

Review of *In Vivo* Bone Strain Studies and Finite Element Models of the Zygomatic Complex in Humans and Nonhuman Primates: Implications for Clinical Research and Practice

FELIPPE BEVILACQUA PRADO,¹ ALEXANDRE RODRIGUES FREIRE,¹
ANA CLÁUDIA ROSSI,¹ JUSTIN A. LEDOGAR,² AMANDA L. SMITH,³
PAUL C. DECHOW,⁴ DAVID S. STRAIT,² TILMAN VOIGT,⁵ AND CALLUM F. ROSS^{5*}

¹Department of Morphology, Anatomy Area, Piracicaba Dental School,
University of Campinas-UNICAMP, Piracicaba, São Paulo, Brazil

²Zoology Division, School of Environmental and Rural Science, University of New England,
Armidale, NSW, Australia

³Department of Anthropology, Washington University in St. Louis, Missouri

⁴Department of Biomedical Sciences Texas A&M University, College of Dentistry, Dallas,
Texas

⁵Department of Organismal Biology & Anatomy, University of Chicago,
Chicago, Illinois

ABSTRACT

The craniofacial skeleton is often described in the clinical literature as being comprised of vertical bony pillars, which transmit forces from the toothrow to the neurocranium as axial compressive stresses, reinforced transversely by buttresses. Here, we review the literature on bony microarchitecture, *in vivo* bone strain, and finite-element modeling of the facial skeleton of humans and nonhuman primates to address questions regarding the structural and functional existence of facial pillars and buttresses. Available bone material properties data do not support the existence of pillars and buttresses in humans or *Sapajus apella*. Deformation regimes in the zygomatic complex emphasize bending and shear, therefore conceptualizing the zygomatic complex of humans or nonhuman primates as a pillar obscures its patterns of stress, strain, and deformation. Human fossil relatives and chimpanzees exhibit strain regimes corroborating the existence of a canine-frontal pillar, but the notion of a zygomatic pillar has no support. The emerging consensus on patterns of strain and deformation in finite element models (FEMs) of the human facial skeleton corroborates hypotheses in the clinical literature regarding zygomatic complex function, and provide new insights into patterns of failure of titanium and resorbable plates in experimental studies. It is suggested that the “pillar and buttress” model of human craniofacial skeleton function be replaced with FEMs that more accurately and precisely represent *in vivo* function, and which can serve as the basis for future

This article includes AR WOW Videos. Video 1 can be viewed at <http://bcove.me/2mla49wp>, Video 2 can be viewed at <http://bcove.me/39ip9imm>, Video 3 can be viewed at <http://bcove.me/e0rpa5s4>.

Grant sponsor: National Science Foundation Physical Anthropology HOMINID; Grant number: NSF BCS 0725219, 0725183, 0725147, 0725141, 0725136, 0725126, 0725122, 0725078.

*Correspondence to: Callum F. Ross, Department of Organismal Biology and Anatomy, University of Chicago, 1027 E. 57th St., Chicago, IL 60637. E-mail: rossc@uchicago.edu

Received 9 March 2016; Revised 16 July 2016; Accepted 27 July 2016.

DOI 10.1002/ar.23486

Published online in Wiley Online Library (wileyonlinelibrary.com).

research into implants used in restoration of occlusal function and fracture repair. *Anat Rec*, 299:1753–1778, 2016. © 2016 Wiley Periodicals, Inc.

Key words: pillars; buttresses; zygomatic fractures; dental implants; zygomaticomaxillary complex

The zygomatic bone is one of the most functionally important and diverse bones of the craniofacial skeleton. It performs many mechanical functions, including dissipating feeding forces, protecting, and positioning the orbital contents, and providing attachments for muscles that move the jaw, lips, and cheeks. The zygomatic bone lies at the center of what is variously referred to as the zygomatic complex (Furst et al., 2001; Devci et al., 2004; Rath and Sharma, 2015), the orbitozygomatic complex (Rohner et al., 2002), the zygomaticomaxillary complex (Hanemann et al., 2005), and zygomaticomaxillary buttress (Linnau et al., 2003; Pollock, 2012). These complexes include not only the body of the zygomatic bone and its processes, but also the zygomatic processes of the frontal and temporal bones, and the zygomaticoalveolar crest on the maxillary and zygomatic bones (Fig. 1). In modern humans, the zygoma and associated bones are said to act as important “buttresses” of the midface, protecting the face against external assaults, providing anchor points for various plates and fixtures, and playing a fundamental role in facial aesthetics through their influence on facial width and projection. Indeed, failure to properly repair fractures of the zygomatic complex can result in a wide range of deformities and dysfunctions to feeding, visual, and respiratory systems (Linnau et al., 2003).

