



The life history of *Ardipithecus ramidus*: a heterochronic model of sexual and social maturation

Gary Clark, Maciej Henneberg

Biological Anthropology and Comparative Anatomy Unit University of Adelaide Medical
School, Australia

ABSTRACT: In this paper we analyse the ontogeny of craniofacial growth in *Ardipithecus ramidus* in the context of its possible social and environmental determinants. We sought to test the hypothesis that this form of early hominin evolved a specific adult craniofacial morphology via heterochronic dissociation of growth trajectories. We suggest the lack of sexual dimorphism in craniofacial morphology provides evidence for a suite of adult behavioral adaptations, and consequently an ontogeny, unlike any other species of extant ape. The lack of sexually dimorphic craniofacial morphology suggests *A. ramidus* males adopted reproductive strategies that did not require male on male conflict. Male investment in the maternal metabolic budget and/or paternal investment in offspring may have been reproductive strategies adopted by males. Such strategies would account for the absence of innate morphological armoury in males. Consequently, *A. ramidus* would have most likely had sub-adult periods of socialisation unlike that of any extant ape. We also argue that *A. ramidus* and chimpanzee craniofacial morphology are apomorphic, each representing a derived condition relative to that of the common ancestor, with *A. ramidus* developing its orthognathic condition via pedomorphosis, and chimpanzees evolving increased prognathism via peramorphosis. In contrast we suggest cranial volume and life history trajectories may be synapomorphic traits that both species inherited and retained from a putative common ancestral condition. Our analysis also provides support for the hypothesis that an intensification of maternal care was central to the process of hominization.

KEY WORDS: facial growth, alloparenting, pedomorphosis, peramorphosis, cooperation, sexual dimorphism

Introduction

Debate over the early stages of human evolution has deepened in recent years with the discovery of two putative fossil hominins, classified as members of the

Ardipithecus genus. *A. ramidus* is thought to have inhabited a forest or woodland niche in Ethiopia approximately 4.5 Ma (Lovejoy 2009). *A. kadabba* inhabited the same region from 5.8 to 5.2 Ma and is believed to be ancestral to *A. ramidus*

(Haile-Selassie and Woldegabriel 2009). Objections have been raised as to whether *A. ramidus* is in actual fact a hominin (Sarmiento 2010; Harrison 2010). In response to these objections it was argued that significant behavioral and anatomical affinities between *A. ramidus* and other hominins (Sayers, Raghanti and Lovejoy 2012), as well as very detailed affinities in the anatomy of the cranial base (Kimbel et al. 2014), confirm its hominin status. In this paper we will proceed under the assumption *A. ramidus* is a hominin, an assumption that may be validated or disproven by future research.

The published analysis of *A. ramidus* indicates an absence of male canine armoury (Suwa et al. 2009b). This conclusion was reached based on a sample of canines from at least fourteen individuals, a sample larger enough for researchers to conclude the presence of males and females. Consequently a lack of canine sexual dimorphism was inferred from the absence of a bimodal distribution. Although reconstruction of the skull morphology was based on one individual, it is safe to infer from the monomorphic canine morphology the lack of a C/P3 complex and consequently an attendant reduction in facial prognathism as species specific traits in both males and females.

Consequently the absence of cranio-facial and postcranial sexual dimorphism has led to the conclusion that the species evolved male reproductive strategies unlike those evident in any other species of extant great ape (Lovejoy 2009). It has been common in the literature on human evolution to use chimpanzee social and mating behaviour as a model for reconstructing the social and mating systems of early hominins (Wrangham and Peterson 1997; Stanford 2001; Stanford

2012). However, the lack of sexual dimorphism and male canine armoury evident in *A. ramidus*, as well as numerous anatomical affinities with Miocene apes, has led researchers to question models of early hominin social behaviour based on extrapolations from chimpanzees (Sayers, Raghanti and Lovejoy 2012), which are most likely derived in relation to the common ancestral condition. Since hominins and chimpanzees both seem to be derived, it has been argued we need to look more carefully at the Miocene ape radiation in order to gain insight into the common ancestral condition from which both lineages evolved (Lovejoy 2014). *A. ramidus* consequently enables a more nuanced consideration of different degrees of differentiation from a Miocene great ape *bauplan* or body plan evident in the chimpanzee and hominin lineages (Lovejoy 2014). In this sense phylogenetic diversity may be explained in terms of differing degrees of differentiation or departure from embryonic form (Baer 1827), a situation in which differing ontogenies assume significant importance in accounting for phylogenetic diversity.

The implication is that in order to develop adult traits such as reduced canines and minimal craniofacial sexual dimorphism, *A. ramidus* must have had an ontogeny that distinguishes it quite clearly from that of chimpanzees. Given that selection does not act on adult characters, but on developmental processes themselves (West-Eberhard 2003), the *A. ramidus* fossils provide evidence for a unique ontogeny at the base of the hominin clade unlike that of any extant primate (Lovejoy 2014). In this sense the fossils contribute a great deal to our understanding of the evolution of early hominin social behaviour and life history.

The ontogeny of primates and hominins was studied quite extensively in the first half of the twentieth century (Bolk 1929; Schultz 1924; Schultz 1936; Portmann 1945). In his *Ontogeny and Phylogeny* (1977) Gould built on this early work in his heterochronic model of human evolution, suggesting that the retention of juvenile characters into sexual maturity was fundamental to the process of hominization (Gould 1977). According to Gould, heterochronic dissociation of developmental trajectories is an important evolutionary mechanism whereby the rates of growth in different ontogenetic fields can be altered in relation to one another. In arguing that taxonomic diversity results from altering an ancestral *bauplan* or body plan, Gould sought to resurrect older models of evolutionary change based on alterations of development timing, an approach that underpins current research in evolutionary developmental biology (Hall 1999; Raff 1996; Coen 2000; West-Eberhard 2003; Kirschner and Gerhart 2005; Laubichler and Maienschein 2007; Carroll 2006; Gould 2002). Gould's model has also been applied in a number of studies of fossil species and of human and primate evolution (Groves 1991; Shea 1983; Alba et al. 2001; Bjorklund and Pellegrini 2002; Konner 2010).

In *Ontogeny and Phylogeny* Gould discussed heterochrony in relation to the craniofacial form of *Australopithecines* and *Homo sapiens*. What is interesting to note is that the orthognathic skull morphology of *A. ramidus* suggests this species may have evolved via heterochronic dissociation of craniofacial growth trajectories from those of sexual maturation. *A. ramidus* therefore provides further support for Gould's original proposition. Consequently the morphology of *A. ramidus*

suggests the dissociation of craniofacial growth from other ontogenetic trajectories that Gould analysed in the *Australopithecines* may have much more ancient origins than he originally assumed.

Over the last fifty years comparative studies of primate morphology have enhanced our understanding of the ontogeny of extinct hominins (Smith and Tompkins 1995; Mann 1975; Bromage 1985). Notably Smith and Tompkins (1995) argued that in hominoids major life history trajectories evolved in tandem with increases in brain size. A significant body of literature has consequently built on these studies, resulting in an increasingly refined understanding of the life history and ontogeny of fossil hominins (Minugh-Purvis and McNamara 2002; Thompson, Krovitz and Nelson 2003; Hawkes et al. 2006; Robson and Wood 2008; Zollikofer and Ponce de León 2010). In terms of craniofacial variation amongst primates, it has been suggested that males and females share juvenile and sub-adult growth trajectories, but diverge significantly during the period of sexual maturation. Consequently, sex-based differences in ontogeny associated with reproductive biology are thought to account for sexual dimorphism in adult craniofacial form (O'Higgins and Jones 1998). It is likely that the lack of craniofacial sexual dimorphism evident in *A. ramidus* may be a result of changes in ontogeny associated with sexual maturation, social behaviour and reproductive strategies – strategies unlike those evident in any other extant nonhuman species of the hominoid clade.

