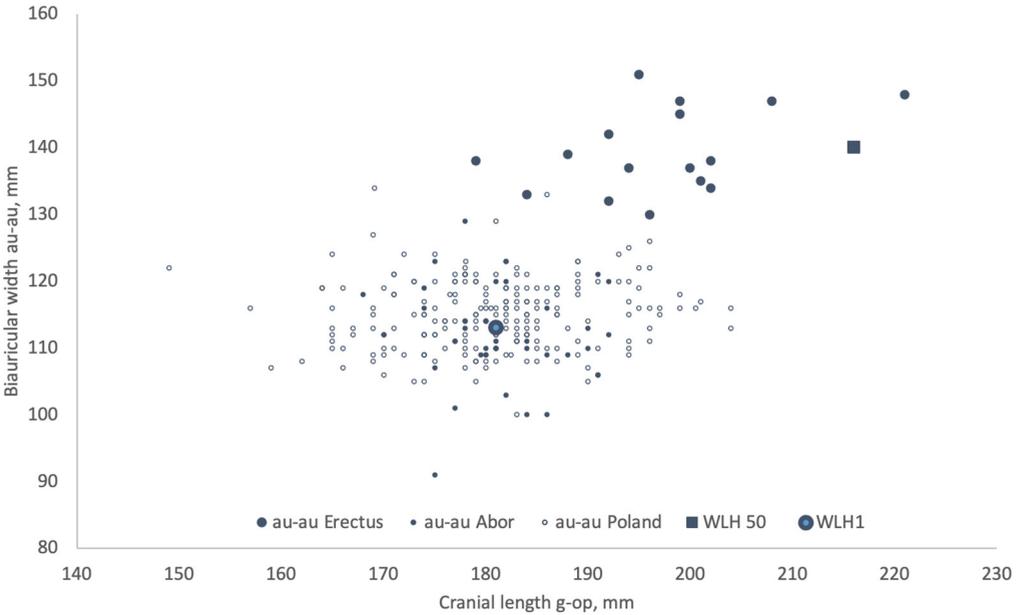


Fig. 3. Measure of the breadth of the cranial base in *Homo erectus* and modern humans against the maximum cranial length Biauricular distances for Willandra Lakes Humans estimated by adding 10 mm to biasterionic distance

Table 1. Averages and standard deviations of craniometric dimensions of *Homo erectus* and three samples of modern humans. Sample sizes for some averages may differ somewhat from the cited one due to missing individual measurements. For *H. erectus* eu-eu diameter has been replaced with biparietal diameter. Ratio modern/erectus is an average of three values

Group		N	g-op	po-v	eu-eu	co-co	ba-n	au-au	ast-ast	ba-pr
<i>H. erectus</i>	avg	33	189.3	97.2	135.9 <sup>a</sup>	109.3	106.4	133.9	118.4	115.3 <sup>b</sup>
	sd		15.3	7.8	10.1	10.6	9.0	9.2	9.5	12.0
Australians	avg	78	180.7*	108.3*	137.5	106.8	97.5*	112.8*	102.8*	99.6*
	sd		10.1	7.1	10.6	5.4	6.1	6.6	6.3	7.0
Ugandans	avg	172	179.1*	111.3*	130.5*	109.9	106.7	115.9*	105.2*	96.8 <sup>+</sup>
	sd		7.3	5.0	5.3	5.5	4.9	5.6	5.3	6.5
Polish	avg	215	181.8*	112.6 <sup>c</sup> *	136.8	114.4*	108.8*	115.1*	107.9*	93.2*
	sd		8.2	4.8	5.3	5.8	5.4	5.2	8.4	5.6
Ratio modern/erectus (averaged)			0.95	1.14	0.99	1.01	0.98	0.85	0.88	0.83

<sup>b</sup> – sample size is only N=4.

<sup>c</sup> – porion-bregma vertical distance.

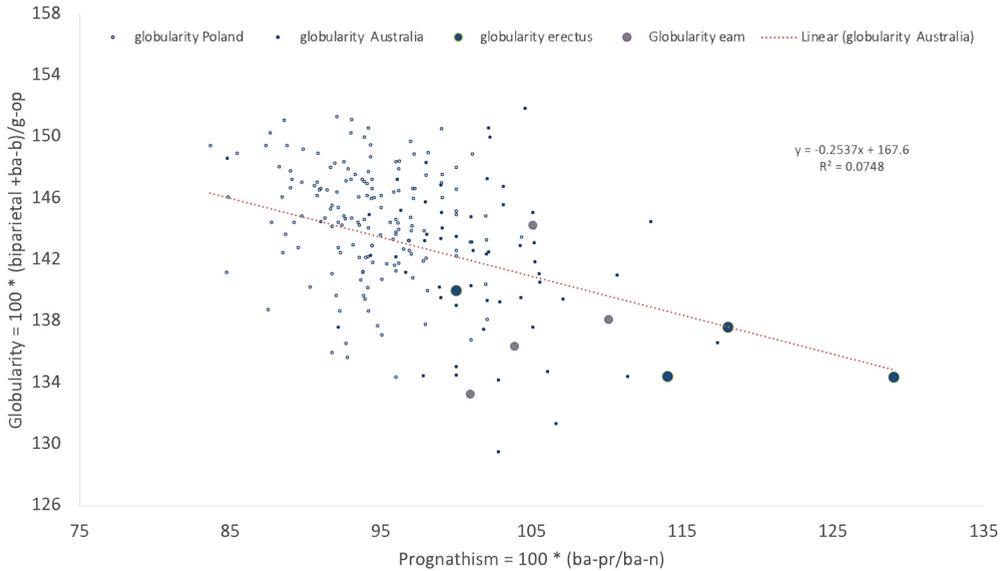
<sup>a</sup> – for *H. erectus* eu-eu is replaced by biparietal distance.