Despite the functional importance of the zygomatic complex, the basic biomechanical principles governing its structure and function are not well understood. The traditional view of skull biomechanics reduces the craniofacial skeleton to a fundamental structure or framework consisting of vertical pillars supported by transverse buttresses (Görke, 1904; Richter, 1920; Benninghoff, 1925; Blüntschli, 1926; Sicher and Tandler, 1928; Roberts and Tattersall, 1974; Couly, 1976; Rak, 1983; Ross, 2001; Ross et al., 2011). The most influential English-language conception of these pillars, derived from Sicher and Tandler (1928), was disseminated by H. Sicher in a series of editions of “Oral Anatomy” following his arrival in Chicago in 1939. In this view, vertical pillars in the facial skeleton are said to resist and transmit forces from the tooththrow to the neurocranium as axial compressive stresses. In particular, bite forces generated during biting or mastication are said to be transmitted by the zygomaticoalveolar crest on the maxilla up to the zygomatic bone, thence up the lateral wall of the orbit to be dissipated over the neurocranium (Fig. 1). Sicher and Tandler (1928) recognized that the facial pillars are not straight, but curved, necessitating the presence of the transverse buttresses to resist the tendency of these curved structures to bend under axial load.

This traditional view of pillars and buttresses persists in the modern dental, orthodontics, and surgical literature (Manson et al., 1980; Gruss and Mackinnon, 1986;

Yamamoto et al., 1998; Cattaneo et al., 2003; Linnau et al., 2003; Nagasao et al., 2005; Andrades et al., 2008; Rodriguez et al., 2008; Pollock, 2012; Yamaguchi et al., 2012) despite the accumulation over the last three decades of *in vivo* bone strain and FEM data suggesting that a different view is warranted. As reviewed here, the contrary data emphasize that the zygomatic complex is not only loaded in compression by bite forces, but is also loaded by muscle forces acting on its temporal and frontal processes, and together the bite and muscle forces subject the facial skeleton to strong bending moments and shearing forces, which are often more important than pure axial tension or compression (Endo, 1966; Rak, 1983; Hylander and Johnson, 1997; Ross et al., 2011).

A better conception of the biomechanics of the zygomatic complex is important for improving methods of craniofacial repair post trauma. One reason that controversies persist about the best location and type of

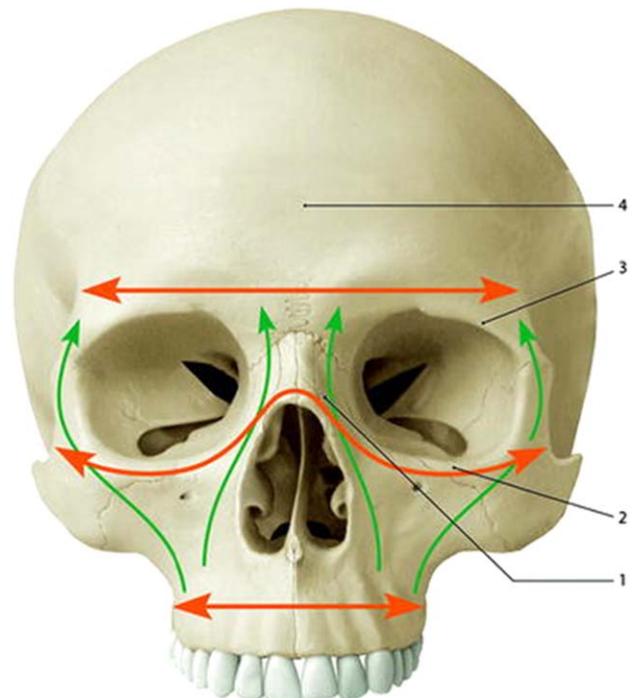


Fig. 1. From Hardt and Kuttenberger, 2010, Chapter 1, *Anatomy of the Craniofacial Region*, in *Craniofacial Trauma: Diagnosis and Management* pp 3-13, Springer. Reproduced with permission from Springer. 1. Frontal process of maxilla, 2. inferior orbital rim, 3. superior orbital rim, 4. frontal bone; orange lines represent transverse supraorbital-frontal, infraorbital, and alveolar buttresses, green lines represent vertical lateral zygomaticomaxillary and anterior medial nasomaxillary “buttresses.”

