

# Protective buttressing of the hominin face

David R. Carrier<sup>1,\*</sup> and Michael H. Morgan<sup>2</sup>

<sup>1</sup>*Department of Biology, University of Utah, 257 S 1400 E, Salt Lake City, UT 84112, U.S.A.*

<sup>2</sup>*Division of Emergency Medicine, The University of Utah School of Medicine, 30 N 1900 E, Salt Lake City, UT 84132, U.S.A.*

## ABSTRACT

When humans fight hand-to-hand the face is usually the primary target and the bones that suffer the highest rates of fracture are the parts of the skull that exhibit the greatest increase in robusticity during the evolution of basal hominins. These bones are also the most sexually dimorphic parts of the skull in both australopiths and humans. In this review, we suggest that many of the facial features that characterize early hominins evolved to protect the face from injury during fighting with fists. Specifically, the trend towards a more orthognathic face; the bunodont form and expansion of the postcanine teeth; the increased robusticity of the orbit; the increased robusticity of the masticatory system, including the mandibular corpus and condyle, zygoma, and anterior pillars of the maxilla; and the enlarged jaw adductor musculature are traits that may represent protective buttressing of the face. If the protective buttressing hypothesis is correct, the primary differences in the face of robust *versus* gracile australopiths may be more a function of differences in mating system than differences in diet as is generally assumed. In this scenario, the evolution of reduced facial robusticity in *Homo* is associated with the evolution of reduced strength of the upper body and, therefore, with reduced striking power. The protective buttressing hypothesis provides a functional explanation for the puzzling observation that although humans do not fight by biting our species exhibits pronounced sexual dimorphism in the strength and power of the jaw and neck musculature. The protective buttressing hypothesis is also consistent with observations that modern humans can accurately assess a male's strength and fighting ability from facial shape and voice quality.

*Key words:* *Australopithecus*, *Paranthropus*, *Homo*, male-male competition, fighting, sexual dimorphism, visual assessment of strength, masculine voices, male facial shape.

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\* Address for correspondence (Tel: 001 (801) 585-7967; Fax: 001 (801) 581-4668; E-mail: carrier@biology.utah.edu).

## I. INTRODUCTION

*Our view is that researchers have failed to understand the evolutionary significance of australopith craniofacial anatomy.* (Daegling *et al.*, 2013)

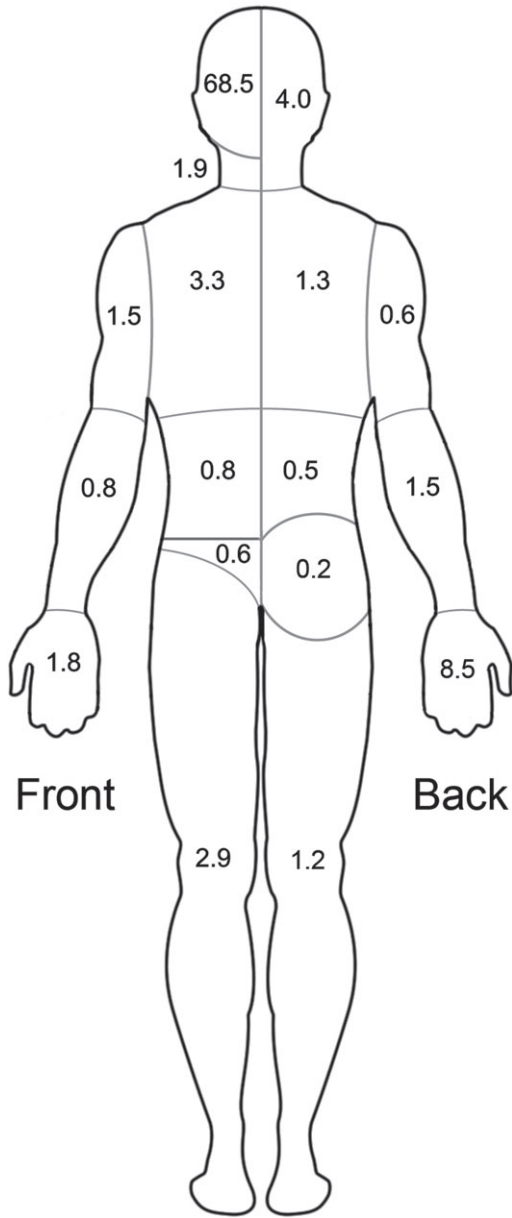
For six decades, the distinctly robust faces of the first bipedal apes, the australopiths, have been recognized as phylogenetically derived and argued to be functionally related to a diet that included hard, difficult to crush objects (Robinson, 1954; Jolly, 1970; Rak, 1983; Kay, 1985; Daegling & Grine, 1991; Teaford & Ungar, 2000; Strait *et al.*, 2013) or abrasive foods such as grasses (Teaford & Ungar, 2000; Ungar *et al.*, 2012). However, analyses of microwear patterns on postcanine teeth suggest that the diet of australopiths included few or no hard objects (Walker, 1981; Grine *et al.*, 2012; Daegling *et al.*, 2013) and although analyses of carbon isotopes suggest that the diet of the hyper-robust species *Paranthropus boisei* was composed primarily of grasses and sedges (Cerling *et al.*, 2011; Sponheimer *et al.*, 2013) microwear analyses suggest a frugivorous rather than a grazing or browsing diet (Walker, 1981; Ungar, Grine & Teaford, 2008). These observations raise questions about the feeding hypothesis. In this review, we suggest an alternative adaptive hypothesis for many of the facial features of australopiths based on the need to protect the face from injury during fighting. Obviously, there are additional possible explanations for the evolution of the derived aspects of the hominin face. The finding that a feature provides a performance advantage for mastication or protecting the face during fighting does not necessarily mean it was selected for these functions. For example, many aspects of the face of early hominins may be a consequence of developmental or phylogenetic constraints on anatomy (Moss & Young, 1960; Shea, 1985; Ravosa, 1988; McCollum, 1999; Lieberman, 2000, 2011; Daegling *et al.*, 2013). Nevertheless, the protective buttressing hypothesis, presented here, represents an additional factor that may have played a role in the evolution of the hominin face and masticatory system.

We have previously suggested that the hand proportions that allow humans to clench their hand into a fist evolved as a result of selection to make the hand a more dangerous weapon (Morgan & Carrier, 2013). If the human fist is a dangerous weapon, it is reasonable to predict that the primary target, specifically the head, would have undergone evolution resulting in increased robusticity and protective buttressing (Nickle & Goncharoff, 2013; also see Puts, 2010). Although the hands of early hominins differ in many ways from those of modern humans (Aiello & Dean, 1990), the proportions of the hand that allow modern humans to form a buttressed fist appear to have been present in the earliest

hominins for which we have a fossil record, at approximately the same time our lineage became habitually bipedal (reviewed in Morgan & Carrier, 2013). Thus, it is in the skulls of the basal hominins that we must look for a correlation between evolution of hand proportions and anatomical changes of the face that might provide protective buttressing against fist strikes.

If hand-to-hand fighting in early hominins was similar to fighting in untrained modern humans, injuries sustained during modern interpersonal violence may provide clues about the parts of the body that were primary targets of interpersonal violence among early hominins (Fig. 1). A study done in the UK that quantified the location of injury resulting from assault found that the face was the most common site, accounting for 53% of all haematomas, 66% of all lacerations and 83% of all fractures (Shepherd *et al.*, 1990). In comparison, this study found that injuries to other parts of the head and neck accounted for only 7% of all haematomas, 10% of all lacerations, and 4% of all fractures. Similarly, the thorax sustained only 14% of all haematomas, 2% of all lacerations and 2% of all fractures. Another study done in Denmark of 1156 male assault victims found that 68.5% of all injuries were facial (Brink, Vesterby & Jensen, 1998). A study of patients treated for domestic violence in the United States found that 81% of victims had maxillofacial injuries and in 69% of the victims the middle third of the face was most often involved (Le *et al.*, 2001). Two other studies of domestic violence that quantified the location of injuries also found that the face was the part of the body most frequently injured (Berrios & Grady, 1991; Petridou *et al.*, 2002). Several studies have quantified which facial bones are most likely to fracture as a result of interpersonal violence (Table 1). Fractures most often occur in the mandible, nasal complex, zygoma, maxilla and orbit. Thus, in modern state societies, the face is the most frequent target of interpersonal violence and, in addition to haematomas and lacerations, fractures of facial bones are common.