<sup>+</sup> – difference from *H. erectus* significant at  $p < 0.05$  (t-test). Note that some differences in cranial width are not significantly different between *H. erectus* and modern humans.

toid region did not develop relative to the parietals – for example as a result of a change in diet - that would yield a more globular paedomorphic form in *H. sapiens*. If this were the case, then we would expect to see a negative correlation between globularity and facial prognathism.

Figure 4 plots the relationship between globularity and facial projection. It shows quite a clear relationship with globularity being negatively correlated with prognathism. This suggests that as prognathism decreases globularity increases. Combined with the data in Figures 2 and 3 this suggests that globularity is related to the reduction of the size of the base, mastoid region and the association of this portion of the skull with the face and the apparatus of mastication. And if the face and base are reduced relative to the calvaria this would yield a more globular form. This would involve the decoupling of the ontogenetic growth trajectories of the face and the base from those of the calvaria. Such retardation of the growth trajectories asso-

ciated with the face and the base, would result in the retention of subadult shape proportions into adulthood. Such retention would result in laterally expanded parietals relative to the base and mastoid region. However, such “expansion” is not so much a result of expansion of the parietals but a reduction of growth in the base and mastoid region which increases the relative dimensions of the parietals giving the impression of expansion. However, what really seems to have happened is other parts of the skull merely did not develop as much in *H. sapiens* they did in *H. erectus*. This process would explain the differences between the Mojokerto child and adult *H. erectus* – and also the similarity of this subadult *H. erectus* fossil with adult *H. sapiens*. Of course, this does not mean that there were no selective pressures operating upon the calvaria – but our results do suggest that an important component contributing to globularity and laterally expanded parietals in modern humans was reduction in the base and mastoid region.



Globularity in *H. erectus* is calculated using po-v height that is approximately 77 % of ba-b height.

Fig. 4. Measure of the globularity and prognathism in *Homo erectus* and modern humans. Some early modern *H. sapiens* (eam) values are shown here – see Fig. 6 and the Discussion for their details. Note that the coefficient of determination of the regression line fitted to the Aboriginal Australian data ( $R^2=0.0748$ ) is significant ( $p=0.015$ ). Regression line for Polish data is similarly significant [not shown].

## Discussion

Our results suggest that during the transition from *H. erectus* to *H. sapiens* selective pressures differentially impacted the cranial base relative to the calvaria. Given the cranial base is believed to be developmentally conservative, and coupled to an early developing neural growth trajectory associated with brain growth (Lieberman, Pearson & Mowbray 2000), the changes we have observed may be related to the more lateral aspects of the base that continue to grow along with the rest of the skeleton and which are associated with mastication (Sejrsen et al. 1997). This view is supported by findings of significant association between the cranial base and facial morphology (Bhattacharya et al. 2014). Additionally, in humans growth of the brain and calvaria achieve

most of their adult size between 6 and 8 years of age whereas the face and the base appear to keep growing throughout the adolescent period of development (Bhattacharya et al. 2014; McKinnon et al. 2018; Roche and Lewis 1976; Roche 1977). These different ontogenetic trajectories may be related to the brain and parts of the neurocranium being on a neural growth trajectory, which is completed much earlier than growth of the face and skeleton, which continues beyond childhood into adolescence (Lieberman 2011, p. 31).

In Figure 5 we illustrate these different ontogenetic trajectories using a sample of Aboriginal Australians. In the lower two trend lines indicating the ontogeny of facial and mandibular growth, there is a virtually constant rate of growth from birth to adulthood, indicating the face

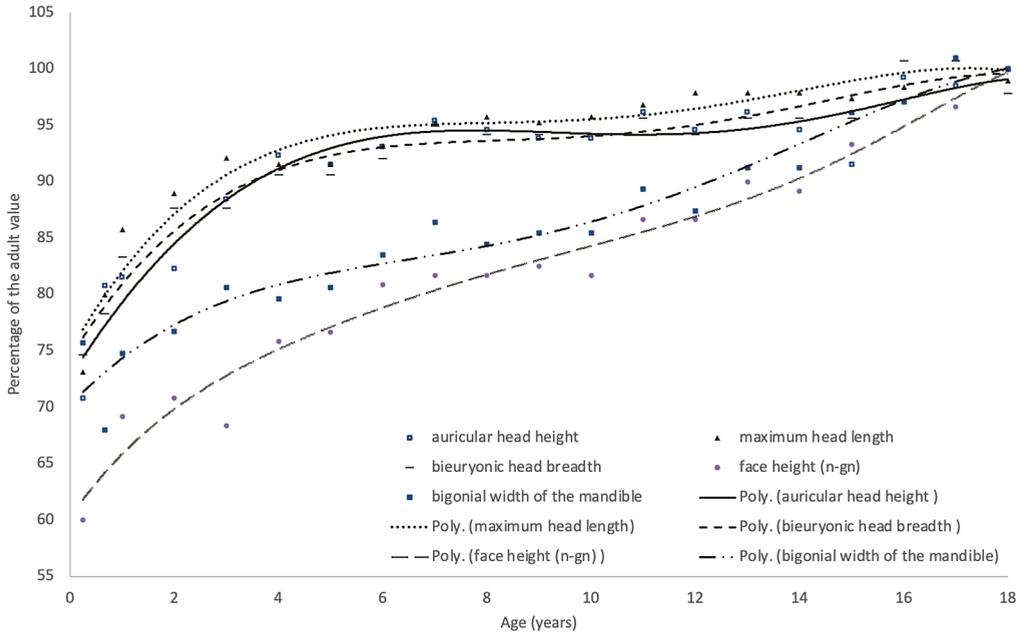


Fig. 5. Growth of calvarial dimensions and facial height and jaw width in Australian Aboriginal males. Data from (Abbie 1975)