fixation for the repair of zygomatic complex fractures is that the basic biomechanics of this region are not well understood (Karlan and Cassisi, 1979; Ellis et al., 1985; Rinehart et al., 1989; Davidson et al., 1990; Ellis, 1991; Rudderman and Mullen, 1992; Swift, 1993; Kasrai et al., 1999; Rohner et al., 2002; Deveci et al., 2004; Hanemann et al., 2005). To further our understanding of the biomechanics of the zygoma, we review and evaluate the literature on *in vivo* bone strain and FEM of the zygomatic region of humans and nonhuman primates and present new data gathered from FEMs to address some important questions regarding facial pillars and buttresses:

1. Do pillars and buttresses exist structurally?
2. Do pillars and buttresses exist functionally?

What do *in vivo* and *in silico* studies tell us about patterns of stress, strain and deformation in the zygomatic complex?

3. How useful is the buttress concept clinically and how can a new concept advance clinical practice?

DO PILLARS AND BUTTRESSES EXIST STRUCTURALLY?

In 1901, Rene Le Fort described the bones of the craniofacial skeleton as including “delicate and spongy” areas as well as columns or “blades of more compact bone” (Le Fort, 1901). A decade later, Jean-Leo Testut described the architecture of the skull as a framed assembly of “dense pillars” separated by “zones of weakness” (Testut, 1911; Testut and Jacob, 1914; Testut, 1943) and Henry Cryer (1916) described the facial skeleton as being composed of buttresses and flying buttresses. In adopting and developing these concepts Sicher and Tandler (1928) hypothesized that the masticatory forces generated at the teeth are transmitted and dissipated from the maxillary alveolar process to the neurocranium via three vertical pillars on each side, supported by transversely oriented buttresses. They described canine-frontal pillars, separated from each other by the nasal cavities, zygomatic pillars separated from the canine-frontal pillars by the orbits and maxillary sinuses, and pterygoid pillars, extending from the hard palate to the skull base. The canine-frontal and zygomatic pillars are connected to each other by buttresses along the supraorbital and infraorbital borders, and the two pterygoid pillars are buttressed by the back of the palate (Fig. 1; Sicher and Tandler, 1928; Hilloowala and Kanth, 2007).

TERMINOLOGY TEXT BOX

Sicher and Tandler clearly distinguished between pillars and buttresses, however many (but not all, Manson et al., 1980) authors use the term “buttress” imprecisely and inaccurately to refer to vertical pillars as well as horizontal buttresses (Linnau et al., 2003; Hardt and Kuttenger, 2010; Pollock, 2012; Smith and Nesi, 2012). The distinction is more than terminological: pillars are oriented predominantly parallel to applied loads, and thereby resist external forces generating compressive stresses, whereas buttresses are oriented perpendicular to pillars, and resist lateral thrust that might cause failure of a pillar due to bending or buckling.

For example, in architecture and engineering a buttress is a “visible concrete or masonry projection or pier built out at right angles to a wall to reinforce its resistance to earth thrust or water pressure” (Herman and Bucksch, 2014). We advocate the use of the terms “pillar” and “buttress” in the senses originally defined by Sicher and Tandler (1928).

A second terminological issue is the use of the same term by different authors to refer either to an entire “pillar” or buttress”, or to only a part of it. For example Linnau et al. (2003) follow Sicher and Tandler’s definition most precisely, referring to the entire zygomatic complex as the zygomaticomaxillary buttress; whereas others use the term lateral zygomaticomaxillary buttress or lateral buttress to refer only to the inferior edge of the body of the zygoma and the zygomaticoalveolar crest (Kasrai et al., 1999; Rohner et al., 2002; Hanemann et al., 2005). We recommend referring to regions of the face using the appropriate anatomical terminology, reserving the use of pillars and buttresses to precisely defined terms.