In order to test the hypothesis that craniofacial growth was decoupled from other ontogenetic trajectories in *A. ramidus*, we compared both its putative age of sexual maturation, and its skull mor-

phology, with a number of other primate species. To establish whether adult skull morphology of *A. ramidus* is paedomorphic, we compared it with infant, juvenile and adult specimens of other primate species. If *A. ramidus* did achieve a paedomorphic form via heterochronic dissociation of growth trajectories, then the species would show evidence of retention of infant or juvenile dimensions into adulthood and the period of sexual maturity.

It should be noted there is an inherent difficulty in undertaking such an analysis for we are comparing infant and juvenile chimpanzees with adult dimensions of *A. ramidus*. This may seem to contradict our previous discussion of the problematic nature of the chimpanzee referential model. Since we lack not only juvenile and adult fossils of the last common ancestor, but also sufficient juvenile fossils of Miocene apes, the use of juvenile and infant chimpanzees is the only option open to us. Further, our approach does find support in the observation that ontogenetic craniofacial shape change is stronger in *Pan* than in *Homo* (Williams and Sutherland 2002, 436) and that the striking resemblance between juvenile pongids and adult humans is obliterated during pongid ontogeny by strong negative allometry of the brain and positive allometry of the jaws (Gould 1977: 353). While we acknowledge humans and chimpanzees do differ in the earliest stages of embryogenesis (Schaefer et al. 2004) those differences become far more pronounced throughout ontogeny. Consequently, the shape dimensions of infants and juveniles of different primates are more similar to each other than are their respective adult forms, which diverge to different degrees from the embryonic stage of develop-

ment (Baer 1827). In this sense we are not testing the hypothesis that *A. ramidus* represents a paedomorphic alteration of chimpanzee craniofacial ontogeny – or that early hominins evolved via alteration of a common ancestral ontogeny that was equivalent to that of chimpanzees. Infant chimpanzees, however, do give us an indication of what the infant craniofacial *bauplan* of the last common ancestor may have looked like, which we can state categorically lacked the prognathic and sexually dimorphic craniofacial morphology of adult great apes. Our objective is to test the hypothesis that craniofacial growth related to shape dimensions in *A. ramidus* departs less from a putative ancestral infant condition than does that of chimpanzees. The best proxies we have for inferring such a condition, in the absence of fossil evidence, are infant and juvenile chimpanzees. However, like many other issues in palaeoanthropology, a more refined and robust understanding of heterochrony in early hominins awaits further fossil discoveries – particularly of sub-adult specimens.

Materials and methods

We used data from the literature (Smith and Tompkins 1995; Ross 1988; Smuts et al. 1987; Kappeler et al. 2003) on correlations between endocranial volume and life history events in order to predict age of M1 eruption and sexual maturation of *A. ramidus*. We also obtained measurements of upper facial projection and subnasal-alveolar projection on a sample of infant, juvenile and adult chimpanzees from CT scans made available on line by the Kyoto University Digital Museum (<http://dmm.pri.kyotou.ac.jp/dmm/WebGallery/index.html>). These were compared with measurements of

facial projection in *A. ramidus* based on published data, as well as our own measurements of dimensions taken from the published CT scan of the skull (Suwa et al. 2009, SOM).

We used ratios similar to those provided by Suwa and colleagues (Suwa et al. 2009a) in their comparison of craniofacial projection in *A. ramidus* and great apes. However, as they were not concerned with an ontogenic analysis in that study, we had to change the landmarks slightly to account for the posterior migration of porion throughout ontogeny as the cranial base opens up in extant apes. Suwa and colleagues measured upper facial projection by calculating distances from porion to landmarks in the facial region. In order to overcome the fact that porion migrates backwards during ontogeny in great apes we calculated distances from opisthocranium to various landmarks in the facial region. These ratios were then compared with measurements of the skull of *A. ramidus* (landmarks in Fig. 3).

In order to assess the ontogeny of facial projection we measured the skulls of 4 infants, 4 juveniles and 19 adult chimpanzees of both sexes. These measurements were used to calculate facial projection by determining the length of nasion to prosthion and nasal aperture point to prosthion in relation to the entire length of the skull. The data published with the CT scan of the *A. ramidus* skull included a measurement of 162.5 mm for direct linear distance from prosthion to opisthocranium (Suwa et al., 2009 SOM). This enabled us to accurately scale our own measurements of the CT scan. We projected vertically onto the Frankfurt horizontal line prosthion, nasal aperture point, nasion and opisthocranium. This allowed all measurements to be

taken at a line being a cross-section of the Frankfurt horizontal plane with the midsagittal plane (Fig. 3). Distances between projected points were prosthion to nasal aperture point 18mm; nasion to prosthion 29mm; nasion to opisthocranium 128mm; prosthion to opisthocranium 158mm. This method of measuring the shape of the skull of different ages allowed us to compare relative projection of the face independent of differences in size.

We also obtained data from the literature (Harrison 1986; Suwa et al. 2009a; Moyà-Solà et al. 2009) in order to determine the position of the zygomatic root in infants, juveniles and adults for a number of extant primate species, as well as two Miocene apes *Anoiapithecus brevirostris* and *Oreopithecus bambolii*. These data indicated a specific ontogenetic trajectory in which the root of the zygomatic bone migrates backwards in relation to the maxillary dentition. We compared the position of the zygomatic root in *A. ramidus* with this sample of primate species in order to assist in the reconstruction of the ontogeny of the species.

Ontogeny of craniofacial growth and sexual maturation in *Ardipithecines*

Life history and heterochrony

A. ramidus has a reconstructed cranial volume similar to that of chimpanzees (Suwa et al., 2009a). Given that cranial volume gives some indication of brain size, and that across primate species, significant correlations exist between brain size and other life history parameters

(Smith and Tompkins 1995), cranial volume may enable us to tentatively reconstruct the ontogeny of various life history trajectories in *A. ramidus*.

Smith and Tompkins have presented data demonstrating that in hominoids the 'general rate of growth and aging evolved in parallel with brain size' (Smith and Tompkins 1995: 257). While

the correlation between various other life history variables has been questioned, the correlation between brain size and maturational rates is still considered to be robust (Deanner et. al. 2003). In this sense the similarity between *A. ramidus* and chimpanzee brain size would indicate similar rates of maturation.