and jaw are associated with both the early neural and later skeletal growth trajectories. The upper trend lines indicating growth of the neurocranium, on the other hand, show significant growth during early childhood, a plateau in growth after 6 years of age, and then a further period of growth during adolescence. While this concurs with the observations of Lieberman and colleagues noted above of the neurocranium being on the early neural growth trajectory, it also illustrates there is a latter period of growth of the neurocranium associated with the skeletal growth trajectory. What is crucial to note here is the lower trend lines depicting growth of the jaw and face are associated with further growth of the neurocranium during the period of puberty as indicated in the upper trend lines – that is from 14 to 18 years of age. This suggests, in contradistinction to the model of Lieberman

and colleagues, the existence of correlated growth between the jaw, the cranial base (which supports the jaw) and the neurocranium – all as part of the skeletal growth trajectory.

This suggests that the extra growth in the cranial base and the associated mastoid region that we see in *H. erectus* relative to *H. sapiens*, may in part be related to correlated growth between the jaw, the base and the neurocranium during adolescence. It also explains why the sub-adult skull shape of *H. erectus* lacks the flared mastoid region evident in adult *H. erectus*. It is possible that the transition from *H. erectus* to *H. sapiens* involved regulatory alteration of gene expression and developmental trajectories associated with the jaw – alteration that can result in phylogenesis of skull form (Parsons and Albertson 2009). In this sense, as *H. erectus* infants passed through childhood

and adolescence and into adulthood, down regulation of genes associated with growth of the jaw and associated components of the cranial base, would yield over time more globular skull shape. But not, as we have suggested, because of lateral expansion of the parietals, but because of reduced growth in the base, mastoid region, and jaw.

Worth noting in this context is that in primates, it has been observed that cranial volume is more stable under differing selective regimes than craniofacial length, suggesting that the brain and neurocranium are less malleable to selective pressures than the face (Isler et al. 2008). Taken together this evidence suggests that the face and the associated aspects of the cranial base are on different ontogenetic trajectories than the brain and calvaria, differences that may account for the results obtained in this study.

Given the face and cranial base seem to be on different growth trajectories than the neurocranium and calvaria, trajectories potentially more subject to environmentally induced phenotypic variation, it is conceivable that growth of the face and base could have slowed relative to the calvaria. This view finds support from observed alterations of the skull morphology of domesticated hominoids, where changes in lifestyle and diet relative to wild individuals result in quite pronounced differences in facial and jaw morphology (Bjork 1950). A similar approach has been proposed where the impact of dietary factors upon the ontogeny of craniofacial growth has been proposed as a possible cause of the phenotypic differences between gracile and robust Australians (Curnoe 2011). Similarly, slowing down of growth trajectories associated with the jaw, base and mastoid

region, could be related to adaptations associated with a change in diet and cultural practices associated with food preparation during the transition from *H. erectus* to *H. sapiens* or even within *H. sapiens* itself – either through increasing use of fire, technological advances facilitating greater extra-oral food processing or changes in the kinds of food consumed.

The globular shape of the skull in modern humans has been attributed to selection for unique cognitive specialisations (Neubauer et al. 2018). Such specialisations are believed to underpin evidence of cognitive and behavioural modernity in the archaeological record during the Middle to the Upper Palaeolithic in Europe around 50,000 to 40,000 years ago, as well as modern forms of language use (Benítez-Burraco and Kempe 2018; Boeckx and Benítez-Burraco 2014; Neubauer et al. 2018; Niego and Benítez-Burraco 2019; Progovac and Benítez-Burraco 2019). More specifically, it has been argued that expansion of the parietals in modern humans results from selection for the uniquely human neural hub associated with the default mode network (Neubauer et al. 2018). The default mode network is believed to be a uniquely human neural hub (Rilling et al. 2007) underpinning theory of mind (Mars et al. 2012), mental time travel (Ostby et al. 2012), the self-reflective capacities of the human ego complex (Carhart-Harris and Friston 2010; Carhart-Harris et al. 2014) as well as meta-cognition – that is the ability to not only have thoughts but also have thoughts about thoughts (Lou et al. 2017; Qiu et al. 2018). Commenting on the relationship between modern human cognition and behaviour, globularity and expansion of the parietals Neubauer and colleagues write: ‘...*parietal bulging in present-day humans has been linked to large*

shape variation in the precuneus....The precuneus is a central node of the default-mode network and an important hub of brain organization.... [therefore] precuneus expansion in *H. sapiens* is related to cognitive specializations' (Neubauer et al. 2018, p. 5).

Our results suggest an alternative to this view. If we consider the more globular shape of the Mojokerto child relative to adult *H. erectus* as illustrated in Figure 1, globularity seems to result from the retention of subadult cranial shape into adulthood. For example, the frontal lobes of the Mojokerto child are anteriorly rounded, the parietal lobes are relatively more developed than those of adult *Homo erectus* with the specimen sharing relative development of the cerebral lobes comparable with modern human adults (Balzeau et al. 2005). Given adult modern humans share these shape

characteristics to a greater degree with subadult rather than adult *H. erectus* it has been argued that *H. sapiens* calvaria shape is paedomorphic relative to *H. erectus* (Antón 1997).