Hypotheses

For these pillars and buttresses to exist structurally, and to have empirical content, we argue that, in these tracts running from the tooththrow to the cranium, there must be one, two, or all of:

- distinct shapes on the external surface of the bone; for example, as with canine-frontal (= anterior) pillars of *Australopithecus africanus* (Rak, 1983);
- increases in bone density, which may include thickened cortical bone, increased density of trabeculae, and/or increased bone mineral density (perhaps recognizable in radiographs, for example, Görke (1904);
- regional variability in material and microstructural properties of human and primate cranial bone, such as trabecular orientation and bone material properties, that strengthen the pillars and buttresses.

Here, we evaluate these hypotheses using data from the literature and from our own scan data on the crania of *Sapajus*.

LITERATURE REVIEW

If the pillars are defined so as to include all connections between the tooththrow and the neurocranium (e.g., Fig. 5 of Linnau et al., 2003), and buttresses to include all transverse connections between pillars, then forces cannot be transmitted to the neurocranium through any structure other than a pillar, pillars are not prevented from buckling by anything other than a buttress, and statements regarding their existence have no empirical content. Hence, for pillars and buttresses to exist, they must be morphologically distinct in some way.

Early qualitative evidence on the existence of pillars in humans and great apes presented by Görke (1904), Benninghof (1925), Wetzell (1930), and Sicher and DuBrul (1970) consists of diagrams, illustrations, and radiographs (Fig. 2). For example, Görke (1904) identified areas of increased bone density in lateral radiographs of the crania of *Pongo*, *Gorilla*, *Pan*, and *Homo*, which he described as pillars, but these features were