Table 1. Brain weight, M1 eruption and age of first breeding for six primate families (data from Smith and Tompkins 1995; Ross 1988; Smuts et al. 1987; Kappeler et al. 2003; Lathouwers and Elsacker 2005; Suwa et al. 2009a; Strauss and Schon 1960)

Family	Genus	Species	Brain Weight	Eruption of M1	First breeding in months
Lemuridae	Lemur	catta	25.6	0.33	30.0
	Lemur	fulvus	25.2	0.50	27.8
	Lemur	macaco	25.6	0.50	
	Varecia	variegatus	34.2	0.50	23.5
	Cheirogaleus	medius	2.9	0.12	
Indriidae	Propithecus	variegatus	27.5	0.33	
Callitrichidae	Callithrix	jacchus	7.9	0.31	17.0
	Saguimus	fuscicollis	9.3	0.37	24.1
	Saguimus	nigricollis	8.9	0.31	
Cebidae	Cebus	albifrons	82.0	1.06	
	Cebus	apella	71.0	1.15	42.0
	Saimiri	sciureus	24.4	0.43	
	Aotus	trivigratus	18.2	0.36	
Cercopithecidae	Cercopithecus	aethiops	59.8	0.84	47.7
	Macaca	fascicularis	109.1	1.34	46.3
	Macaca	mulatta	95.1	1.36	43.3
	Macaca	nemestrina	106	1.37	47.3
	Papio	cynocephalus	175.1	1.54	
Hominidae	Pan	troglydotes	389.0	3.30	138.0
	Pan	paniscus	350.0	3.00	130.0
	Gorilla	gorilla	457.0	3.50	
	Pongo	pygmaeus	302.0	3.50	118.2
	Ardipithecus	ramidus	300.0	2.57	100.7
	Homo	sapiens	1300.0	6.50	232.0
	Oreopithecus	bambolii	350.0	2.85	109.0

Table 1. gives data for brain size and life history parameters for twenty five primate species. We used these data, excluding *A. ramidus*, to plot brain size against age of M1 eruption. In Figure 1 we used this correlation to estimate age of M1 eruption for *A. ramidus* as well as the Miocene species *Oreopithecus bambolii*. Although variation and error need to be accounted for it is clear that both fossil species cluster around the great ape age of M1 eruption, with *A. ramidus* having an estimated age of M1 eruption between 2.5 and 3 years. Our analysis concurs with the findings of Smith and Tompkins (1995) who postulated quite strong correlations between brain size and age of M1 eruption.

Ross (2003) also found a strong correlation between brain size and age of

first reproduction across primate taxa. Here we are defining sexual maturation as age of first birth. As is illustrated in Figure 2 we used data obtained from the literature to estimate the age of sexual maturation of *A. ramidus*. Our estimate for *A. ramidus* age of first reproduction shows affinities with chimpanzees and other great apes. However, it is possible that *A. ramidus* had an age of reproduction different from what we have predicted, given differences within and between species of chimpanzees resulting from ecologically induced variation in age of first birth (Lathouwers and Elsacker 2005). However, this is not so much of an issue if we make a distinction between chronological and developmental age. For heterochrony to have occurred in the life history of *A. rami-*

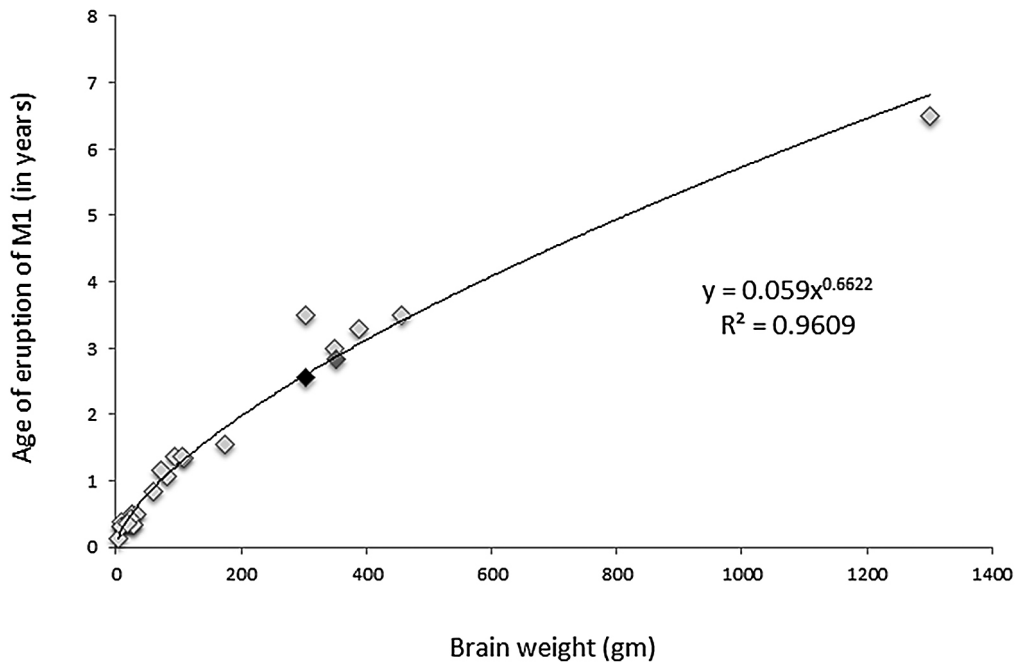


Fig. 1. Brain weight in grams plotted against age of M1 eruption *A. ramidus* black, *Oreopithecus* dark grey. Note the grade shifts between New World monkeys, lesser apes, great apes and humans (see text for details).

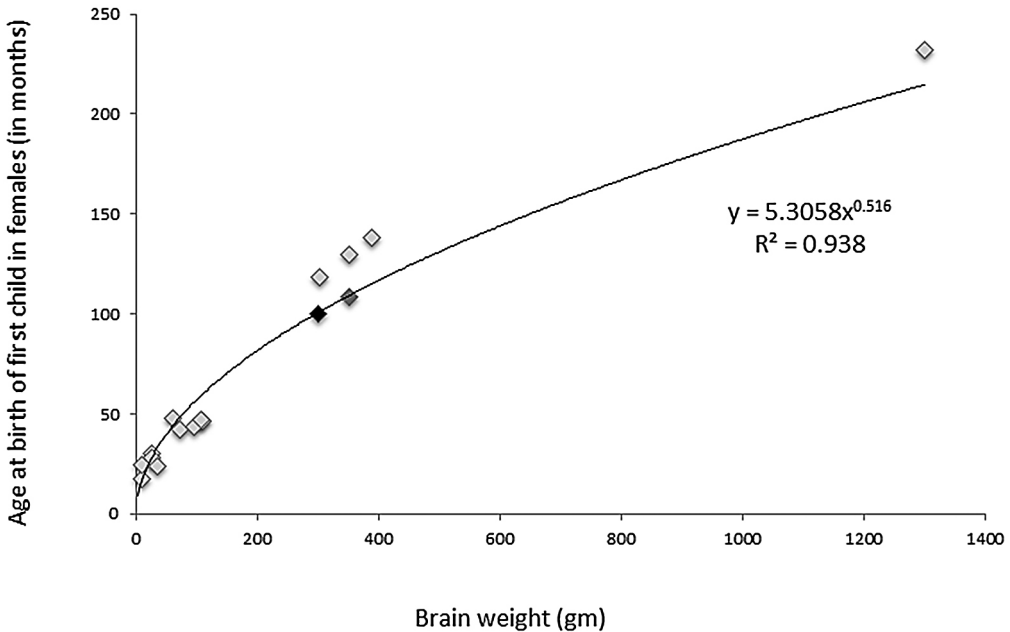


Fig. 2. Age of first reproduction in *A. ramidus* predicted from brain weight
A. ramidus black, *Oreopithecus* dark grey. Note the grade shifts between New World monkeys, lesser apes, great apes and humans (see text for details).

us it is only necessary that craniofacial growth was halted at a juvenile stage prior to first reproduction, whatever that may have been in years. In contrast chimpanzee craniofacial growth develops in tandem with sexual maturation (Cobb and O'Higgins 2007). Consequently, this issue is not dependent on *A. ramidus* having a specific chronologic age at first reproduction, although affinities with other great apes are themselves illuminating. The essential point is that if we consider developmental age as opposed to chronological age, it seems that *A. ramidus* attained sexual maturity while retaining juvenile craniofacial dimensions.