A frequent criticism of the hypothesis that selection for fighting ability influenced the evolution of hominin hands is that the human fist is too fragile to be used as a weapon (King, 2013). This suggestion is not supported by epidemiological data, which indicate that in modern societies interpersonal violence is the most frequent cause of fracture of the facial skeleton (Table 2), and the fist is the weapon most often used, causing 46–67% of the fight-associated facial fractures (Shepherd *et al.*, 1990; Boström, 1997; Brink *et al.*, 1998; Le *et al.*, 2001). Additionally, the study done in Sweden reported 63 facial fractures and 57 concussions inflicted by fists, but only eight fractures of the metacarpal or phalangeal bones (Boström, 1997). Thus, human fists are common and effective weapons and, when humans fight, faces break much more frequently than fists.



**Fig. 1.** Sites of injuries due to interpersonal violence in 1156 men attending the Accident and Emergency Departments and examined in the Department of Forensic Medicine in Aarhus, Denmark during a 1 year period from August 1993 to July 1994 (Brink *et al.*, 1998). Numbers represent the percentage of the total 1808 injuries that occurred in each region of the body. Note that the majority of injuries were inflicted on the face.

**II. PROTECTIVE BUTTRESSING OF THE FACE OF HOMININS**

**(1) Basal hominins**

When humans fight, the face is a vulnerable target. Given that the hand proportions that allow humans to form a buttressed fist appear to have been present in the

**Table 1.** Facial bones fractured as a result of interpersonal violence

	Christchurch Hospital <sup>a</sup>	Bristol Royal Infirmary <sup>b</sup>	Sabbatsbery Hospital (Stockholm) <sup>c</sup>
Mandible	40.8	41.3	4.8
Nasal complex	4.3	29.4	75.0
Zygoma	29.6	26.6	7.2
Orbit	17.3	1.4	5.6
Maxilla	7.8	1.4	6.4

Values are percent of total facial fractures.

<sup>a</sup>Lee (2009).

<sup>b</sup>Shepherd *et al.* (1990).

<sup>c</sup>Boström (1997).

earliest hominins, do the faces of early hominins exhibit evidence of increased robusticity and buttressing that would be protective in instances of interpersonal violence? Specifically, do the bones most susceptible to fracture during fighting, the mandible, zygomatic arch, nasal region, orbit and maxilla, exhibit increased robusticity?

The genus *Australopithecus* is characterized by robust mandibles (Fig. 2). Most dramatically, the mandibular corpus (i.e. body) of both gracile and robust australopiths is substantially broader, mediolaterally, than in chimpanzees (*Pan*), orangutans (*Pongo*) and gorillas (*Gorilla*) (Hylander, 1988; Daegling & Grine, 1991; Lockwood, Kimbel & Johanson, 2000; Kimbel *et al.*, 2004; Lieberman, 2011). This difference presumably gave australopiths great resistance to loading in torsion and shear, and combined with short corpus length also resulted in high resistance to mediolateral bending (Daegling & Grine, 1991). Compared to great apes the mandibular symphyses of australopiths are tall and deep (Lieberman, 2011). Additionally, the condylar processes of robust australopiths are relatively large, being more similar in size to those of gorillas than chimpanzees (Lieberman, 2011). The mandible of australopiths was also relatively broad in the transverse plane with the bi-articular breadth and breadth of the articular eminence approaching or equalling the values observed in much larger male gorillas (Kimbel *et al.*, 2004).

In both absolute and relative dimensions, the zygomatic bones of *A. afarensis*, *Paranthropus robustus* and *P. boisei* are large and massively built (Kimbel *et al.*, 2004; Figs 2 and 3). Robusticity is most pronounced anteriorly in the height and breadth of the zygomatic arch, in the frontal process and in the thickness of the inferior zygomatic margin. The zygoma of *A. afarensis* is more robust than that of *P. robustus* and *P. boisei*, but all three species exhibit robusticity equivalent to or exceeding that of the much larger-bodied male gorilla.

The australopith orbit was also well buttressed. Among *A. afarensis*, *P. robustus* and *P. boisei*, the frontal process, which forms the lateral margin of the eye, was exceptionally thick and wide; equalling, and in the case

Table 2. Mechanism of facial and mandible fracture

	Christchurch <sup>a</sup> (facial)	United States <sup>b</sup> (facial)	Seoul <sup>c</sup> (facial)	Montreal <sup>d</sup> (mandible)	Richmond, USA <sup>e</sup> (mandible)	Ankara <sup>e</sup> (mandible)
IPV	44	37	37.8	41	53.7	26.7
Falls	14	24.6	27.2	18	7.1	22.4
Sports	22	—	19.5	10	2.1	2.4
MVA	11	12.1	15.5	26	28.1	36.2
Other	10	16.3	0	3	7.5	12.4

IPV, interpersonal violence; MVA, motor vehicle accidents.

Values are percent of total facial (including mandible) or mandible fractures.

<sup>a</sup>Lee (2009).

<sup>b</sup>Allareddy *et al.* (2011).

<sup>c</sup>Suh & Kim (2012).

<sup>d</sup>Czerwinski *et al.* (2008).

<sup>e</sup>Simsek *et al.* (2007).

of *A. afarensis*, greatly exceeding, the same dimensions of male gorillas (Kimbel *et al.*, 2004). Although similar comparative data do not appear to exist for the supra-orbital torus, the general dimensions and shape of the frontal process were maintained as it arched medially to form the torus. In *A. afarensis*, the lateral wall of the orbit and the squama region of the frontal bone, above the supraorbital torus was also thicker than in chimpanzees and gorillas (Kimbel *et al.*, 2004).

The nasal bones of australopiths were similar to those of chimpanzees and gorillas in being relatively small and recessed in-line with the profile of the face, rather than protuberant as in *Homo*. Presumably as a consequence of this plesiomorphic configuration, the nasal bones of australopiths were less vulnerability to injury than is the case in modern humans. Additionally, the lateral margins of the nasal aperture were well supported by the relatively broad infraorbital region of the maxillary bones (Kimbel *et al.*, 2004), and in the case of *A. africanus* and *P. robustus* by stout anterior pillars of the maxilla (Rak, 1983).