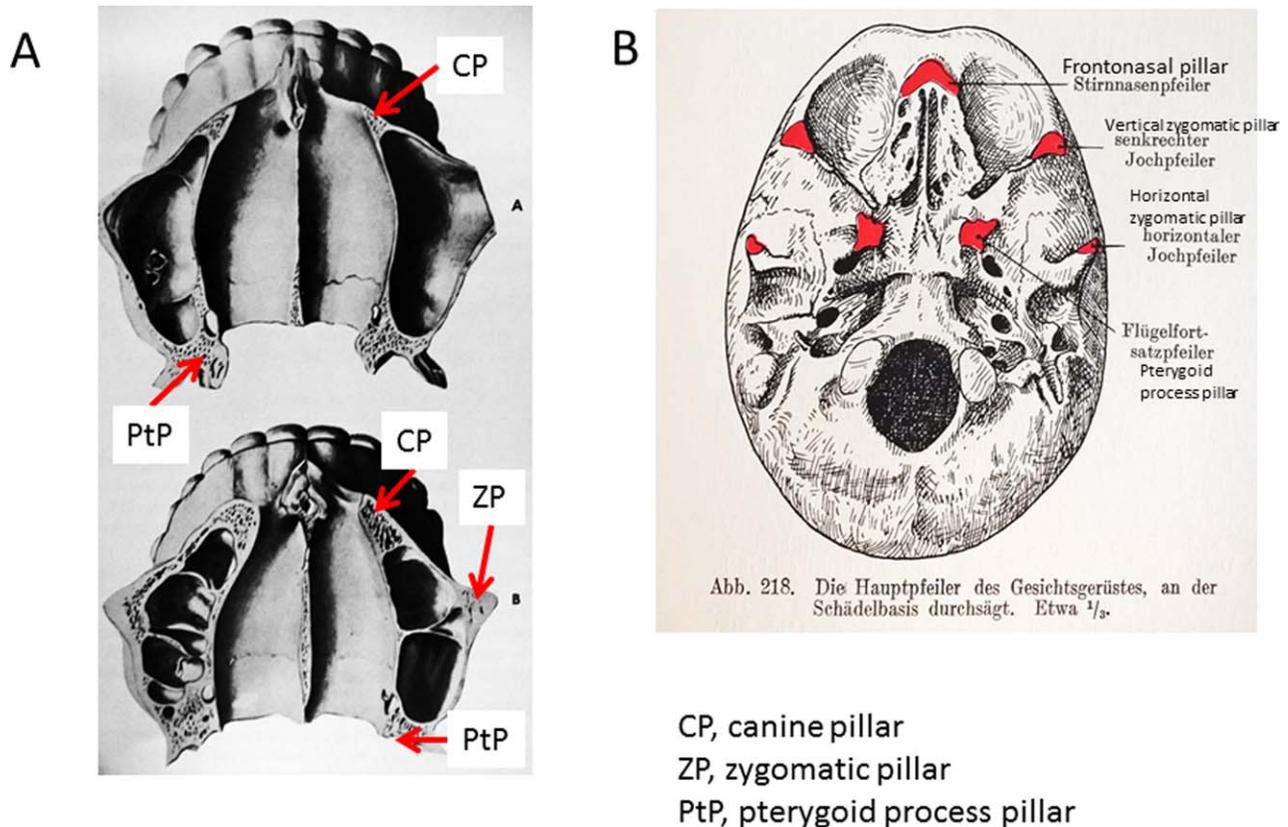


Fig. 2. **A.** Figure 219 from H. Sicher and E.L. Du Brul 1970, *Oral Anatomy*, 5th edition, Published with permission. Figure originally published as Figures 267 and 268, H. Sicher and J. Tandler, *Anatomie für Zahnärzte*, Berlin and Vienna, Verlag von Julius Springer. Arrows and labels added by

authors: CP, canine-frontal pillar, ZP, zygomatic pillar, PtP, pterygoid pillar. **B.** From Figure 218 in G. Wetzel, 1930, *Lehrbuch der Anatomie für Zahnärzte und Studierende der Zahnheilkunde*. Jena, Verlag von Gustav Fischer. English translations of labels added by authors.

not quantified. Similarly, Wetzel (1930) and Sicher and DuBrul (1970) presented diagrams of human facial skeletons cut in transverse section, giving either verbal descriptions or colored indicators of where the pillars are found (Fig. 2). Descriptions of the diversity in pillar and buttress morphology in hominids (extant great apes, humans, and their fossil relatives), while also qualitative, benefit from precise definition, description, and appreciation of intraspecific and interspecific diversity (Rak, 1983; Kimbel et al., 2004; Villmoare and Kimbel, 2011). For example, consider Rak's (1983) description of the anterior pillars of *A. africanus*:

"In a frontal view of the facial mask, attention is drawn to two prominent solid structures that extend as an elongated blunt ridge running alongside the nasal aperture down to the alveolar process. In the gorilla, chimpanzee and modern man, and many other primates, the homologous site is flat and thin, and it is referred to as the anterior, or canine, buttress by those who wish to convey the notion of a functional unit connecting the front of the dental arcade and the calvaria. It appears cylindrical and bulging only at its lower end, along the underlying root of the canine, where it is nothing more than the canine eminence ... However, in *A. africanus* the columnlike buttress

extends much farther than the tip of the canine root ... Although the two terms anterior pillars and anterior buttresses of the face are used synonymously in the literature to denote the site adjacent to the nasal aperture, (for example Griesman, 1945; Sicher and DuBrul, 1975), a distinction is maintained here whereby the term anterior pillars refers only to the columnlike structures of the type found in *A. africanus*." (Rak, 1983: 11-2).

Hence, the anterior pillars present in most *A. africanus* are characterized by a column-like bulge extending beyond the apex of the canine root (and hence are more than just canine eminences), along the lateral margin of the nasal aperture (giving the lateral margin of the piriform aperture a blunt, rounded edge, rather than a sharp edge), and are delineated from the infraorbital region laterally by a distinct groove, the maxillary furrow (rather than the canine fossa seen in great apes and humans). This definition enables the distribution of these pillars among extant and fossil hominids to be clearly documented: they are absent in *Pan*, *Gorilla*, *Pongo*, and *Homo*, *Australopithecus afarensis*, *A. sediba*, and *A. boisei*, but present in *A. africanus*, and *A. robustus*. Most recently, Villmoare and Kimbel (2011) used computed tomography (CT) to show that the internal structure of the canine-frontal pillar varies among those