Upper facial and sub-nasal alveolar projection in *A. ramidus*

The data on *A. ramidus* published by Suwa and colleagues (2009) demonstrate the species did not develop the degree of upper facial or sub-nasal alveolar projection evident in other great apes (Suwa et al. 2009a). The authors argue that what overlap does exist between *A. ramidus* and extant great apes, clusters around the less pronounced projection evident in female members of *P. paniscus*. However, that analysis did not consider the ontogeny of facial projection in *A. ramidus*, nor has the ontogeny of this species been dealt with in the extant literature on early hominins.

To measure the ontogeny of upper facial projection, we calculated the distance from nasion to prosthion as a per-

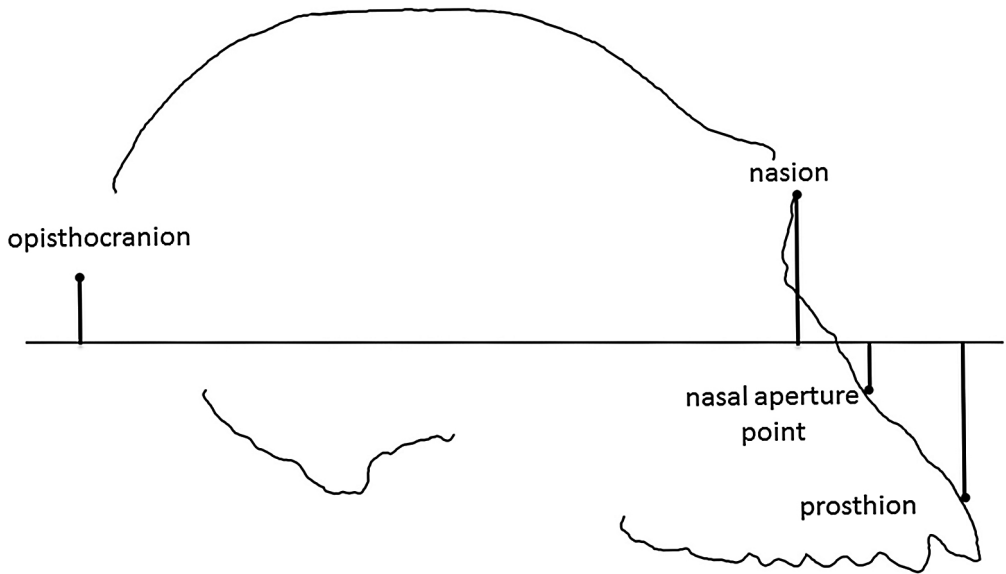


Fig. 3. Drawing of *A. ramidus* skull showing landmarks associated with facial projection. We measured the published CT scan of the skull. We measured distances in the sagittal plane between perpendicular projections of opisthocranium, nasion, nasal aperture point and prosthion onto the Frankfurt horizontal (Drawing based on CT scan in Suwa et al. 2009 SOM)

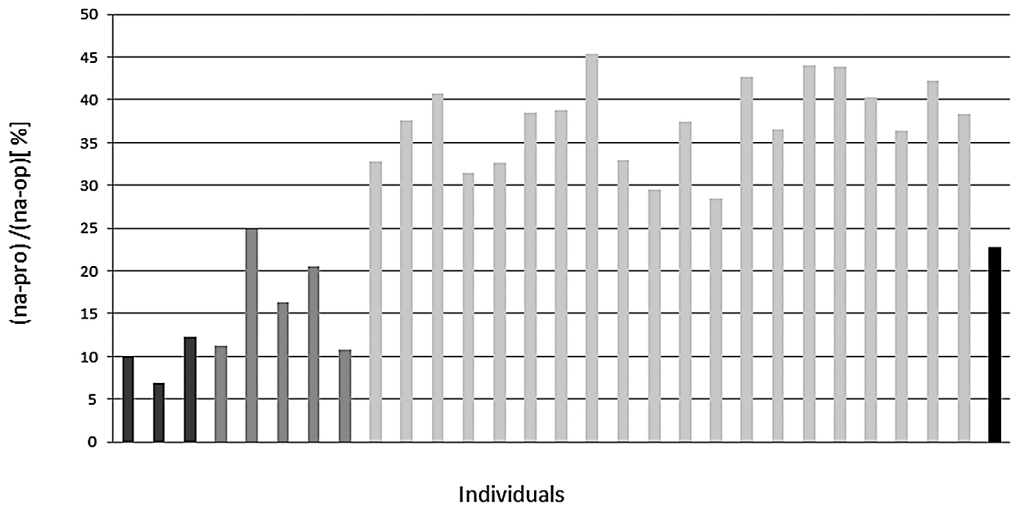


Fig. 4. Graph showing upper facial projection measured as nasion to prosthion as a percentage of nasion to opisthocranium

A. ramidus in black, adult chimpanzees in light grey, juveniles in grey, and infants in dark grey. This ratio indicates the relative degree of upper facial projection in relation to the length of the cranial vault from opisthocranium to nasion. *A. ramidus* shows greater affinity with juvenile than with adult chimpanzees (see text for details)

centage of nasion to opisthocranium. As can be seen from Figure 4 *A. ramidus* has upper facial projection of approximately 23 %, which clusters with juvenile chimpanzees, being significantly less than all adult specimens.

For subnasal alveolar projection we calculated the length of the entire skull from prosthion to opisthocranium in multiples of nasal aperture point to prosthion (Fig. 3). This means less projection in the subnasal alveolar region will yield a higher figure. As can be seen from Figure 5 we obtained a ratio for *A. ramidus* of approximately 9, which clusters around the mid-range of juvenile chimpanzees, also showing affinity with infants. It is also distinctly different from all adult specimens. As we have no evidence of the common ancestral adult or infant dimensions we are uncertain how to interpret this result. What is most likely is that the

dimensions of *P. troglodytes* are a result of peramorphic increase in canine size, with accompanying increases in subnasal alveolar projection, which have been shown to facilitate occlusion of larger canines (Cobb and O'Higgins 2007). It also suggests *A. ramidus* is paedomorphic in relation to the common ancestral condition. This conclusion finds support in the more robust canine morphology of its putative ancestor, *A. kadabba* (Haile-selassie and Woldegabriel 2009). Consequently there seems to be a slow process of gracilization occurring from a hypothesized common ancestral condition to *A. kadabba* through to *A. ramidus*.