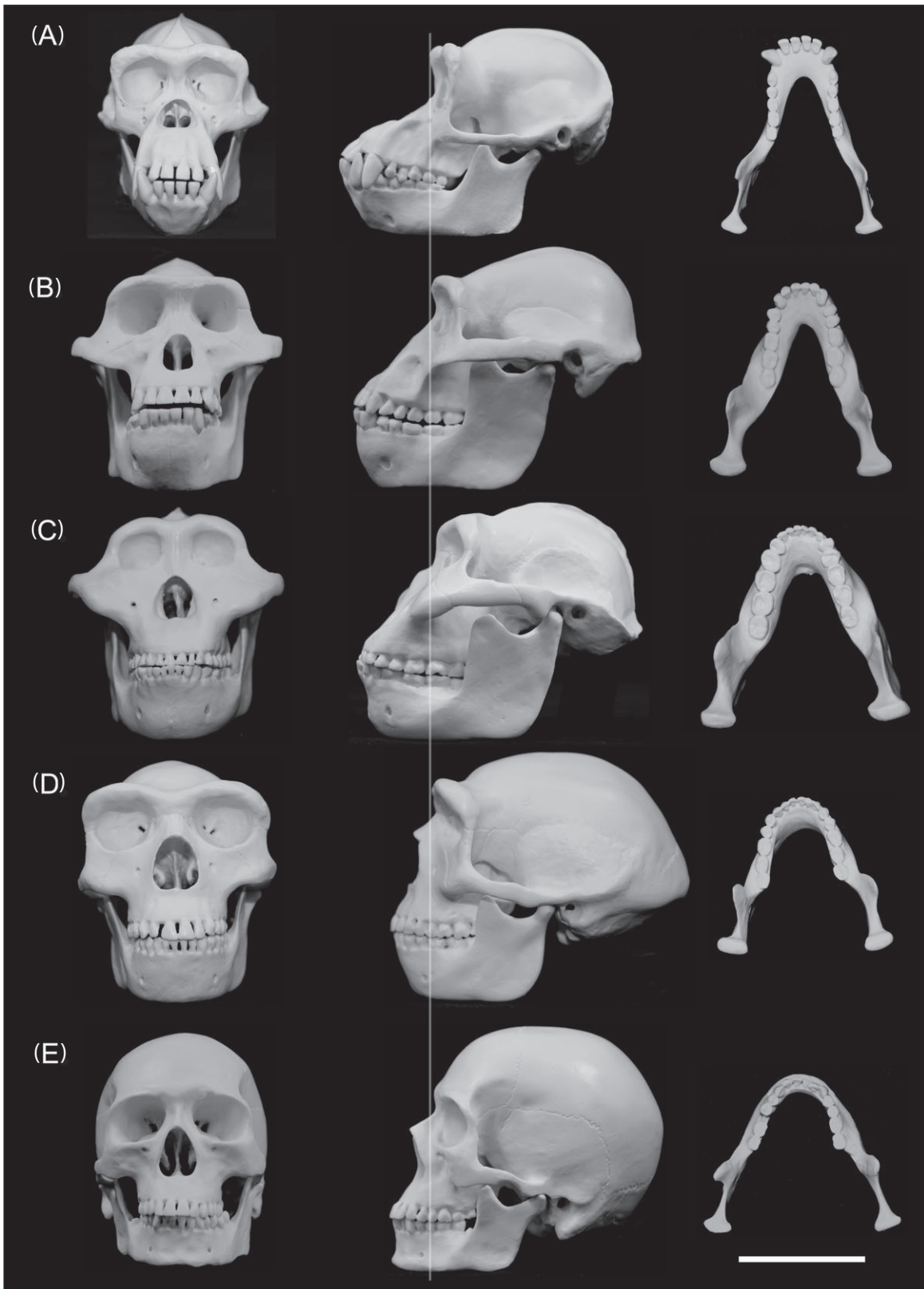
Beginning in early hominins, the trend towards a more vertically oriented, orthognathic face (Rak, 1983; Lieberman, 2011; Fig. 2) reduced the rotational moment on the skull from a blow applied in the region of the mandibular symphysis. At the same time, this change in shape of the face increased the mechanical advantage of the jaw adductor and neck muscles that may provide protective energy absorption when the chin is struck.

Thus, the evolution of hand proportions that allow the formation of a buttressed fist is roughly coincident with the evolution of facial robusticity. The parts of the facial skeleton that are most subject to fracture during interpersonal violence in modern humans tend to exhibit disproportionately large dimensions in australopiths, often equal to or exceeding values reported in much larger-bodied male gorillas. Regardless of the evolutionary reasons for these features, the facial skeleton of australopiths was well proportioned to withstand strikes.

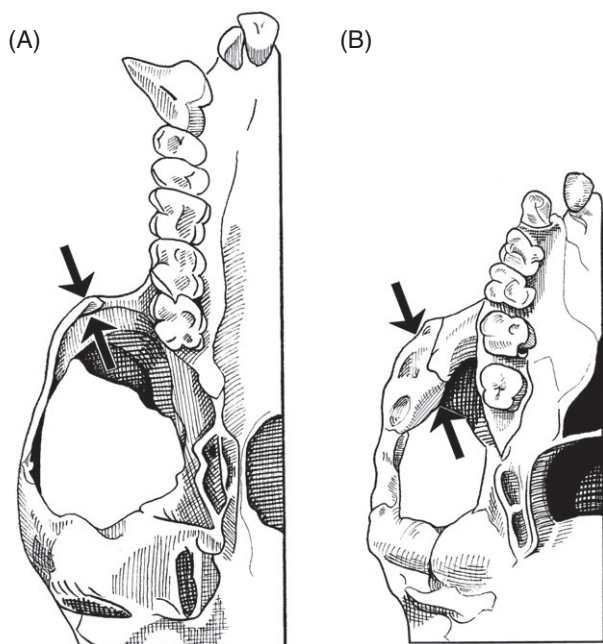
## (2) Adaptation for fighting may explain some aspects of facial robusticity in primates

The facial skeleton of primates is generally assumed to be an adaptive response to the demands of mastication. If all facial bones are adapted to minimize bone tissue and maximize strength for countering loading during mastication and incision of food, bone strain produced by chewing would be relatively uniform throughout the facial skeleton. However, *in vivo* measurements of bone strain during chewing and incision are highly variable among regions of the primate face (Ravosa, Johnson & Hylander, 2000a; Ross & Metzger, 2004). Most notably, bone strains during chewing are relatively low in the middle and posterior portions of the zygomatic arch (Hylander & Johnson, 1997), around the orbit (Hylander, Picq & Johnson, 1991*a,b*; Ross & Hylander, 1996; Ravosa *et al.*, 2000*a,b*; Ravosa, Vinyard & Hylander, 2000c), and in the lingual and subcondylar regions of the mandible (Ross & Metzger, 2004). Finite element analyses of the cranium of *A. africanus* and *Macaca fascicularis* simulating molar and premolar biting indicate that masticatory strains are low in the skeletal tissue below and above the orbit, nasal pillar, and frontal process of the zygomatic arch (Strait *et al.*, 2010). These observations suggest that at least some parts of the primate facial skeleton are overbuilt for mastication.

Regions of the primate facial skeleton that have been shown to experience relatively low strain during chewing are known to exhibit relatively high levels of sexual dimorphism. A detailed and phylogenetically broad analysis of craniofacial sexual dimorphism in primates found that metrics of orbital margin, mandible and zygomatic robusticity are among the most dimorphic (Plavcan, 2002). Greater robusticity of the mandible and zygomatic arch in male primates may be associated with stronger adductor muscles (Demes & Creel, 1988; Plavcan, 2002) and higher loading of these skeletal structures during biting behaviour that occurs in many species during male–male contest competition. By contrast, sexual dimorphism of the orbital margin



**Fig. 2.** Photographs of skull reconstructions comparing chimpanzees with four hominins: (A) *Pan troglodytes*; (B) *Australopithecus afarensis*; (C) *Paranthropus boisei*; (D) *Homo erectus*; (E) *Homo sapiens*. Images are (from left to right) frontal and lateral views of the skulls, and dorsal view of the mandibles. The lateral views are aligned by the bridge of the nose (vertical line). Scale bar, 100 mm. Reconstructions were supplied by Skulls Unlimited (Oklahoma City, OK, USA).



**Fig. 3.** Ventral view of the skulls of (A) a male gorilla and (B) a male *Australopithecus afarensis* (A. L. 444-2) illustrating the difference in thickness of the zygomatic arches of these species. Arrows compare the attachment sites of the anterior portion of the masseter muscle. Although male gorillas are three- to fourfold more massive in body size, the arch of *A. afarensis* was much more robust. Modified from Kimbel *et al.* (2004).

may be better explained as buttressing to protect the eye from injury when being bitten or struck by an opponent. Indeed, among researchers who have investigated skeletal strain during chewing, robusticity of the orbital margin is interpreted to prevent structural failure due to accidental trauma (Hylander *et al.*, 1991*b*; Ravosa *et al.*, 2000) as might occur during fighting. Thus, the observation that those regions of the face that exhibit the lowest levels of skeletal strain during chewing are also regions that tend to be highly sexually dimorphic raises the possibility that the proportions of these parts of face may be a result of sexual selection on fighting performance.