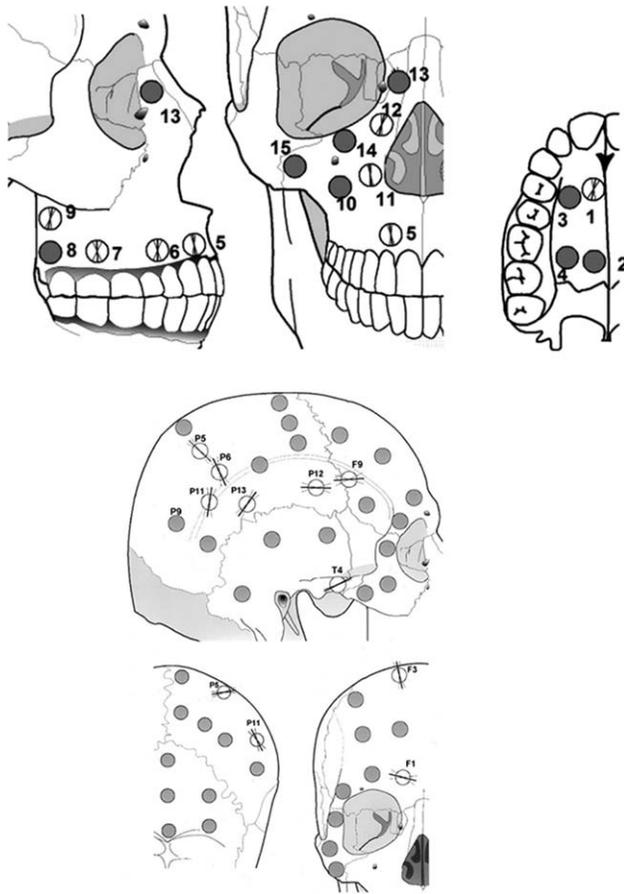


Fig. 3. Composite of Figure 5 from Peterson and Dechow (2003) and Figure 10 from Peterson et al. (2006). Orientation of axes of maximum stiffness in dentate human maxilla, zygomatic and calvaria. Significant orientations are shown with central line and two lines showing 95% CI. Non-significant orientations are shown as shaded. (Published with permission from Wiley).

fossil hominids that possess them. The authors evaluated the fossil specimens using direct observation and/or examination of CT data to document the internal morphology of the nasal margin, maxillary sinus, and maxilla. CT data were collected from a variety of sources and include all available CT scans of relevant specimens from the species analyzed. They used two software packages (ImageJ 1.42 - National Institutes of Health and Amira 4.1.2 - Mercury Computer Systems) to examine the CT data and extracted the data from trabecular bone of the specimens. In *Australopithecus africanus*, exemplified by Sts 5, the pillar is a hollow shell of cortical bone, whereas in robust australopithecines, *A. robustus* and *A. boisei*, the “pillars” on either side of the nasal aperture consist of cortical bone shells enclosing a trabecular core. Thus, although the morphological existence of an externally apparent canine-frontal pillar is restricted to *A. africanus* and *A. robustus*, these two species differ in the internal anatomy of this pillar. Clearly, further CT-based, quantitative work on the morphology of this region in hominids, including humans, would be of great interest.

The morphological reality of the zygomatic buttress is difficult to assess because of the morphological complexity

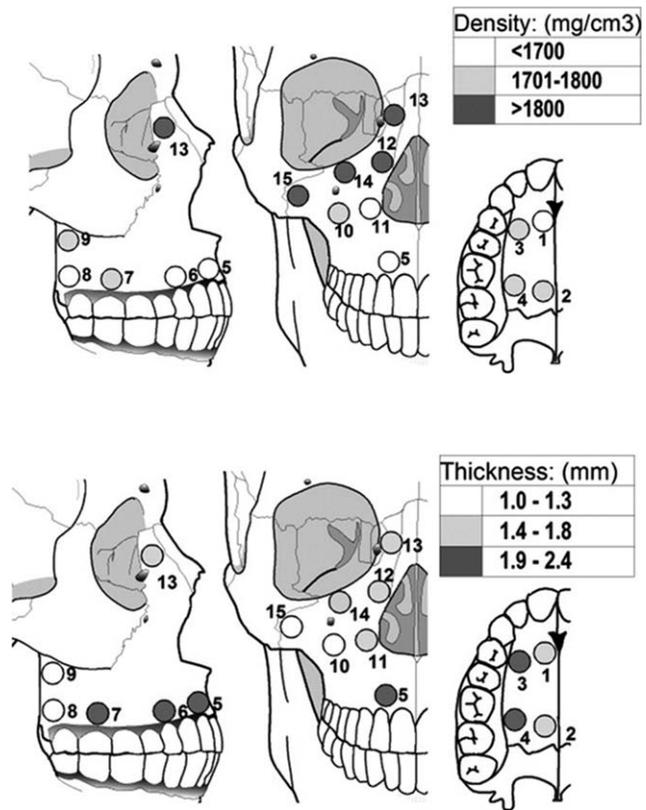


Fig. 4. Composite of Figures 2 and 3 from Peterson et al. (2006). Distributions of density and cortical bone thickness across the dentate maxilla in humans. (Published with permission from Wiley).