However, until we have a richer fossil record at the base of the hominin clade this issue cannot be decided with any degree of accuracy. What our result suggests is that *A. ramidus* reduced subnasal alveolar projection while *P. troglodytes*

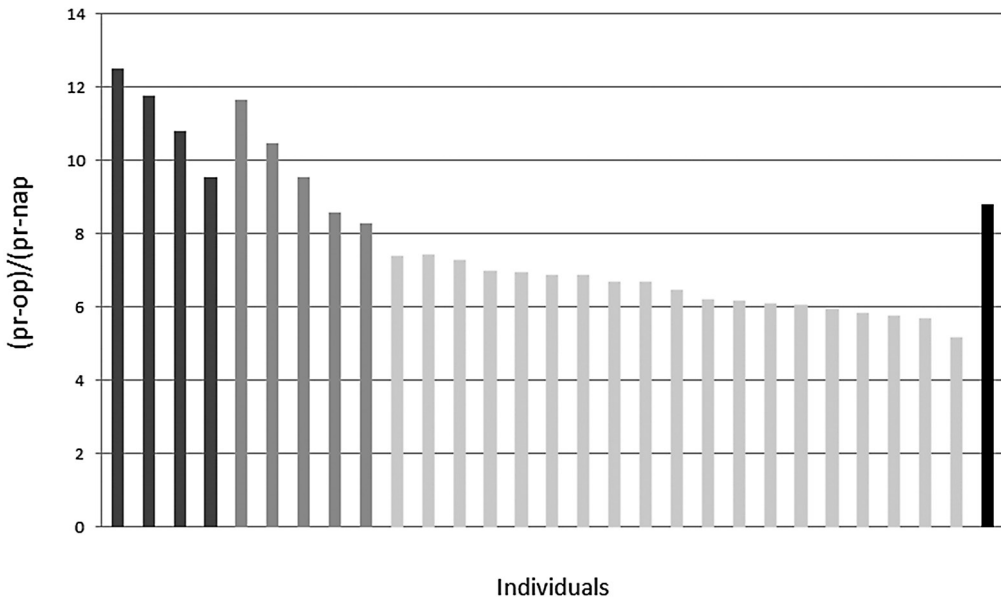


Fig. 5. Graph showing sub-nasal alveolar projection, measured as length of the entire skull from prosthion to opisthocranium in multiples of nasal aperture point to prosthion *A. ramidus* in black, adult chimpanzees in light grey, juveniles in grey, and infants in dark grey. *A. ramidus* shows greater affinity with juvenile than with adult chimpanzees (see text for details).

may have increased it, each species departing from its own infant and juvenile morphology to different degrees. Given it is highly unlikely *A. ramidus* evolved from a more gracile ancestor, the reduction of facial projection in sexually mature individuals represents an example of heterochronic dissociation of growth trajectories, an evolutionary trend that was continued in later hominins who evolved distinctive orthognathic craniofacial morphology.

Position of the zygomatic root

The growth in projection of the face in primates is accompanied by a change in zygomatic root position, which is located in a more posterior position as facial pro-

jection increases (Harrison 1986). Consequently the position of the zygomatic root in relation to the maxillary dentition changes throughout ontogeny in most primate species. The position of the root is also associated with interspecific variation in prognathism or projection of the face.

In Table 2 data on zygomatic root position taken from the literature (Harrison 1986; Suwa, et al. 2009; Moyà-Solà et al. 2009) are given for a number of primate species. The data include a range of samples, from the anteriorly placed root of infant *P. troglodytes*, to the posteriorly placed root of adult *Papio*. In the Miocene ape *O. bambolii* the zygomatic root is anteriorly placed in relation to extant primates, being above maxillary P4/M1.

Table 2. Position of the zygomatic root in relation to the maxillary dentition in a number of extant and fossil primates

Individuals	N	Post M3	Mid M3	Ant M3	M2/M3	Post M2	Mid M2	Ant M2	M1/M2	Post M1	Mid M1	Amt M1	P4/M1	Post P4	Mid P4
<i>Pan troglodytes</i> infant	5													60	40
<i>Symphalangus</i> infant	2													50	50
<i>Pan troglodytes</i> juvenile	2								50		50				
<i>Gorilla gorilla</i> juvenile	2													50	50
<i>Oreopithecus bambolii</i>	2													100	
<i>Anoiapithecus brevirostris</i>	1											100			
<i>Homo</i>	20								5	27	40	25	3		
<i>Ardipithecus ramidus</i>	1											100			
<i>Symphalangus</i>	15				27	7	40	13	13						
<i>Pan troglodytes</i>	25				12	8	8	16	44	8	4				
<i>Gorilla gorilla</i>	26					3.9	11.6	34.7	34.7	15.4					
<i>Papio</i>	13	30.8	30.5	30.8											

As can be seen, in infant and juvenile specimens, the placement of the zygomatic root is above the anterior dentition. Throughout ontogeny it 'migrates backwards', being positioned more posteriorly in extant adult specimens. However, in late Miocene and early Pliocene fossil primates such as *A. ramidus*, *A. brevirostris* and *O. bambolii*, the placement is more akin to that of infant and juvenile than adult extant primates. *Homo* shows greatest affinity with these extinct species. (data taken from Harrison 1986; Suwa, et al. 2009a; Moyà-Solà et al. 2009; infant and juvenile measurements taken from CT scans obtained from Kyoto University Digital Museum: <http://dmm.pri.kyoto-u.ac.jp/dmm/WebGallery/index.html>).

Accompanying this anterior placement of the zygomatic root *O. bambolii* also has dramatically reduced projection of the face, yielding an unusually orthognathic morphology that differs dramatically from extant ape species. At the other extreme is *Papio*, with a highly prognathic facial morphology in which the zygomatic root is posteriorly positioned above M3.

As Table 2 indicates over 90% of *H. sapiens* specimens have placement of the zygomatic root above M1. The same placement is evident in *A. ramidus*. Also, *H. sapiens* shows greater affinity with the three Miocene and early Pliocene fossil species, than with any of the other extant adult specimens. For example, in *P. troglodytes* 88% of the specimens have placement of the zygomatic root either between M1 and M2, or more posteriorly, with some specimens having the root positioned between M2 and M3. The anterior placement of the zygomatic root also differentiates *A. ramidus* from *P. troglodytes*, which has greater facial prognathism and consequently more posterior placement of the zygomatic root.

Table 2 also illustrates ontogenetic changes in zygomatic root position. In infant specimens of *Symphalangus* and *P. troglodytes* it is placed above P4 and its position becomes more posterior throughout ontogeny. For example in juvenile specimens of *P. troglodytes* the root is positioned either above M1 or between M1 and M2. Only a small number of adults from this species show similar placement to juveniles, with the majority having placement between M1 and M2 or with further posterior placement above M2 or in between M2 and M3. This indicates a slow movement posteriorly of the placement of the zygomatic root throughout ontogeny, with the ma-

ior differences evident between infants and adults.

What is significant is the similarity in zygomatic root position that exists between adult specimens of Miocene and early Pliocene species such as *A. brevirostris*, *O. bambolii* and *A. ramidus*, and juvenile and infant specimens of extant apes. For example, in *O. bambolii* the root is positioned in an extremely anterior position, one that shows greatest affinity with the infants of extant species. Consequently it has been suggested that this species is paedomorphic, and that it evolved through heterochronic decoupling of growth trajectories (Alba et al. 2001). *A. brevirostris* similarly shows greater affinity with juvenile specimens with zygomatic root placement above M1. *A. ramidus*, with placement of the root above M1, also shows affinities with juvenile *P. troglodytes* specimens. It is also placed in a more anterior position than in adult *P. troglodytes* where 44% of specimens have placement of the root above M2 or between M2 and M3. Although the remaining 56%, which have root placement between M1 and M2 or above M1 do show some overlap with *A. ramidus*, that overlap is slight and exists only at the very extreme end of variation. Given the monomorphic canine morphology of the species it is likely that variation in the position of the zygomatic root would not have been as pronounced as species with significant canine sexual dimorphism. Given that the development of facial projection and the accompanying changes in the ontogeny of zygomatic root position are more pronounced in more prognathic species with large canines, the absence of large dimorphic canines in *A. ramidus* would suggest the zygomatic root position in this individual may be indicative of the species norm

in both sexes. Further, given male great apes have greater prognathism than females the slight overlap between *A. ramidus* and chimpanzees would most likely be a result of affinities with females and not males. The data we used did not differentiate between the zygomatic root placement in males and females so this is a supposition, but a justified one given the widely acknowledged sexual dimorphism of great ape craniofacial morphology (Schaefer et al. 2004; Cobb and O'Higgins 2007).