### (3) Preflex protection of the hominin jaw

Several observations suggest that the temporalis and masseter muscles of humans are overbuilt for mastication. Unilateral measurements of maximum bite force between pairs of opposing teeth in the molar region tend to average from 300 to 600 N (Hagberg, 1987; Bakke *et al.*, 1989; van der Bilt *et al.*, 2008). Chewing forces during feeding are estimated to be from one-third to roughly the same as these maximum bite forces, depending on the hardness of the food (Pruim, De Jongh & Ten Bosch, 1980; Bakke *et al.*, 1989). However, higher bite forces occur when the occlusal area

increases from one pair of opposing molar teeth to several pairs of opposing teeth (Bakke, 1993; Waltimo & Könönen, 1994). This suggests that the adductor muscles can generate forces that exceed those they produce during chewing. A similar conclusion can be drawn from studies in which the periodontal receptors are anaesthetized. Although there are conflicting results in the literature (Teenier, Throckmorton & Ellis, 1991), maximum bite forces between two antagonistic molar teeth increase by approximately 30% when periodontal receptors are blocked with local anaesthesia (Orchardson & MacFarlane, 1980). Similarly, a 30–40% increase in electromyographic activity of the masseter and temporalis muscles has been observed during maximum clenching efforts when the periodontal receptors are anaesthetized (Manns *et al.*, 1991). These observations suggest that human jaw adductor muscles are capable of producing larger forces than those produced during chewing. Overbuilt jaw adductors might make sense if biting was used to injure opponents during interpersonal aggression, but humans rarely bite when they fight (Shepherd *et al.*, 1990; Boström, 1997).

In addition to mastication and biting, jaw adductor muscles may function to protect the mandible when the lower jaw is punched during fighting. If the adductors are active isometrically, either with the teeth in occlusion or with the mouth held partially open through co-activation of antagonistic jaw depressors, a horizontally and/or downward-directed blow to the front or side of the mandible will act to laterally rotate and/or open the jaw, resulting in stretching of the active masseter and temporalis muscles. The instantaneous increase of force generation when active muscle is suddenly stretched (Katz, 1939; Edman, 1988) may act as a preflex (Baratta *et al.*, 1988; Loeb, 1995; Blickhan *et al.*, 2007) to stabilize the lower jaw, protecting it from dislocation. At the same time, stretching of active jaw adductors would absorb energy that may reduce bone strain and prevent fracture (reviewed by Burr, 2011). This possibility is supported by the observation that activation of the jaw and neck muscles stiffens the connection between the head and body, decreases acceleration of the brain upon impact and therefore reduces the risk of concussion (Viano, Casson & Pellman, 2007; Hasegawa *et al.*, 2013).

Although the jaw adductor muscles appear to be overbuilt for mastication, they are small compared to the muscles of the arm and trunk and might be unable to provide effective protection to the mandible. However, a simple estimate of the percentage of the energy of a strike that jaw muscles are capable of absorbing suggests that they can provide protection. Recordings of Olympic boxers striking the face of a Hybrid III dummy demonstrated average punch energy of 20.2 J (Walilko, Viano & Bir, 2005). In males, average maximum bite force ranges from 547 to 847 N (Waltimo & Könönen, 1993; Raadsheer *et al.*, 2004). The mechanical advantage of the human adductor muscles at the molars where

bite force is measured is 0.7 (Lieberman, 2011), which translates to a maximum adductor muscle force ranging from 781 to 1210 N. The increase in force when human muscles are stretched from an isometric contraction ranges from 25 to 122% (Linnamo, Strojnik & Komi, 2006; Choi & Widrick, 2010). If we conservatively assume at the time the mandible is struck that (i) the adductor muscles are 50% isometrically activated, such that they are generating a total force of 450 N; (ii) an instantaneous increase in force of 40% as the adductor muscles are stretched due to opening of the jaw; (iii) that the muscle fibres are stretched mainly over the peak of the length–tension relationship such that they generate an average of 80% of peak force; (iv) a 4.0 cm opening displacement at the incisors as a result of the strike; and (v) a mechanical advantage of the adductor muscles against the force of the strike, also at the incisors, of 0.3, then the adductor muscles would produce approximately 6.1 J of negative work; 30% of the average punch energy of Olympic boxers. Thus, it is reasonable to expect that human adductor muscles are able to dissipate a significant portion of the energy of a punch to the lower jaw and therefore greatly reduce the risk of dislocation and fracture.

Massive jaw adductor muscles characterized australopiths (Rak, 1983; Demes & Creel, 1988; Lieberman, 2011; Eng *et al.*, 2013). In *A. afarensis* the inferior border of the zygomatic bone, the massetric scar to which the masseter muscle attaches, is extremely thick, much thicker than that chimpanzees and even male gorillas (Kimbel *et al.*, 2004, Fig. 3). The relatively large size of the massetric scar characterizes the hominins and is largest in *A. robustus* and *P. boisei* (Kimbel *et al.*, 2004). Temporal lines and crests, as well as nuchal crests indicate that australopiths also possessed well-developed temporalis muscles (Rak, 1983; Kimbel *et al.*, 2004; Lieberman, 2011). Recent, anatomically based estimates of maximum bite force indicate that the jaw adductors of australopiths were as strong as those of much larger-bodied male orangutans and gorillas (Eng *et al.*, 2013). If the masseter and temporalis muscles do protect against dislocation and fracture of the mandible during fighting, australopiths appear to have been well protected.

#### (4) Postcanine teeth may transfer punch energy from the lower jaw to the skull

Australopiths are distinguished from other great apes by the massive size and thick enamel of their postcanine teeth (Rak, 1983; Kimbel *et al.*, 2004; Lieberman, 2011). The summed occlusal area of the premolar and molar teeth averages approximately 450–500 mm<sup>2</sup> in chimpanzees, 760–850 mm<sup>2</sup> in gracile australopiths and 970–1228 mm<sup>2</sup> in robust australopiths (Wood, 1991; Lieberman, 2011). The large size and thick enamel of these teeth has traditionally been interpreted to be an

adaptation to a very hard and/or abrasive diet (Teaford & Ungar, 2000).

Regardless of their role in chewing, the large, thickly enamelled, bunodont postcanine teeth of australopiths may have allowed energy from an upward strike to the jaw to be transferred from the lower jaw to the skull. The energy in an upward blow to the lower jaw can presumably be absorbed by stretching of active depressor muscles of the mandible (e.g. digastric, geniohyoideus, sternohyoideus, omohyoideus, sternothyroideus muscles), and/or transferred to the skull through the occlusal contacts of the teeth, resulting in acceleration of the head and stretch of potentially active muscles of the neck (e.g. sternomastoideus, scalene, and hypo-branchial muscles). If the lower jaw is a punching target during fighting then postcanine teeth are potentially vulnerable to fracture as a result of sudden impact of occlusal surfaces. Although epidemiology indicates that injury to the postcanine teeth rarely occurs as a result of interpersonal violence in modern humans (Bastone, Freer & McNamara, 2000), large size, thick enamel and the rounded cusps of bunodont molars (Berthaume *et al.*, 2010) would reduce the risk of injury if the jaws were suddenly slammed together with high energy.

#### (5) Reduced buttressing in the face of *Homo*

The facial skeleton of *Homo* presents a challenge to the protective buttressing hypothesis (Nickle & Goncharoff, 2013). The skull of *Homo* is distinguished from that of *Australopithecus* by a reduction in the masticatory system (reviewed by Lieberman, 2011). Compared to the gracile australopiths, early *Homo habilis* and *H. erectus*, were characterized by reductions in the medio-lateral dimensions of the maxilla and zygomatic bones. Although metrics of jaw and molar robusticity group *H. habilis* with the australopiths, a general reduction in the size of the molar crowns characterizes *H. erectus* (Wood & Collard, 1999). Associated with this reduction in molar size in *H. erectus* are clear indications of weaker jaw muscles, narrower mandibular condyles and less-robust zygomatic arches. The trend of reduced facial and dentition size continues in species of late archaic *Homo* and in *H. sapiens*. Estimates of overall size indicate that the face of *H. sapiens* is 15–25% smaller than in taxa of archaic *Homo* and a 6% decrease in facial length of *H. sapiens* occurred during the last few thousand years (Lieberman, 2011). If the facial structure of australopiths is, in part, a function of selection for protective buttressing against strikes from fists, why did the face of *Homo* evolve to be less robust?