A question that needs to be addressed is whether our analysis applies to fossil specimens of *H. sapiens*. In Figure 6 we present a comparison of Palaeolithic skulls attributed to *Homo sapiens* (early anatomically modern sapiens) in order to address this question. As can be seen these earlier members of *H. sapiens* did not differ significantly from *H. erectus*. The exception to this similarity is *H. sapiens* having higher cranial vault (po-v) and tending to have somewhat smaller basicranial and gnathic dimensions. These, however, were not significantly different from those of *H. erectus* because values of their z-scores are less

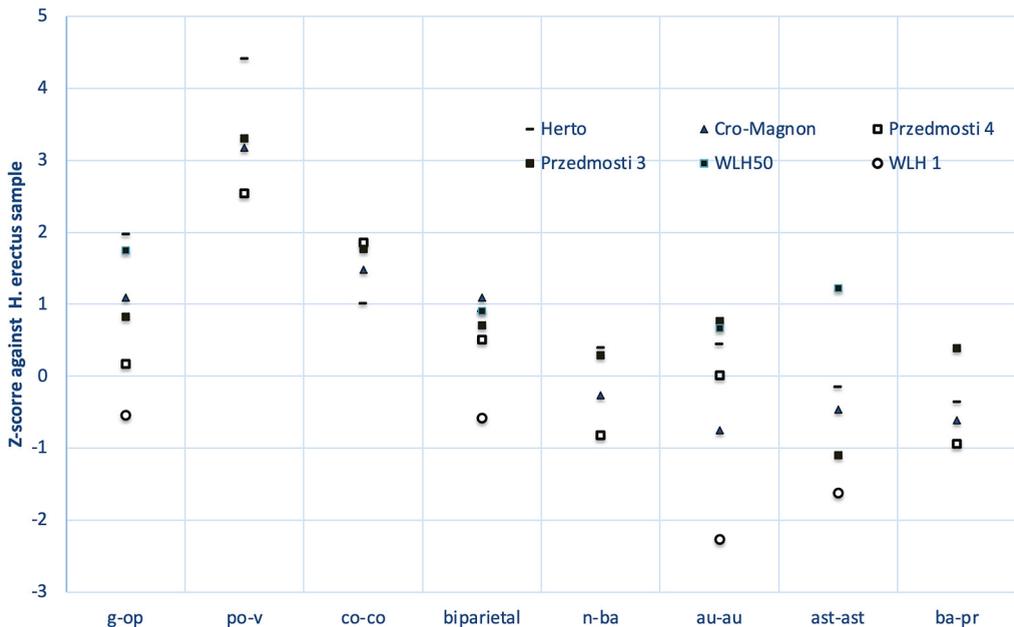


Fig. 6. Comparison of Palaeolithic *Homo sapiens* and *H. erectus* averages and standard deviations (from Table 1) Z-score is the difference between values of the cranial dimension divided by its standard deviation. Data for specimens shown are from (Lubsen and Corruccini 2011; Morant 1930; Webb 2018b; White et al. 2003).

than 3 standard deviations away from the *H. erectus* means. Additionally, values of their globularity and prognathism indices fit within the range of both Australian fossils (WLH 50 and WLH 1) and *H. erectus* (Fig. 4).

As already noted, the thesis that changes in skull shape such as increasing globularity and expansion of the parietals provide evidence of selection for unique cognitive capacity and brain architecture, is based on the apparent co-occurrence of increased evidence of behavioural and cognitive modernity in the archaeological record and changes in skull shape (Neubauer et al. 2018). However, there is no indubitable evidence as far as we are aware that the causal arrow tends in this direction – that is that changes in skull shape and putative attendant changes in neural architecture are what resulted in the production of the artefacts we find in the archaeological record. For example, it is possible that increasing technological capability in *H. erectus* such as the use of fire and extra-oral food processing, resulted in changes in diet that eventually led to the changes in skull architecture in *H. sapiens* noted by the above authors. In this sense, the cognitive specialisations proposed as unique to modern humans would have already been present in *H. erectus* – with those specialisations creating the selective regime that resulted in environmentally induced changes in the growth trajectories of the mastoid region and cranial base, yielding the paedomorphic form of modern humans. From this perspective the skull shape of modern humans was not a result of selection for unique cognitive specialisations. Instead, it was the result of earlier specialisations that resulted in a changed social, cultural and technological niche associated with improved resource exploitation and food

preparation. That is the causal arrow is operating in the opposite direction from that proposed by the above authors.

There has been a great deal of discussion in the extant paleoanthropological literature regarding reduced robusticity and prognathism, and increased globularity and gracilisation of the skull. Some researchers have argued this trend begins at the base of the hominin clade with *Ar. ramidus* some 4–5 Ma, which shows evidence of paedomorphic morphogenesis of the skull possibly via the process of self-domestication and selection for increased levels of prosociality in social and mating behaviour (Clark and Henneberg 2015; Clark and Henneberg 2017). A similar process has been proposed for the trend towards more gracile skull architecture in the *Homo* genus. For example, it has been noted that the male skull has tended to become feminised, paedomorphic and more globular as a result of selection for social tolerance and that such a process accounts for behavioural modernity (Cieri et al. 2014; Hare 2017). While we accept that this process may have been part of the adaptive suite leading to modern humans, our results also suggest a role for changes in diet and masticatory stress in the evolution of paedomorphic and globular skull form. One way of reconciling these two views, is to consider changes in diet and reduced masticatory stress resulting from extra-oral food processing, would have removed selective pressure for a more robust face and cranial base. Once this selective pressure was removed, then paedomorphic morphogenesis via the process of self-domestication and selection for pro-sociality, could have occurred. In this sense our findings do not contradict the evolution of social tolerance via self-domestication thesis – they

merely postulate an additional factor acting synergistically with the processes of social selection.