What is clear is that in terms of zygomatic root placement *A. ramidus* is pedomorphic in relation to *Pan troglodytes*. As with the issue of facial projection, it is uncertain the degree to which this is a result of peramorphosis in *Pan troglodytes* or pedomorphosis in *A. ramidus* as we have no data on the common ancestral condition.

What is interesting to note are the affinities between modern humans and the three fossil species. This suggests that zygomatic root position in modern humans is a retention from late Miocene and early Pliocene ape cranio-facial morphology. Although *O. bambolii* does not have the reduced canines evident in *A. ramidus*, it lacks the zygomatic root position associated with facial prognathism, and its sub-nasal alveolar projection is dramatically reduced in relation to extant great apes and its own putative ancestor *Dryopithecus* (Alba 2002: 28–50). Given that the basic foundation of hominoid life history seems to have been laid down during the Miocene (Kelley 1997: 173–208) it is interesting to consider the degree to which aspects of modern human ontogeny are retentions or mere elaborations of this basic Miocene ape *bauplan*. Given that we are the only extant primate with a pedomorphic zygomatic root

position, combined with the fact that this heterochronic alteration of primate morphology existed in a number of Miocene apes, in this feature at least modern humans retain phylogenetically deep traits that are absent in all other extant primates. This analysis concurs with that of Lovejoy (2009; 2014) who has shown phylogenetically deep affinities between Miocene apes, *A. ramidus*, *Orrorin tugenensis*, *Sahelanthropus tchadensis* and modern humans in various aspects of skull and locomotor morphology. One of the most fruitful avenues of research in future studies of hominin phylogeny will be the degree to which, not just features of craniofacial morphology, but also the socio-behavioral suites of modern humans have their roots in Miocene hominoid life history and ontogeny.

Discussion

Our analysis has suggested that *A. ramidus* shares with chimpanzees similar brain volume and consequently similar maturational rates associated with the age of eruption of M1 eruption and sexual maturation. However, while this predicted affinity in chronological age of first birth is illuminating, it is not a necessary condition for heterochrony to have occurred. In this sense we make a distinction between chronological and developmental age. Consequently we can postulate evolution via heterochrony in *A. ramidus* if the species reached the developmental stage of first birth, whatever that may have been in years, while retaining juvenile craniofacial dimensions.

In comparison with chimpanzees *A. ramidus* shows distinct differences in terms of craniofacial growth. However, we are not suggesting this conclusion indicates *A. ramidus* represents an altered

chimpanzee ontogeny nor that chimpanzees provide a useful model for early hominin social and mating behaviour. What the differences indicate when analysing *A. ramidus* and the more robust yet closely related chimpanzee, is that both species seem to have evolved different developmental alterations of the common ancestral *bauplan*. Given that we are dealing with sexually mature individuals, our analysis indicates that developmental trajectories associated with craniofacial growth may have been dissociated from those of cranial volume and sexual maturation in *A. ramidus*. Consequently brain volume and associated maturational trajectories in both chimpanzees and *A. ramidus* may be considered synapomorphic traits, with little divergence from a common ancestral condition – although given ecologically induced variation of age of first reproduction amongst great apes, this may be more relevant to considerations of brain size than life history parameters. What is significant is that craniofacial projection seems to be apomorphic, each species representing a derived condition relative to a putative common ancestor.

This analysis concurs with the observation that in primates cranial volume is more stable under differing selective regimes than craniofacial length (Isler et al. 2008). The implication is that selective pressures may alter aspects of facial growth without altering cranial volume. The fact that *A. ramidus* shares a similar cranial volume and associated brain size with chimpanzees, yet its facial morphology is distinctly different suggests that selection has operated on craniofacial morphology to a greater degree than brain volume and related life history parameters. Yet the degree to which these differences can be attributed to

decreased prognathism in *A. ramidus* or increased prognathism in chimpanzees is unclear as we lack fossils of the common ancestral condition. It is most likely that the craniofacial morphology of *A. ramidus* is more gracile than that of both its putative ancestor *A. kadabba*, and also the common ancestral condition. Our study suggests this process of gracilisation was achieved through heterochronic dissociation of growth trajectories. Given such heterochronic dissociations of developmental trajectories are considered important sources of evolutionary innovation (Gould 1977; Gould 2002), we suggest it is through such means that *A. ramidus* diverged from a more robust ancestral condition.

In this context it is interesting to note the chronology of cranial base, neuro-cranial and craniofacial facial ontogeny in primates. What is significant is that formation of the cranial base and the neuro-cranium in primates occurs prior to formation of the face (Lieberman et al., 2000). Daniel Lieberman has succinctly described this phenomenon in the context of human ontogeny:

“The brain and its associated capsules, the neuro-cranium and cranial base, grow especially fast during the first two post-natal years and then reach adult size within six to eight years. In contrast, most of the face grows more slowly, along with the rest of the skeleton, with spurts after birth and during adolescence, reaching adult size between ages fourteen and twenty” (Lieberman 2011: 31).

This human pattern is an elaboration on the basic chronology of primate maturation in which a spurt in craniofacial growth occurs during sexual maturation. What is worth noting is that it is during the period of sexual maturation that head morphology becomes sexually

dimorphic in chimpanzees and baboons (O'Higgins and Jones 1998; Cobb and O'Higgins 2007). In this sense growth rates associated with sexual maturation may have been implicated in selection for the idiosyncratic ontogeny of *A. ramidus*, which suggests craniofacial growth rates were retarded or slowed down at a juvenile stage of development. What is interesting to note in this context is that *A. ramidus* shares with modern humans reduced development of facial projection during puberty – an observation suggested by the halting of growth at a juvenile stage in *A. ramidus*. Modern humans have very idiosyncratic growth trajectories at this age that are unlike any other extant or fossil primate. However, evidence of that singular pattern of development, at least in incipient form, shows its first appearance at the very base of the hominin clade in *A. ramidus*.

In this context it is worth noting that in a number of primate species males and females share a common ontogenetic trajectory until sexual maturity. The sexual dimorphism evident in facial morphology in these species is largely attributable to ontogenetic divergence as juveniles become reproductively active; consequently it has been suggested such developmental factors may be under hormonal changes associated with puberty (Cobb and O'Higgins 2007: 188; O'Higgins and Collard 2002: 270).

For example, at puberty male and female African apes develop significant sexual dimorphism in the mesiodistal dimensions of their maxillary canines – yet very little sexual dimorphism is evident in the post-canine dentition (Cobb and O'Higgins 2007). Also there is no obvious shape dimorphism in the region where the developing canines are housed. Consequently, it is not so much

the larger male canine that contributes to differences in craniofacial shape, but the requirements of canine occlusion, which are facilitated by a diastema mesial to the maxillary canine. Therefore, the divergence at sexual maturation of male and female craniofacial shape can be accounted for by larger male canine size *and* more importantly the larger diastema that effectively increases the distance between maxillary I2 and P3. The result is that such increased distance between I2 and P3 contributes to increased male subnasal alveolar projection in relation to females. The lack of craniofacial sexual dimorphism in *A. ramidus* suggests that in males growth in the facial region did not develop to the degree it does in more dimorphic species, males retaining into adulthood juvenile craniofacial dimensions.