The reduction in facial and masticatory system size in *Homo* may be associated with a general reduction in upper body strength. Throughout the evolutionary history of *Homo*, a decrease in skeletal robusticity of the arm indicates a more-or-less continuous reduction in upper body strength (Ruff *et al.*, 1993; Trinkaus, 1997). Additionally, between late archaic *Homo* and early

modern humans there was a decrease in the robusticity of the caudal cervical vertebral spinous processes that serve as attachment sites for parts of the trapezius, rhomboideus and levator scapulae muscles; decreases in the size and rugosity of the proximal humeral insertion sites of the extrinsic arm muscles; and marked reduction in palmar carpal tuberosities indicating a reduction in the size and mechanical advantage of both the extrinsic and intrinsic hand musculature (Trinkaus, 1997). Thus, as the strength of the upper body decreased in *Homo*, striking power must have decreased and the level of buttressing necessary to protect the face against fist strikes during fighting would also have declined.

### III. SEXUAL DIFFERENCES IN VIOLENCE AND FACIAL ROBUSTICITY

#### (1) Human violence and postcranial dimorphism

As is the case in other species of great apes, human males perpetrate the vast majority of violence and most of these acts of aggression are directed at other males (Adams, 1983; Chagnon, 1988; Daly & Wilson, 1988; Keeley, 1996; Wrangham & Peterson, 1996; Walker, 2001; Ellis, 2008; Puts, 2010). Consequently, it is not surprising that human males suffer more injuries to the face from interpersonal violence than do females: 92.1% (Lee, 2009), 84% (Shepherd *et al.*, 1990), 82% (Brink *et al.*, 1998), 83% (Suh & Kim, 2012), 68% (Allaredy, Allaredy & Nalliah, 2011), 78% (Czerwinski *et al.*, 2008), 90% (Boström, 1997), and 84 and 76% (Simsek *et al.*, 2007).

Although humans are generally viewed as exhibiting low to moderate levels of sexual dimorphism (McHenry, 1994; Plavcan, 2001, 2012; Reno *et al.*, 2003), the relatively low body mass dimorphism of humans is largely a consequence of human females having substantial fat stores (Pond & Mattacks, 1987). When fat-free masses are compared, men are 41% more massive (Mayhew & Salm, 1990; Lassek & Gaulin, 2009) and have 48–65% more muscle mass than women (Illner *et al.*, 2000; Abe, Kearns & Fukunaga, 2003; Kim *et al.*, 2004; Shen *et al.*, 2004). As in gorillas (Zihlman & McFarland, 2000) and australopiths (McHenry, 1986, 1991, 1996), the upper body of humans exhibits more sexual dimorphism in size and strength than do the legs (Abe *et al.*, 2003; Raadsheer *et al.*, 2004; Lassek & Gaulin, 2009; Price *et al.*, 2012). Among young adults, the muscles of the arm are 69–109% stronger in males than in females, whereas strength dimorphism of leg muscles range from only 23 to 66% (Bohannon, 1997). The most sexual dimorphic part of the human body, in terms of muscular strength, may be the neck. Maximum moments produced by the muscles of the neck are 100–150% greater in men than in women (Vasavada, Li & Delp, 2001). Pronounced sexual dimorphism in cervical muscles is surprising given that humans do

not fight by biting with the jaws. However, as discussed above, energy absorption by the muscles of the neck can protect against concussion when the head is struck. Thus, humans do show very high levels of sexual dimorphism in the parts of the postcranial musculoskeletal system that appear to be most important in fighting (Lassek & Gaulin, 2009; Puts, 2010; Carrier, 2011; Sell, Hone & Pound, 2012; Morgan & Carrier, 2013).

Because sexual dimorphism is often greatest in those characters that enhance a male's capacity to dominate other males (Clutton-Brock & Harvey, 1977; Parker, 1983; Andersson, 1994), the observation that the face is the primary target when males fight leads to the expectation of sexual dimorphism in buttressing of the human face (Puts, 2010). The protective buttressing hypothesis predicts that the most dimorphic parts of the hominin skull will be those that are most frequently injured during fighting, namely the mandible, nasal region, zygomatic arch, orbit and maxilla.

#### (2) Human dentition and facial skeleton

In humans and primates in general, metrics of the face are more sexually dimorphic than metrics of the neurocranium (Plavcan, 2002). Among the great apes, the pattern for the dentition is complex. Humans exhibit dramatically lower sexual dimorphism of the canine teeth than other ape species, as would be expected in a species that does not fight with its teeth. Nevertheless, the molar teeth of humans are more dimorphic than those of chimpanzees and slightly less dimorphic than in gorillas and orangutans (Wood, 1976; Frayer & Wolpoff, 1985; Wood, Li & Willoughby, 1991). The pattern of dimorphism in the mandible mirrors that of the molar teeth; human mandibles are more dimorphic than chimpanzees but less dimorphic than gorillas and orangutans (Wood, 1976; Frayer & Wolpoff, 1985; Wood *et al.*, 1991). The mandibular metrics that are the most dimorphic in humans include condylar and coronoid height, condylar width and anterior–posterior diameter, breadth of the ramus, minimum ramus breadth, bigonial breadth, and height and thickness of the symphysis (Wood, 1976; Wood *et al.*, 1991; Steyn & İşcan, 1998). Metrics of the human face that are the most dimorphic include size of supraorbital tori (ridges), interorbital breadth (width of nose between the eyes), maximum width and length of the nose (nasion-nasospinale), breadth of the maxilla, and bizygomatic breadth (Wood, 1976; Wood *et al.*, 1991; Steyn & İşcan, 1998; Bass, 2005; Franklin, Freedman & Milne, 2005).

As predicted, the parts of the human facial skeleton that exhibit marked sexual dimorphism are also the parts of the skull that most frequently fracture when people fight (Table 1). First, as described above, the face of humans exhibits much more sexual dimorphism than the neurocranium and fractures of the face as a result of fighting are much more common than fractures



of the neurocranium (Shepherd *et al.*, 1990; Boström, 1997). Second, although relative frequency of fracture type varies among the studies included in Table 1, the sites of facial fracture are the same in each study. Of the mandibular fractures in the Bristol study, 25.4% were to the condyle or coronoid, 35.6% were to the ramus, 35.6% to the angle, and 3.4% to the symphysis. Additionally, the nasal region, zygoma and orbit are also sites of frequent injury and exhibit relatively high sexual dimorphism. Thus, a dramatic correspondence exists between the parts of the skull that are most sexually dimorphic and the parts that most frequently fracture during fighting.

### (3) Human jaw muscles

Given that humans have relatively small canine teeth, exhibit low canine sexual dimorphism (Frayer & Wolpoff, 1985; Wood *et al.*, 1991; Plavcan & van Schaik, 1997) and rarely bite during fighting (Shepherd *et al.*, 1990; Boström, 1997), it is puzzling that humans exhibit significant sexual dimorphism in the strength of their jaw adductor muscles. Five studies that measured maximum bite force in men and women indicate that, on average, men produce  $34.3 \pm 10.5\%$  (mean  $\pm$  S.D.) greater forces than women (Klatsky, 1942; Waltimo & Könönen, 1993; Braun *et al.*, 1995; Raadsheer *et al.*, 2004; van der Bilt *et al.*, 2008). This level of sexual dimorphism is only 7–20% below estimated sexual dimorphism in bite force of gorillas and orangutans (Demes & Creel, 1988; Eng *et al.*, 2013); species in which biting is an important male fighting behaviour. The human masseter muscle also exhibits substantial gender differences in the proportion of fast-twitch (type II) muscle fibres. The average cross-sectional area of type II fibres in the masseter muscle averages 66.9% in males and only 8.3% in females (Tuxen, Bakke & Kenrad, 1992; Tuxen, Bakke & Pinholt, 1999). Type II muscle fibres shorten faster and generate force more quickly when stimulated than type I fibres (Close, 1967). Although human sexual dimorphism in adductor muscle strength and fibre type cannot be explained by aggressive biting behaviour during fighting or by mastication, because diets of human males and females are largely similar, the observed human dimorphism is consistent with the hypothesis of protective buttressing of the face. If the jaw adductor muscles do function to protect against mandibular dislocation and fracture, as suggested above, greater muscle strength and shorter force activation times in males would be expected because of their higher incidence of fighting and facial injury.