Our results also suggest that the selective forces resulting in the different forms of skull architecture evident in *H. erectus* and modern *H. sapiens* may not be related to selection on brain structure and neural organisation. A corollary of this position is that the major behavioural and cognitive adaptations we associate with modern humans were already evident in *H. erectus*. In support of this notion numerous authors have argued that many of the socio-cognitive adaptations characteristic of modern humans were already in place in *H. erectus* (Bednarik 2013, 2015; Sterelny 2012; Webb 2006). Some of the evidence for this position is based on the discovery of stone tools at approximately 800ka ago on the island of Flores in Indonesia (Brumm and Moore 2012). This island is on the eastern side of the Wallace line – a stretch of water that is presumed to necessitate the building and navigation of maritime craft in order to establish a founder population on its eastern side (Bednarik 1995; Bednarik 2011, 2013, 2015; Webb 2006). While others have argued these migrations may have resulted from passive dispersal not requiring complex forms of cognition or technological competencies (Dennell et al. 2014; Leppard 2015) the existence of stone tools and possible maritime travel – if it occurred – suggests that *H. erectus* possessed the technological competencies as well as the social structure necessary to accumulate technological knowledge and transfer it from one generation to another (Sterelny 2012).

Further evidence for putative advanced cognitive capacities in *H. erectus* has been found in China. For example, increasing evidence of intentional tool manufacture

involving enhanced planning and technical competence continues to emerge from China, indicating the development of quite complex and sophisticated lithic traditions involving the making of Acheulean-like bifacial tools (Kuman et al. 2014; Li et al. 2014; Shen et al. 2011; Wang et al. 2012; Yamei et al. 2000; Yang et al. 2017). Significantly, fMR studies have suggested Acheulean toolmaking recruits brain regions involved in planning, learning and social scaffolding associated with the default mode network (Stout et al. 2015). We noted above that researchers have argued that expansion of parietals in modern humans is associated with evolution of the default mode network (Neubauer et al. 2018). However, the fact that the making of Acheulean tools requires engagement of the default mode network suggests such abilities associated with this neural hub were already in place in *H. erectus*. Consequently, the changes in skull architecture that we see in the transition from *H. erectus* to *H. sapiens* may not be a result of selection for cognitive capacities associated with expansion of the parietal lobes.

In support of the notion that behavioural and cognitive modernity existed in *H. erectus*, it is worth noting research that suggests the up regulation of the dopaminergic system may have occurred in this species (DeLouize et al. 2017). Dopamine is believed to be involved in cognitive skills such as human language, motor planning, working memory, cognitive flexibility and abstract reasoning – abilities that are believed to have facilitated endurance running, hunting and the demographic expansion of early hominins (Previc 1999; Previc 2009). Given the ability of *H. erectus* to make Acheulean tools and the possibility of maritime craft manufacture and

navigation, the role of dopamine in novelty-seeking, exploratory behaviour and tool manufacture, suggests the dopaminergic system may have been central to the evolution of *H. erectus* (DeLouize et al. 2017). And such up regulation of the dopaminergic system – a system that is central to the uniqueness of modern human populations – could be selected for in the absence of the emergence of more globular skull shape. Additionally, such changes in neurochemical profiles could occur in the absence of brain size increases. Interestingly, there seems to be greater overlap of brain size distributions between *H. erectus* and some modern human populations than occurs between specific modern populations themselves – which indicates brain size difference between these putative species are negligent and unrelated to differing cognitive capacities (Clark and Henneberg, this volume, pp. 405–429).

Other evidence that behavioural and cognitive modernity is unrelated to globularity and cranial gracilisation is to be found in the Australian fossil record. Australian fossil populations are renowned for possessing a wide range of variation from gracile to extremely robust (Curnoe 2011; Durband 2009; Thorne 1976). Yet these Pleistocene populations were nevertheless capable of complex ritual and symbolic culture such as burial and cremation (Bowler et al. 1970; Hiatt 1969). For example, in Figure 2, we have plotted two Australian fossils from the Willandra Lakes region, WLH 1 and WLH 50. WLH 50 has been dated to between 12.2 and 32.8k years (Grün et al. 2011). WLH1 is believed to be approximately 40k years old, with evidence of occupation of the region between 50–46k years (Bowler et al. 2003). Significantly, the site contains the oldest evidence in the world of a buri-

al with ochre dated at approximately 30k years (Bowler and Thorne 1976; Bowler et al. 2003). Cross cultural ethnographic analysis suggests that ochre is symbolically associated with blood and ritual power – and particularly with fertility rites and the blood of hunted animals (Knight 1995, 2009; Knight et al. 2008; Power 2004). Some researchers have argued the earliest evidence for the use of red ochre in a symbolic context can be dated between 500 and 300k years (Watts et al. 2016). Whether these claims are valid or not is yet to be decided – but the presence of an ochre burial in Pleistocene Australia does suggest the deep antiquity of such symbolic customs in the region.

The implications of these findings are that Pleistocene Australians possessed symbolic capacities at a quite early date. What is worth noting is that Pleistocene Australians seem to represent a range of variation that overlaps with modern humans and *H. erectus*. This can be seen in Figure 2 where WLH 1 sits firmly within the modern human sample – while WLH 50 clusters with two of the larger *H. erectus* skulls. Significantly, it has been suggested that measures of globularity be used as a means of establishing taxonomic inclusion into *Homo sapiens* – with the caveat that such inclusion does not apply to WLH 50 (Lieberman et al. 2002, 1138). This assertion is based on the assumption that WLH 50 sits outside of the range of variation for *Homo sapiens* due to pathology of the skull. This view has been challenged more recently, with the robustness of WLH 50 being considered an allometric result of size increase akin to that evident in contemporary Indigenous Australians, and consequently not pathological but part of the variation evident in *Homo sapiens* (Curnoe and Green 2013). These observations suggest

a broader conception of cognitive modernity – one which includes evidence of more robust humans found in the Australian fossil record.