The increased distance that develops in male ontogeny between maxillary I2 and P3, itself a result of increase in the size of the diastema in males relative to females, is necessary to facilitate interlocking canines and the C/P3 honing complex. This complex is found in all non-human primates and is particularly pronounced in species in which male on male conflict is the major avenue for reproductive success (Holloway 1967; Harvey, Kavanagh and Clutton-Brock 1978; Plavcan and van Schaik 1992), although some authors have suggested both predation (Plavcan, Van Schaik and Kappeler 1995) and diet combined with sexual selection (Hylander 2013) may explain some interspecific variation.

Some fossils attributed to *A. kadabba*, the species thought to be ancestral to *A. ramidus*, do possess a small facet on the mesio-buccal crown of the mandibular P3 caused by contact with the lingual surface of an interlocking upper canine.

Yet other samples have led researchers to conclude that *A. kadabba*, while retaining some evidence of honing canines, has a C/P3 complex which seems to be less pronounced than in other primates. Consequently the species shows an incipient trend towards the hominin condition, a conclusion suggested by the lack of consistently expressed functional honing (Haile-Selassie 2004). The complex is no longer evident in *A. ramidus*, in which the process of gracilisation has continued (Haile-Selassie and Wolde-Gabriel 2009: 213). Accompanying this development is greatly reduced distance between maxillary I2 and P3, due to the absence of a diastema for interlocking canines, reduced upper facial and sub-nasal alveolar projection, and retention of the sub-adult position of the zygomatic root into adulthood.

The absence of a C/P3 complex in a forest and woodland dwelling species such as *A. ramidus* has profound implications for our understanding of the origins of human social and mating systems (Suwa et al. 2009; Sayers, Raghanti and Lovejoy 2012). Trivers (1972) has observed that increased parental investment on the part of males disproportionately decreases male reproductive effort invested in male-male competition to inseminate females. In this context we suggest metabolic resources directed towards growth of the craniofacial region of the skull and male on male conflict over females, may have been redirected into provisioning of females and offspring as a male reproductive strategy - either in terms of direct investment or if males became part of an extended system of allo-parental care and co-operative breeding. Growing a projecting face with a C/P3 complex is metabolically expensive - and so is competing with other

males for sexual access to females. It may be that in *A. ramidus* energy expenditure for growth was moved away from craniofacial growth to provisioning, laying the foundation of human social and mating systems. This may account for *A. ramidus* males being reproductively successful in the absence of canine armoury. Although Hylander (2013) argues that reduction in male hominin canines is related to changes in diet and jaw gape, he does concede that in *A. ramidus* changes in mating patterns would have also been important.

Slowing down of development is a distinguishing feature of primate phylogenies, a trend that has been extended in humans (Portmann 1990). The slow rate of somatic development in humans, in which developmental immaturity is extended post-natally relative to other primates, has been described by Portmann as 'secondary altriciality' (Portmann 1990: 38), a concept that has become the basis of some important thinking in hominin life history theory and developmental palaeoanthropology (Martin 1983; 2008; 2013; Zollikofer and Ponce de León 2010; Dunsworth et al. 2012). It has also been suggested by Portman and other researchers that the associated phenomenon of foetal brain growth rates being extended ex-utero, and the increase in metabolic requirements this necessitates, may have been facilitated in the hominin lineage by an intensification of parental care (Portmann 1990: 57; Smith and Tompkins 1995: 271; Martin 2007: 78). Recent work has refined these insights, leading to improved understanding of the ontogeny of fossil hominins, with estimations of increasing birth weights in *Australopithecines* suggesting the trend towards secondary altriciality may have been facilitated in this genus by allo-parents

providing extra metabolic resources to mothers (DeSilva 2011a).

Advocates of the maternal energy hypothesis have extended Portman's thesis, arguing that secondary altriciality, extension of foetal brain growth rates ex-utero and increased brain size, were facilitated by an intensification of parental care in the hominin lineage (Martin 1996, Martin 1998; Martin et al. 2005, Martin 2007: 74). This thesis finds support in the observation that shared parenting among primates increases individual growth and/or litter size (Burkart et al. 2007) and that distributing the costs of reproduction over several, or merely two individuals, yields an energetic benefit for mothers (Isler and Van Schaik 2012: 2).

Given that the adaptation of co-operative breeding in primates is not dependent on high cognitive abilities, Isler and Van Schaik (2012) have suggested that alloparental care may have evolved in the hominin lineage prior to increases in body and brain size. Previous researchers have argued that the increases in body and brain size evident in *H. erectus* provide evidence for the emergence of alloparental care in the hominin lineage (Hawkes et al. 2003). However, evidence of alloparenting and increased body and brain size in *H. erectus* is by no means evidence that these two traits evolved simultaneously.

Evidence for the emergence of co-operative breeding and care of offspring by individuals in addition to the mother may be found in craniofacial correlates of social and mating systems, not necessarily in increases in body and brain size. It is most likely that cooperative breeding is a prerequisite for increases in body and brain size – which is quite different from postulating their simultaneous emergence. Primate species that have systems

of co-operative breeding have been found to extend cooperative behaviour into the broader social system, resulting in higher levels of generalised pro-social behaviour than species without such systems of care (Burkart et al. 2007). Such a generalised system of co-operation, developing out of a system of cooperative breeding, would have provided the social context for increasing maternal metabolic allocation to infants in later periods of hominin evolution. In this sense cooperative breeding, which we suggest may have emerged with *A. ramidus*, would have been 'exapted' (Gould and Vrba 1982) in consequent periods of hominin evolution, facilitating the increases in body and brain size evident in *H. erectus*. Consequently, our complex social structures most likely evolved prior to the emergence of large bodied and large brained hominins, having their origin at the base of the hominin clade (Lovejoy 2014).

We suggest that the transfer of metabolic energy from craniofacial growth and male on male conflict into the maternal energy budget would have required very specific patterns of social behaviour. If *A. ramidus* provides evidence of social and mating systems unlike those evident in chimpanzees and the putative ancestral condition, it is also most likely the context of infant and juvenile socialisation was different in this early hominin. As evolution does not act on adult characters, but on developmental processes themselves (West-Eberhard 2003), evolving a specific adult socio-behavioural suite would have required an ontogeny and period of infant and juvenile socialisation divergent from that of chimpanzees and the putative common ancestral condition. As we have noted development of craniofacial projection in *A. ramidus* seems to have halted prior to

sexual maturation. However, craniofacial projection in chimpanzees, and other primate species with a projecting face, continues throughout sub-adult ontogeny into adulthood, with sexual maturation and increased craniofacial projection developing in tandem. The issue we wish to consider is what happens in the period between the cessation of craniofacial growth and sexual maturation in *A. ramidus*? In other words what may the fossil anatomy tell us about the possible pattern of infant and juvenile socialisation?