### (4) Australopith dentition and facial skeleton

Early hominins (*Australopithecus* and *Paranthropus*) appear to have had pronounced sexual dimorphism in body size with males being bigger than females (McHenry, 1996; Gordon, Green & Richmond, 2008),

and the highest levels of postcranial dimorphism are observed in metrics of the forelimbs (McHenry, 1986, 1991, 1996). For an alternative perspective on body size dimorphism in *Australopithecus afarensis* see Reno *et al.* (2010). Nevertheless, if early hominins did fight by striking with their fists and the face was the primary target, the pronounced postcranial sexual dimorphism observed in great apes and humans lead to expectations of high levels of sexual dimorphism in the facial skeleton of early hominins.

Patterns of sexual dimorphism in the face and dentition of australopiths are consistent with the protective buttressing hypothesis. As in other primates, the most dimorphic parts of australopith skulls were aspects of the face (Plavcan, 2003). Although the fossil record limits sample size for analysis, aspects of the face that appear to be highly dimorphic in australopiths are the size and robusticity of the mandible (Frayer & Wolpoff, 1985; Lockwood *et al.*, 2000), zygomatic (malar) height (Lockwood, 1999; Plavcan, 2003), anterior pillars in *A. africanus* (Lockwood, 1999), and supraorbital tori (Lockwood, 1999). The development of cranial crests indicates significant sexual dimorphism in size of the jaw adductor muscles (Kimbel *et al.*, 2004; Lieberman, 2011). The magnitude of facial dimorphism in australopiths appears to have been roughly equivalent to that of the most dimorphic great apes, gorillas and orangutans (Wood, 1991; Lockwood *et al.*, 2000). Additionally, the level of dimorphism in the face of australopiths appears to be similar or greater in magnitude than the level of dimorphism observed in their postcranial skeleton (Lockwood, 1999; Plavcan, 2003). Finally, as would be expected from the protective buttressing hypothesis, the most facially robust species *P. boisei* and *P. robustus* appear to have been more sexually dimorphic than the gracile species (Chamberlain & Wood, 1985; Lockwood, 1999; Lockwood *et al.*, 2000).

### (5) Conclusion

Although the mechanics of chewing are generally accepted to explain the evolution of facial and dental robusticity in hominins, it is hard to see how they can explain pronounced sexual dimorphism in facial and dental robusticity because male and female diets are largely similar in extant apes. Facial dimorphism in most species of primates is likely to be a function of the importance of the canine teeth in male–male fighting. However, the relatively small size and low sexual dimorphism in the canines of australopiths and *Homo* (Plavcan & van Schaik, 1997) indicate that facial dimorphism in hominins is not a result of sexual selection on offensive weapons. Furthermore, the observation that, in hominins, the postcanine teeth and facial structures are more sexually dimorphic than the canine teeth and neurocranium suggests that dimorphism of the face and postcanine dentition are not a simple allometric consequence of males being larger than females. Rather,

sexual dimorphism in cheek teeth, facial robusticity and jaw muscle strength in australopiths and humans is likely associated with sexual selection to protect the face against injury during fighting with fists.

#### IV. WHY WAS THE MASTICATORY SYSTEM OF EARLY HOMININS ROBUST?

It is possible that many aspects of the early hominin face were not a consequence of natural selection. For example, the large browridges of many primate species, including early hominins, may develop as a consequence of the spatial relationship of the orbits and face in front of the neurocranium (Moss & Young, 1960; Shea, 1985; Ravosa, 1988; Lieberman, 2000, 2011). Projection of the upper face occurs through differential growth of the inner and outer layers of cortical bone (referred to as 'tables') of the frontal bone, which are parts of the neurocranium and face, respectively. As the orbits grow anteriorly relative to the anterior cranial fossa, the browridge forms as a result of growth of the outer table. How much the face projects in front of the anterior cranial fossa is a function of the relative anteroposterior growth of the anterior cranial fossa itself, the anterior cranial base, and the face. Variation in browridge size may partially be a function of brain size, such that hominins with larger skulls have proportionally more facial projection, and therefore longer browridges (Ravosa, 1988; Lieberman, 2000). Additionally, browridge size is at some level a function of facial size (Shea, 1986; Ravosa, 1991; Lieberman, 2000). Hominins with larger faces relative to cranial size tend to have more facial projection and longer browridges. The size of the dentition also has developmental consequences on the size and shape of the face. McCollum (1999) argued that the robust postcanine but small anterior teeth of australopiths require a pattern of facial growth that may explain all of the synapomorphies of the *Paranthropus* face.

If, however, facial structure of early hominins is at some level a function of natural selection on musculoskeletal performance, the anatomy of the australopith masticatory system presents us with an enigma. The facial and dental traits that distinguish australopiths have generally been assumed to be adaptations to a diet requiring excessively high bite forces to process hard, stress-limited objects such as seed and nuts (Robinson, 1954; Jolly, 1970; Rak, 1983; Kay, 1985; Daegling & Grine, 1991; Teaford & Ungar, 2000; Ungar *et al.*, 2008; Strait *et al.*, 2009, 2010, 2013; Berthaume *et al.*, 2010; Lieberman, 2011) or adaptations that allow the consumption of large volumes of tough food, such as grasses or roots encrusted with soil, that resulted in high wear damage to the teeth (Teaford & Ungar, 2000; Ungar & Sponheimer, 2011; Ungar *et al.*, 2012). However, analyses of patterns of microwear on postcanine teeth and carbon isotopes suggest that,

with the exception of *P. robustus*, australopiths did not consume significant amounts of hard objects (Walker, 1981; Scott *et al.*, 2005; Ungar & Sponheimer, 2011; Grine *et al.*, 2012; Ungar *et al.*, 2012; Sponheimer *et al.*, 2013) and, with the exception of *P. boisei*, australopiths did not consume large volumes of foods that were tough such as leaves and grasses (van der Merwe, Masao & Bamford, 2008; Cerling *et al.*, 2011; Sponheimer *et al.*, 2013).

The comparative morphological and biomechanical evidence supporting a diet that required high bite forces in early hominins is compelling. The enlargement of the crowns of the molar and premolar teeth, as well as molarization of the premolars, is consistent with selection for elevated bite forces (Robinson, 1954; Rak, 1983; Teaford & Ungar, 2000; Strait *et al.*, 2009, 2013; Lieberman, 2011). Additionally, reduction in the size and steepness of crests of the occlusal surfaces of the molar and premolar teeth, resulting in a bunodont configuration, is consistent with specialization to resist fracture of the teeth during high-force biting (Berthaume *et al.*, 2010). Medio-lateral robusticity of the mandibular corpus is consistent with the need to resist elevated torsional stress intrinsic to high-force biting due to high torsional moments applied by the adductor muscles on the non-biting side of the jaw (Daegling & Grine, 1991). The very large attachment sites for the masseter on the ventral surface of the zygomatic arch (Fig. 3) and the large temporal fossa and sagittal and nuchal crests that serve as attachment sites for the temporalis muscle indicate relatively massive jaw adductor muscles (Rak, 1983; Kimbel *et al.*, 2004). Finally, the trends towards a more orthognathic face, more anterior-placed attachment sites for the masseter muscle, and the development of paranasal anterior pillars increase the capacity for elevated bite forces by the premolar teeth (Rak, 1983; Strait *et al.*, 2009, 2010; Lieberman, 2011). These facial features distinguish hominins from the other great apes and, in the absence of other data, provide a persuasive argument for a diet requiring very high bite forces.