The implication of the above discussion is that Pleistocene Australians possessed a complex symbolic and ritual culture despite being comprised of populations in which numerous individuals lacked globular and gracile skull morphology. Additionally, such hominins were able to navigate the oceans from South East Asia to Australia as early as 65ka (Clarkson et al. 2017) – with some more speculative dates of shell middens and fire suggesting a much earlier arrival of 120k years (Bowler et al. 2018). The picture that emerges from this evidence is seafaring, technologically advanced hominins with a complex ritual life and symbolic culture. And the presence of robust and nonglobular skull morphology in these populations of fossil Australians (Curnoe 2011; Durband 2009; Thorne 1976) seems to have presented no real obstacle for such achievements (Webb 2006).

In this essay we presented data suggesting there has been greater evolutionary alteration of the cranial base and the mastoid region than the calvaria in the transition from *H. erectus* to *H. sapiens*. This may have resulted from greater selective pressure on the parts of the jaw and skull associated with mastication. Additionally, such reduction in the cranial base and mastoid region results in a morphology that gives the *impression* of laterally expanded parietals – when in fact what seems to have occurred is the cranial base and mastoid region grow less relative to the parietals in *H. sapiens*. This reduction of growth in the cranial base and mastoid region seems to have evolved by paedomorphic morphogene-

sis of the skull. Evidence suggests such reduction may be related to changes in diet and food preparation. Our findings, however, do not necessarily contradict the social tolerance thesis of paedomorphic skull evolution through the process of self-domestication. In fact, changes in diet and food preparation may have co-evolved synergistically with changes in social structure and attendant technological innovation.

### Authors' contribution

GC was the main author and primary researcher. Both authors collaborated on the data collection and analysis. MH assisted with the statistical analysis.

### Conflict of interest

The authors declare no conflict of interests.

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### References

- Abbie A. 1975. Studies in Physical Anthropology, vol.II. Australian Institute of Aboriginal Studies, Canberra.
- Antón SC. 1997. Developmental age and taxonomic affinity of the Mojokerto child, Java, Indonesia', *Am J Phys Anthropol* 102(4):497–514.
- Balzeau A, Grimaud-Hervé D, Jacob T. 2005. Internal cranial features of the Mojokerto child fossil (East Java, Indonesia). *J Hum Evol* 48(6):535–53.

- Bednarik RG. 1995. Concept-Mediated Marking in the Lower Palaeolithic. *Curr Anthropol* 36(4):605–34.
- Bednarik RG. 2011. *The Human Condition*. New York: Springer New York.
- Bednarik RG. 2013. *Creating the Human Past: An Epistemology of Pleistocene Archaeology*. Archaeopress.
- Bednarik RG. 2015. *The First Mariners*. Bentham Science Publishers.
- Benítez-Burraco A, Kempe V. 2018. The Emergence of Modern Languages: Has Human Self-Domestication Optimized Language Transmission?. *Frontiers in Psychology* 9(551) April-17.
- Bhattacharya A, Bhatia A, Patel D, Mehta N, Parekh H, Trivedi R. 2014. Evaluation of relationship between cranial base angle and maxillofacial morphology in Indian population: A cephalometric study. *J Orthodon Sci* 3(3):74–80.
- Bjork A. 1950. Some biological aspects of prognathism and occlusion of the teeth. *Acta Odontol Scand* 9(1):1–40.
- Boeckx C, Benítez-Burraco A. 2014. The shape of the human language-ready brain. *Fron Psychol* 5(282) 2014-April-04.
- Bolk L. 1909. On the position and displacement of the foramen magnum in the primates. *Verh Akad Wet* 12:362–377.
- Bowler JM, Johnston H, Olley JM, Prescott JR, Roberts RG, Shawcross W, Spooner NA. 2003. New ages for human occupation and climatic change at Lake Mungo, Australia. *Nature* 421(6925):837–40.
- Bowler JM, Jones R, Allen H, Thorne AG. 1970. Pleistocene human remains from Australia: a living site and human cremation from Lake Mungo, Western New South Wales. *World Archaeology* 2(1):39–60.
- Bowler JM, Price DM, Sherwood J, Carey SP. 2018. The Moyjil Site, South-West Victoria, Australia: Fire And Environment In A 120,000-Year Coastal Midden —Nature Or People?. *The Royal Society of Victoria* 130:71–93.
- Bowler JM, Thorne AG. 1976. Human Remains from Lake Mungo. In: RL Kirk and AG Thorne (editors). *The Origin of the Australians*. Australian Institute of Aboriginal Studies, Canberra, Australia, pp. 127–38.
- Carhart-Harris RL, Friston KJ. 2010. The default-mode, ego-functions and free-energy: a neurobiological account of Freudian ideas. *Brain* 133(4):1265–83.
- Carhart-Harris RL, Leech R, Hellyer PJ, Shanahan M, Feilding A, Tagliazucchi E, Chialvo DR, Nutt D. 2014. The entropic brain: a theory of conscious states informed by neuroimaging research with psychedelic drugs. *Front Hum Neurosci*. doi.org/10.3389/fnhum.2014.00020.
- Cieri RL, Churchill SE, Franciscus, RG, Tan J, Hare B. 2014. Craniofacial Feminization, Social Tolerance, and the Origins of Behavioral Modernity. *Curr Anthropol* 55(4):419–43.
- Clark G, Henneberg M. 2015. The life history of *Ardipithecus ramidus*: a heterochronic model of sexual and social maturation. *Anthropol Rev* 78(2):109–32.
- Clark G, Henneberg M. 2017. *Ardipithecus ramidus* and the evolution of language and singing: An early origin for hominin vocal capability. *HOMO* 68(2):101–21.
- Clarkson C, Jacobs Z, Marwick B, Fullagar R, Wallis L, Smith M et al. 2017, Human occupation of northern Australia by 65,000 years ago. *Nature* 547:306–10.
- Curnoe D. 2011. A 150-year conundrum: cranial robusticity and its bearing on the origin of Aboriginal Australians. *Int J Evol Biol* 2011:632484.
- Curnoe D, Green H. 2013. Vault thickness in two Pleistocene Australian crania. *J Archaeol Sci* 40(2):1310–8.
- Dean MC, Wood BA. 1984. Phylogeny, Neoteny and Growth of the Cranial Base in Hominoids. *Folia Primatologica* 43(2–3)157–80.
- DeLouize AM, Coolidge FL, Wynn T. 2017. Dopaminergic systems expansion and the advent of *Homo erectus*. *Quaternary International* 427:245–52.
- Durband AC. 2009. Southeast Asian and Australian paleoanthropology: a review of the last century. *J Anthropol Sci* 87:7–31.