Portman noted the different growth trajectories evident in humans and great apes after the permanent dentition begins erupting (1990: 106–111). In both humans and chimpanzees slowing of brain growth and the emergence of the permanent dentition occur at approximately the same age – in chimpanzees at approximately 3.5 years and in humans at approximately 6.5–7.0 years. At these ages juveniles in both species have grown most of their adult brain weight. As Portman noted, in chimpanzees, at approximately 3.5 years when brain growth virtually stops and the permanent dentition begins erupting, the snout begins to grow, eventually yielding the prognathic morphology evident in adults. In humans, at the equivalent developmental milestone, in between approximately 6.5–7.0 years, as with chimpanzees, growth of the brain slows and the permanent dentition begins erupting – however *a snout fails to grow*. This seems a very obvious and banal point to make, but it has profound implications.

Portman highlighted differences in ontogeny when he noted that in apes, following the intense period of brain growth, growth of the snout begins, whereas in humans there is no ‘growth in the alveolar’ section of the jaw fol-

lowing the period of initial growth of the brain (Portmann 1990: 110). Significantly, unlike *H. sapiens*, *A. ramidus* retains a chimpanzee-like pattern of brain and tooth development, yet the species – this being the interesting point – is similar to *H. sapiens* in that it did not develop a projecting snout and the associated C/P3 complex when brain growth rates would have decreased. This would lead to the conclusion that a three or four year old *A. ramidus* child, as it enters puberty, would be developing a different suite of behavioural repertoires than a chimpanzee of the same age. As Portman noted in modern humans, the period after the eruption of the permanent dentition is when increasing socialisation begins, with learning and the forming of social bonds assuming greater importance.

The contrast with chimpanzees is instructive, for when humans start developing broader social bonds after the permanent dentition begins erupting, at the same developmental milestone, chimpanzee facial projection increases. In other words humans seem to have replaced craniofacial growth with an extended and intensified period of socio-emotional development. As *A. ramidus* no longer has an ontogeny that results in the development of a prognathic jaw with a C/P3 complex (which is one of the most important means by which males vie for status within the mating hierarchies of other primate species), young and sub-adult members of the species must have pursued other avenues by which to become reproductively successful members of the social group. The implication of these interspecific differences is that *A. ramidus* would have most likely had a period of infant and juvenile socialisation different from that of chimpanzees. Consequently, it is possible that in *A. ramidus* we see the

first, albeit incipient trend toward human forms of child socialisation and social organisation.

It has been suggested that the process of hominization from *Australopithecines* through the various species of the *Homo* genus would have required a change in juvenile and sub-adult socialisation (Zihlman 1978). According to this matri-focal view of primate and hominin evolution, the mother infant bond that characterises primate societies was intensified in the hominin lineage, with the result that a greater period of maternal socialisation resulted in higher degrees of sociality in male offspring. Increased pro-social association between males, their siblings and their mothers, would according to this view, result in a greater degree of pro-social behaviour in adult males. If sub-adult males were socialised in this way, and if they extended such behaviours into adulthood, then adult male pro-social behaviours could differentially proliferate through female mate preference of less aggressive males.

Support for this theory is based on the observation that the small canines of male hominins suggest they were 'more sociable and less aggressive in their interactions with other males and females' than primates that use canine armoury in male on male conflict (Tanner and Zihlman 1976). This thesis finds support from field studies of non-human primates highlighting the importance of the mother infant bond in chimpanzees and baboons (Goodall 1968; Altmann 2001) as well as that of female sexual selection in baboons (Smuts 2007). If female mate selection is important in highly dimorphic species such as baboons, an intensification of that tendency in hominins where females choose less aggressive and more co-operative mates willing to

invest in offspring may be inferred from the reduced craniofacial sexual dimorphism in *A. ramidus*.

The lack of sexual dimorphism in *A. ramidus* also gives support to the suggestion that bonobos may illuminate the early stages of hominin evolution (Zihlman et al. 1978). Bonobos are less sexually dimorphic than chimpanzees in terms of both body (Shea 1984: 99) and canine size (McIntyre et al. 2009, 361). Further, adult skull morphology of bonobos resembles that of a juvenile chimpanzee (Coolidge 1933), the degree of cranial-base flexion in relation to chimpanzees is juvenilised or paedomorphic (Laitman and Heimbuch in Susman 1984) and bonobo sexual behaviour is thought to be more juvenilised than chimpanzees (Blount 1990). It has also been argued that bonobo social structures are female-centric, with infant growth slower than in chimpanzees, sustained mother-son dyads extending past puberty with male kinship ties focused on the mother as opposed to brothers (de Waal and Lanting 1998: 60 and 86). Studies have also shown female mate choice of males willing to share food is a significant component in bonobo social and mating systems (de Waal 1987 and 1996).

This suite of adaptations combining slowed infant maturation, increased maternal care, the trading of sex for food by males and reduced aggression relative to chimpanzees may have developed via 'self-domestication' (Hare, Wobber and Wrangham 2012), a process which is thought to have given rise to the paedomorphic morphology and idiosyncratic social psychology of bonobos. Of course *A. ramidus* differs significantly from bonobos, bonobos having retained a functional canine honing complex. However,

the fact that *A. ramidus* shares with bonobos reduced sexual dimorphism, and a more paedomorphic form relative to chimpanzees, suggests that the developmental and social adaptations evident in bonobos may be of assistance in future reconstructions of early hominin social and sexual psychology. In fact the trend towards increased maternal care, female mate selection and self-domestication may have been stronger and more refined in *A. ramidus* than what we see in bonobos.

Bipedalism in *A. ramidus* has been explained as evidence of male provisioning of females, with males expanding their feeding range and carrying food back to a more sedentary female with whom the male is pair-bonded (Lovejoy 2009). However, bipedalism would have also facilitated an intensification of maternal care, as bipedal mothers would be more adept at carrying of infants, particularly as they became more altricial and increasingly unable to cling to the mother while she foraged for food (Zihlman 1981). Although there is no direct evidence of secondary altriciality in *A. ramidus*, its first emergence has been postulated in *Australopithecines* (DeSilva 2011). If this theory is correct it may be that the social and mating systems that facilitated this process were already in place in *A. ramidus*. In this sense bipedalism, co-operative breeding, an intensification of maternal care and increased levels of social co-operation, may have been an integrated adaptive suite essential to the process of hominization. This is of course highly speculative. However such an interpretation does find some support from the idiosyncratic craniofacial morphology of *A. ramidus*, suggesting the origins of human sociality may have been laid down in the late Miocene and early Pliocene forests and woodlands of Africa.

Conclusion

In this study we have shown that sexually mature *A. ramidus* individuals retained juvenile craniofacial dimensions. We argue that this represents a heterochronic decoupling of growth trajectories, with craniofacial growth being dissociated from growth of the brain and associated life history trajectories. We also consider the possibility that brain size, dimensions of the cranial vault and the ontogeny of life history trajectories are synapomorphic traits in *A. ramidus* and chimpanzees. Conversely we consider craniofacial morphology to be apomorphic. The consequent reduction of facial projection in *A. ramidus* suggests a reduction in male on male aggression, and a more general change in social and mating systems at the base of the hominin clade. We suggest this may have entailed co-operative breeding and changes in patterns of infant and juvenile socialisation.

Authors' contributions

GC was the main author and primary researcher; MH was collaborative researcher.

Conflict of interest

The authors declare that there is no conflict of interest.

Corresponding author

Gary Clark
Bacaru, Medical School, The University
of Adelaide, Australia 5005
e-mail address:
megafauna@hotmail.com

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