The microwear patterns on the teeth of early hominins, however, suggest these species rarely fed on hard objects (Scott *et al.*, 2005; Grine, Ungar & Teaford, 2006a; Grine *et al.*, 2006b, 2012; Suwa *et al.*, 2009; Ungar *et al.*, 2012). Specifically, the postcanine teeth of *A. anamensis*, *A. afarensis*, *A. africanus*, *P. boisei* and *H. habilis* do not have the high complexity texture values or the heavily pitted surfaces of hard-object feeders (Ungar & Sponheimer, 2011; Ungar *et al.*, 2012). Among the australopiths, only *P. robustus* exhibits microwear patterns consistent with a diet that includes hard objects (Grine, 1986; Grine & Kay, 1988; Scott *et al.*, 2005; Grine *et al.*, 2012), exhibiting a pattern most comparable to hard-object fallback feeders such as gray-cheeked mangabeys (*Lophocebus albigena*) (Scott *et al.*, 2005).

Microwear patterns may also provide evidence about food types with a high capacity to abrade teeth, such

as grasses or roots carrying soil. Teeth of *A. anamensis*, *A. afarensis* and *A. africanus* have low to moderate anisotropy, with few values equivalent to the upper ranges of living folivorous primates, suggesting that they did not eat tough leaves or grass (Ungar & Sponheimer, 2011; Ungar *et al.*, 2012). The microwear patterns from the teeth of *P. boisei* also suggest a diet similar to extant frugivores such as African apes (Walker, 1981; Ungar *et al.*, 2008, 2012; Suwa *et al.*, 2009; Grine *et al.*, 2012). Nevertheless, recent carbon isotope analyses of the teeth of *P. boisei* indicate that their diet was primarily composed of tough C<sub>4</sub> grasses, sedges, and/or grazing animals that ate grasses and sedges (van der Merwe *et al.*, 2008; Cerling *et al.*, 2011). Thus, although the microwear data suggest that australopiths, as a group, did not feed on tough vegetation such as leaves and grasses, the carbon isotope data from *P. boisei* imply that its diet was primarily composed of grasses and sedges.

The suggestion that *P. boisei* was herbivorous, with a diet composed primarily of grasses and sedges, is hard to reconcile with its hyper-robust oral-facial anatomy. Although herbivores generally have hypsodont or selenodont teeth, which maintain shearing crests on the occlusal surfaces as the teeth wear, the teeth of gracile australopiths, such as *A. afarensis*, exhibited less occlusal relief than either chimpanzees or gorillas (Ungar, 2004) and among australopiths the teeth of *P. boisei* had the most rounded (i.e. bunodont) crests (Kay, 1985; Ungar *et al.*, 2008; Berthaume *et al.*, 2010). Because shearing crests appear to be critical in primates for processing tough foods (Kay, 1977; Lucas, 2004; Lucas *et al.*, 2008), it is difficult to argue that the bunodont premolar and molar teeth of *P. boisei* were adaptations to the consumption of grasses and sedges (Kay, 1981; Teaford & Ungar, 2000; Strait *et al.*, 2009). Additionally, the microstructure and great thickness of the enamel of the cheek teeth of *P. boisei* are more consistent with selection for cracking large hard objects than selection to prolong tooth lifetime in situations in which chewing causes progressive erosion of the surface (Lucas *et al.*, 2008; Lawn *et al.*, 2009). The architecture of the mandible also provides relevant clues. In contrast to australopiths, the mandibles of most mammalian herbivores that eat tough leaves and grasses are poorly configured to resist torsional loading. Although the mandibular corpus of mammalian herbivores is often deep, dorso-ventrally, it is generally relatively thin medio-laterally. Further, the mandibular symphysis is weak or poorly formed in many artiodactyls, lagomorphs and rodents that primarily eat grasses. These observations indicate that torsional loads on the mandibular corpus are not large in most species specialized for eating leaves and grasses. Yet the hyper-robust mandible of *P. boisei* was shaped in ways that would have provided very high resistance to torsional loads (Daegling & Grine, 1991). Thus, although analyses of carbon isotopes indicate that the diet of *P. boisei* was primarily composed of grasses and

sedges, it appears that selection for eating these foods cannot explain the evolution of its masticatory system (Strait *et al.*, 2013).

Current hypotheses that attempt to explain the evolution of the robusticity of the face and dentition of early hominins lead to different testable predictions (Table 3). Four facets of these predictions can be evaluated with available data. (i) If facial structure was primarily a response to the mechanical demands of chewing on hard or tough foods, strain of the skeleton during chewing should be of roughly similar magnitude throughout the mandible and face, including the zygomatic arch and browridges. However, as discussed above, strain recordings and finite element analyses simulating molar and premolar biting in primates suggest that this is not the case. (ii) Predictions for the size, shape and enamel thickness of the postcanine teeth are similar for the 'feeding on hard objects' and 'protective buttressing' hypotheses but differ for the 'feeding on tough objects' hypothesis. Additionally, if anatomy of the postcanine teeth is at some level a function of selection to protect the face from fist strikes, microwear and carbon isotope evidence of diet need not be consistent with morphological specialization of the teeth, as appears to be the case. (iii) The predicted strength of the jaw adductor muscles also varies among the functional hypotheses. To be consistent with the feeding hypotheses, jaw muscle strength should reflect maximum masticatory forces because hominins are thought not to have fought by biting. However, jaw adductor muscle strength that exceeds masticatory forces is predicted by the 'protective buttressing' hypothesis, as appears to be the case in modern humans. (iv) Sexual dimorphism of the face, jaw adductor muscles and cheek teeth are consistent with the 'protective buttressing' hypothesis. Because diet does not differ substantially between male and female apes and biting appears not to have been important in the hominin fighting, the feeding hypotheses predicts sexual dimorphism of the postcanine teeth, mandible, zygomatic arch and jaw adductor muscles to be equivalent to observed dimorphism of the canine teeth and/or neurocranium. However, as is predicted by the 'protective buttressing' hypothesis, sexual dimorphism is substantially greater in all of these variables than that observed in the canine teeth and neurocranium.

In conclusion, although the comparative morphological and biomechanical evidence suggests that the derived features of the australopith face were a function of selection acting on the mechanics of mastication, recent attempts to reconstruct the diet of these early hominins raise the possibility that this was not the case. The protective buttressing hypothesis provides an alternative functional explanation for the evolution of the hominin face. As a result of the evolution of habitual bipedalism (Carrier, 2011) and hand proportions that made possible a clenched fist (Morgan &

Table 3. Predictions of hypotheses for the evolution of facial robusticity in early hominins

Structure	Hypotheses			
	Feeding on hard objects	Feeding on tough foods	Development/ pleiotropy	Protective buttressing
Mandible robusticity	Massive with robust symphysis, ramus and condyl; uniform facial and mandibular strain during mastication	Ramus deep dorso-ventrally but narrow laterally; weak symphysis; uniform strain during mastication	Massive to accommodate large postcanine teeth (McCollum, 1999)	Massive with robust symphysis, ramus and condyl; facial strain during mastication not uniform
Browridge size	Small; strain during feeding uniform and similar in magnitude to that in mandible	Small, strain during feeding uniform and similar in magnitude to that in mandible	Large due to spatial relationship of the orbits, face and neurocranium	Large
Zygomatic arch robusticity	Large and robust; strain during feeding uniform and similar in magnitude to that in mandible	Intermediate, strain during feeding uniform and similar in magnitude to mandible	Similar to ancestral state or equivalent to interspecific scaling	Large and very robust to resist forces from blows transmitted directly and through the masseter muscle
Postcanine teeth size and enamel thickness	Large and thick; consistent microwear and carbon isotopes	Large and thick; consistent microwear and carbon isotopes	Similar to ancestral state or equivalent to interspecific scaling	Large and thick; microwear and carbon isotopes not consistent with tooth anatomy
Postcanine teeth shape	Bunodont	Hypsodont or selenodont	Similar to ancestral state	Bunodont
Jaw adductor muscle strength	Very large; maximum bite forces used during feeding	Intermediate; maximum bite forces used during feeding	Equivalent to interspecific scaling	Very large; maximum bite forces exceed those used in feeding
Mandible sexual dimorphism	Equivalent to canine and/or neurocranial sexual dimorphism	Equivalent to canine and/or neurocranial sexual dimorphism	Equivalent to interspecific scaling	Greater than canine and/or neurocranial sexual dimorphism
Zygomatic arch sexual dimorphism	Equivalent to canine and/or neurocranial sexual dimorphism	Equivalent to canine and/or neurocranial sexual dimorphism	Equivalent to interspecific scaling	Greater than canine and/or neurocranial sexual dimorphism
Postcanine teeth sexual dimorphism	Equivalent to neurocranial sexual dimorphism	Equivalent to canine neurocranial and/or sexual dimorphism	Equivalent to interspecific scaling	Greater than canine and neurocranial sexual dimorphism
Jaw adductor muscle sexual dimorphism	Equivalent to neurocranial sexual dimorphism	Equivalent to neurocranial sexual dimorphism	Equivalent to interspecific scaling	Large