- Fox CL, Martín AG, Civit SV. 1996. Cranial variation in the Iberian Peninsula and the Balearic Islands: Inferences about the history of the population. *Am J Phys Anthropol* 99(3):413–28.
- Górny S. 1957. *Crania africana: Uganda*. Wrocław: PWN.
- Gould SJ. 1977. *Ontogeny and Phylogeny*. Belknap Press of Harvard University Press.
- Grün R, Spooner N, Magee J, Thorne A, Simpson J, Yan G, Mortimer G. 2011. Stratigraphy and chronology of the WLH 50 human remains, Willandra Lakes World Heritage Area, Australia. *J Hum Evol* 60(5):597–604.
- Hare B. 2017. Survival of the Friendliest: *Homo sapiens* Evolved via Selection for Prosociality. *Annu Rev Psychol* 68:155–86.
- Hiatt B. 1969. Cremation in Aboriginal Australia. *Mankind* 7(2):104–19.
- Hylander WL. 2013. Functional links between canine height and jaw gape in catarrhines with special reference to early hominins. *Am J Phys Anthropol* 150(2):247–59.
- Isler K, Kirk CE, Miller JM, Albrecht GA, Gelvin BR, Martin RD. 2008. Endocranial volumes of primate species: scaling analyses using a comprehensive and reliable data set. *J Hum Evol* 55(6):967–78.
- Knight C. 1995. *Blood Relations: Menstruation and the Origins of Culture*. New Haven and London: Yale University Press.
- Knight C. 2009. *Early Human Kinship was Matrilineal*. New Jersey: Blackwell Publishing Ltd., Hoboken, pp. 61–82.
- Knight C, Power C, Watts I, Power C. 2008. The Human Symbolic Revolution: A Darwinian Account. *Cambridge Archaeological Journal* 5(1):75–114.
- Kuman K, Li C, Li H. 2014. Large cutting tools in the Danjiangkou Reservoir Region, central China. *J Hum Evol* 76:129–53.
- Li H, Li C, Kuman K. 2014. Rethinking the “Acheulean” in East Asia: Evidence from recent investigations in the Danjiangkou Reservoir Region, central China. *Quaternary International* 347:163–75.
- Lieberman D. 2011. *The Evolution of the Human Head*. Harvard University Press.
- Lieberman D, McBratney BM, Krovitz G. 2002. The evolution and development of cranial form in *Homo sapiens*. *Proc Natl Acad Sci U S A* 99(3):1134–9.
- Lieberman D, Pearson OM, Mowbray KM. 2000. Basicranial influence on overall cranial shape. *J Hum Evol* 38(2):291–315.
- Lou HC, Changeux JP, Rosenstand A. 2017. Towards a cognitive neuroscience of self-awareness. *Neurosci Biobehav Rev* 83:765–73.
- Lovejoy CO. 2009. Reexamining Human Origins in Light of *Ardipithecus ramidus*. *Science* 326(5949):71–78, 74e71–74e78.
- Lubsen K, Corruccini RS. 2011. Morphometric Analysis of the Herto Cranium (BOU-VP-16/1): Where Does It Fit?. *J Contemp Anthropol* 2:1–16.
- Mars RB, Neubert F-X, Noonan MP, Sallet J, Toni I, Rushworth MFS. 2012. On the relationship between the “default mode network” and the “social brain”. *Fron Hum Neurosci* 6:189.
- McKinnon MR, Simpson EK, Henneberg M. 2018. Growth Patterns and Individual Variation in Mid-sagittal Facial Soft Tissue Depth from Childhood to Adulthood. *J Foren Sci* 63(6):1641–51.
- Milicerowa H. 1955. *Crania Australica*. Wrocław: PWN.
- Morant GM. 1930. Studies of Paleolithic Man. *Annals of Eugenics* 4(1–2):109–214.
- Neubauer S, Hublin J-J, Gunz P. 2018. The evolution of modern human brain shape. *Science Advances* 4(1):eaao5961.
- Niego A, Benítez-Burraco A. 2019. Williams Syndrome, Human Self-Domestication, and Language Evolution. *Fron Psychol* 10(521).
- Ostby Y, Walhovd KB, Tamnes CK, Grydeland H, Westlye LT, Fjell AM. 2012. Mental time travel and default-mode network functional connectivity in the developing brain. *PNAS* 109(42):16800–4.
- Parsons KJ, Albertson RC. 2009. Roles for *Bmp4* and *CaM1* in Shaping the Jaw:

- Evo-Devo and Beyond. *Annu Rev Genet* 43(1):369–88.
- Power C. 2004. Women in Prehistoric Rock Art. In: G Berghaus (editor). *New Perspectives on Prehistoric Art*. Praeger, Westport, CT/London, pp. 75–103.
- Previc FH. 1999. Dopamine and the Origins of Human Intelligence. *Brain Cogn* 41(3):299–350.
- Previc FH. 2009. *The Dopaminergic Mind in Human Evolution and History*. Cambridge University Press.
- Progovac L, Benítez-Burraco A. 2019. From Physical Aggression to Verbal Behavior: Language Evolution and Self-Domestication Feedback Loop. *Front Psychol* 10(2807) 2019-December-18.
- Qiu L, Su J, Ni Y, Bai Y, Zhang X, Li X, Wan X. 2018. The neural system of metacognition accompanying decision-making in the prefrontal cortex. *PLOS Biology* 26(4):e2004037-e2004037.
- Rightmire GP. 2013. Homo erectus and Middle Pleistocene hominins: brain size, skull form, and species recognition. *J Hum Evol* 65(3):223–52.
- Rilling JK, Barks SK, Parr LA, Preuss TM, Faber TL, Pagnoni G, Bremner JD, Votaw JR. 2007. A comparison of resting-state brain activity in humans and chimpanzees. *PNAS* 104(43):17146–51.
- Roche AF, Lewis AB. 1976. Late Growth Changes in the Cranial Base. In: JF Bosma (editor). *Symposium on Development of the Basicranium*, University of Michigan, Michigan, USA.
- Roche AF, Lewis AB, Wainer H, McCartin R. 1977. Late Elongation of the Cranial Base. *J Dental Res* 56(7):802–8.
- Russo GA, Kirk EC. 2017. Another look at the foramen magnum in bipedal mammals. *J Hum Evol* 105:24–40.
- Sejrsen B, Jakobsen J, Skovgaard LT, Kjaer I. 1997. Growth in the external cranial base evaluated on human dry skulls, using nerve canal openings as references. *Acta Odontol Scand* 55(6):356–64.
- Shen C, Gao X, Wei Q. 2011. The Earliest Hominin Occupations in the Nihewan Basin of Northern China: Recent Progress in Field Investigations. In: CJ Norton, and DR Braun (editors). *Asian Paleoanthropology: From Africa to China and Beyond*. Dordrecht Springer Netherlands, pp. 169–180.
- Sterelny K. 2012. *The Evolved Apprentice*, MIT Press.
- Stout D, Hecht E, Khreisheh N, Bradley B, Chaminade T. 2015. Cognitive Demands of Lower Paleolithic Toolmaking. *PLOS ONE* 10(4):e0121804.
- Suwa G, Asfaw B, Kono RT, Kubo D, Lovejoy CO, White TD. 2009. The Ardipithecus ramidus Skull and Its Implications for Hominid Origins. *Science* 326(5949):68–68, 68e61–68e67.
- Thorne AG. 1976. Morphological contrasts in Pleistocene Australians. In: RL Kirk, and AG Thorn (editors). *The Origin of the Australians*, Australian Institute of Aboriginal Studies. Canberra, Australia, pp. 95–112.
- Wang W, Lycett SJ, von Cramon-Taubadel N, Jin JJH, Bae CJ. 2012. Comparison of Handaxes from Bose Basin (China) and the Western Acheulean Indicates Convergence of Form, Not Cognitive Differences. *PLOS ONE* 7(4):e35804.
- Watts I, Chazan M, Wilkins J. 2016. Early Evidence for Brilliant Ritualized Display: Specularite Use in the Northern Cape (South Africa) between 500 and 300 Ka. *Curr Anthropol* 57(3):287–310.
- Webb S. 2006. *The First Boat People*. Cambridge University Press.
- Webb S. 2018a. Chapter 10 – Willandra Lakes Skeletal Collection: A Photographic and Descriptive Catalogue. In: S Webb (editor). *Made in Africa*. Academic Press, pp. 301–400.
- Webb S. 2018b. *Made in Africa: Hominin Explorations and the Australian Skeletal Evidence*, Elsevier Science.
- Weidenreich F. 1943. *The Skull of Sinanthropus Pekinensis: A Comparative Study on a Primitive Hominid Skull*, Geological Survey of China.
- White TD, Asfaw B, DeGusta D, Gilbert H, Richards GD, Suwa G, Clark Howell F. 2003. Pleistocene Homo sapiens

- from Middle Awash, Ethiopia. *Nature* 423(6941):742–7.
- Wokroj F. 1953. Wczesnośredniowieczne czaszki polskie z Ostrowa Lednickiego. *Materialy i Prace Antropologiczne*, vol. 1.
- Yamei H, Potts R, Baoyin Y, Zhengtang G, Deino A, Wei W, Clark J, Guangmao X, Weiwen H. 2000. Mid-Pleistocene Acheulean-like Stone Technology of the Bose Basin, South China. *Science* 287(5458):1622.
- Yang S-X, Petraglia MD, Hou Y-M, Yue J-P, Deng C-L, Zhu R-X. 2017. The lithic assemblages of Donggutuo, Nihewan basin: Knapping skills of Early Pleistocene hominins in North China. *PLOS ONE* 12(9):e0185101.