Carrier, 2013), early hominins are suggested to have become much more effective than their arboreal ancestors at striking with their forelimbs. Improved punching performance, in turn, made the bones of the face more vulnerable to fracture, increasing the risk of injury to sensory organs and the masticatory and respiratory systems. Under these conditions, facial anatomy that increased the strength of the skeleton would have been favoured by sexual selection. In this scenario, features of the face and masticatory system that distinguish early hominins were not necessarily adaptations to a hard or tough diet but were adaptations associated with changes in the way males fought when competing for mates and protecting their families. Nevertheless, the feeding and protective buttressing hypotheses are not entirely mutually exclusive. Selection for both feeding mechanics and

for protection of the face during fighting may have contributed to the evolution of increased facial robusticity in early hominins.

## V. ASSESSING FIGHTING ABILITY FROM FACIAL ROBUSTICITY AND VOICE

In species with aggressive social interactions, selection favours the evolution of mechanisms to assess an opponent's fighting ability (Parker, 1974; Szamado, 2008). In humans, masculine characters of the face appear to provide important clues about an individual's formidability. Experimental manipulations of male photographs that increase facial masculinity strongly increase the appearance of social dominance (reviewed

by Puts, Jones & DeBruine, 2012*b*; but see Hill *et al.*, 2013, for an alternative interpretation). Participant ratings of men's facial masculinity from photographs are also positively correlated with handgrip strength (Fink, Neave & Seydel, 2007; Windhager, Schaefer & Fink, 2011). A broad study that included samples from US college students, Bolivian horticulturalists and Andean pastoralists found that participants could accurately judge a man's relative strength and fighting ability from photographs of the face alone (Sell *et al.*, 2009). Facial structure of males has also been found to be a reliable indicator of aggressive behaviour (Carré & McCormick, 2008; Carré, McCormick & Mondloch, 2009; Carré *et al.*, 2010; Třebický *et al.*, 2013), and males with more masculine faces appear better able to survive violent confrontations (Stirrat, Stulp & Pollet, 2012).

The facial features that allow observers to assess a male's strength, fighting ability and propensity to behave aggressively include the ratio of facial width to height (Carré *et al.*, 2009, 2010), face width, chin breadth, eyebrow prominence and nose size (Windhager *et al.*, 2011; Třebický *et al.*, 2013). These metrics represent aspects of the skull that experience high rates of fracture due to interpersonal violence and are features that increased in robusticity coincident with the evolution of hand proportions that allow the formation of a fist (discussed above). Generally, facial masculinity is viewed as an honest signal conveying information about formidability (Sell *et al.*, 2009; Puts *et al.*, 2012*b*; Třebický *et al.*, 2013). Puts (2010) proposed that, in addition to acting as a signal, the greater facial robusticity of males may have evolved to protect the face from injury when males fight, as we are suggesting here. It is also likely that masculine features of the face convey direct information about the degree to which the face, the primary target during interpersonal violence, is vulnerable to injury. Male contest competition involves both offence and defence and a robust facial skeleton may make an individual more formidable simply because he is less susceptible to serious injury.

People are also able accurately to assess a man's upper body strength and fighting ability from his voice (Sell *et al.*, 2010), although it is not known what aspects of the voice communicate this information (reviewed by Puts *et al.*, 2012). Puts *et al.* (2012*a*) suggest that mean standardized formant frequency (formant position) of a voice is an important indicator of physical formidability. Men who speak with a lower formant position are taller, heavier, stronger and report more physical aggression. Although the influence of the size and shape of the different components of the vocal tract is not known, the frequency of formants 1, 2 and 3 does appear to be influenced by the volume of the oral and/or pharyngeal cavities in professional female singers (Yan, Xue & Man, 2011), during adolescent development (Xue, Cheng & Ng, 2010) and among races (Xue, Hao & Mayo, 2006). Thus, the size and robusticity of aspects of the

face associated with the oral cavity may impact the formant frequencies of a male's voice in ways that convey information about fighting ability and the potential of the facial skeleton to resist fracture when struck.

## VI. CONCLUSIONS

(1) The face is a primary target when modern humans fight and, at least in Western societies, interpersonal violence is the most common cause of fracture of facial bones. The facial bones that suffer the highest rates of fracture during interpersonal violence are the parts of the skull that exhibit the greatest increase in robusticity during the evolution of basal hominins and are the most sexually dimorphic parts of the skull in both australopiths and humans. These correlations are consistent with the evolution of protective buttressing of the facial skeleton for fighting. Protective buttressing of the early hominin face may be part of a suite of adaptations for intraspecific fighting in australopiths that include the evolution of hand proportions (Morgan & Carrier, 2013), the evolution of habitual bipedalism (Carrier, 2011), and the retention of short legs for over 2 million years (Carrier, 2007).

(2) The protective buttressing hypothesis provides an evolutionary explanation for many of the features that distinguish the face and masticatory system of early hominins, including the trend towards a more orthognathic face; expansion and bunodont form of postcanine teeth; increased robusticity of the orbit and the masticatory system, including the mandibular corpus and condyle, zygoma, and anterior pillars of the maxilla; and increased size of the jaw adductor muscles.

(3) The protective buttressing hypothesis provides a compelling explanation for the patterns of sexual dimorphism of the face and masticatory apparatus of hominins.

(4) The protective buttressing hypothesis provides an explanation for the conflicting anatomical and dietary evidence emerging from the fossil record of early hominins. The face of australopiths may be distinguished not by feeding adaptations to crack hard objects, but by adaptations to resist injury when being struck by fists. If this is correct, differences in the face of robust *versus* gracile australopiths may primarily be a function of differences in mating system. The greater level of facial buttressing in robust australopiths may indicate a more polygynous mating system. The observation that the most facially robust species *P. boisei* and *P. robustus* appear to have had more sexually dimorphic faces than the gracile species (Chamberlain & Wood, 1985; Lockwood, 1999; Lockwood *et al.*, 2000) is consistent with a difference in mating system.

(5) The evolution of reduced robusticity of the face and masticatory system in *Homo* is temporally associated with the evolution of reduced strength of the upper body

and forelimb. Both these trends may be a consequence of invention of improved weapon technology in early *Homo* that decreased the importance of physical strength and power during fighting. Reduced selection for muscle strength and power in early *Homo* may have allowed (i) the evolution of a more gracile postcranial musculoskeleton in response to selection for locomotor economy (Carrier, 2004), and (ii) the evolution of reduced facial robusticity in association with a decreased need to protect the face because of decreased striking power.

(6) Muscles of the limbs and trunk have long been thought to protect the skeleton against injury (Loeb, 1995). The large size of the jaw adductor muscles of australopiths, in light of evidence against a hard diet, raises the possibility that the adductor muscles of hominins may play an important role in protecting the jaw from injury during fighting. This protective role may explain the puzzling observation in modern humans that the jaw adductor muscles of males are 34% stronger and contain eight times more fast fibres than those of females. Similarly, the need to protect the brain from concussion during fistfights may explain the pronounced sexual dimorphism in the muscles of the neck of modern humans.

(7) The protective buttressing hypothesis is consistent with observations that modern humans can accurately assess a male's strength and fighting ability from facial shape and voice quality. Because successful contest competition involves effective defensive strategies, facial shape and voice may also convey relevant information to potential opponents about susceptibility of the face (the primary target) to injury. An individual may be more formidable simply because his face is more resistant to injury.

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