and diversity in this region among extant and fossil hominids (Rak, 1983; Kimbel et al., 2004; Ledogar et al., in review) and the fact that Sicher and Tandler (1928) originally included the zygomatic arch in this “pillar.” Even if we exclude the zygomatic arch from this discussion of the zygomatic pillar on the grounds that it is neither orthogonal to the palatal plane, not subjected primarily to compression (Hylander and Johnson, 1997; Ross et al., 2011), the complexity of the zygomatic complex makes it difficult to assess whether this pillar exists morphologically (see Ledogar et al., in review).

Several authors have suggested that the prominent supraorbital tori of *Pan*, *Gorilla*, and fossil hominids serve as buttresses (Russell et al., 1985), resisting forces associated with feeding. However, strains in the supraorbital torus are uniformly low, both *in vivo* (Hylander et al., 1991), and in *in silico* models (Ross et al., 2005; Chalk et al., 2011; Ross et al., 2011; Prado et al., 2013; Freire et al., 2014; Janovic et al., 2014, 2015; Fitton et al., 2015) of macaques, fossil hominids, and humans, suggesting that their size and shape are not optimized for dissipating feeding forces. Indeed, alternate explanations for the existence of the supraorbital tori refer to the need to protect the brain and eyes, and growth of the tori along with the face (Sicher and DuBrul, 1970; Ravosa, 1991). As summarized by Ross (2013: 64):

“The available data suggest that selection for integration of the browridges with the rest of the face was

TABLE 1. Summary of studies that evaluated bone density in regions related to the zygomatic complex in humans

Reference	N	Sample	Method	Superior to midline of orbit	alveolar process (around first molar)	Density values in regions related to zygomatic pillar					Unit of measurement	
						Zygoma	Zygomatic arch	Supra-orbital arch	Region below zygomatic-maxillary suture	Anterior Root of the zygomatic process		Lateral orbital wall
Dechow et al. (1993)	15	Unembalmed (frozen) whole or partial human heads	Ultrasonic wave technique (3D)	1.591	-	-	-	-	-	-	-	Mean (g/cm ³)
Southard et al. (2000)	41	Periapical radiographs from dentate Caucasian women	In periapical radiographs (aluminum step wedges)	-	3.82 (20 - 29 yr) 3.69 (30 - 39 yr) 3.77 (40 - 49 yr) 3.28 (50 - 59 yr) 3.44 (60 - 69 yr) 3.27 (70 - 79 yr)	-	-	-	-	-	-	mm Al equivalent
Peterson and Dechow (2003)	15	unembalmed, fresh-frozen, whole human cadaver heads	Apparent density: Archimedes' principle	-	-	1.868	1.654	1.812	-	-	-	Grand mean (g/cm ³)
Peterson et al. (2006)	15	Dentate unembalmed, fresh-frozen whole cadaver heads.	Apparent density: Archimedes' principle	-	1.72	-	-	-	1.90	1.72	-	Mean (g/cm ³)
Dechow et al. (2010)	15	Edentulous human skulls	Apparent density: Archimedes' principle	-	-	1.60 to 1.90	1.60 to 1.90	1.80 to 1.90	1.80 to 1.90	1.60 to 1.69	1.80 to 1.90	g/cm ³

The columns list: the authors; year of publication; number of individuals; method; density values in regions related to zygomatic pillar; and unit of measurement.

necessary to ensure that there was always enough bone there to protect the orbital contents from blows to the head (Hylander et al., 1991) in the context of neuro-orbital disjunction caused by klinorhynchty or increases in facial size (Weidenreich, 1941; Shea, 1986a, b; Ravosa, 1988, 1991). In this sense, the brow-ridges are part of the facial module as a whole. Subsequent selection for increases or decreases in size of the face would then also act on browridge size, making browridges a nice example of how functional integration producing functional modules can be achieved through developmental integration to produce developmental modules, and this in turn creates a genetically integrated evolutionary module (Cheverud, 1982).”

A transversely oriented infraorbital buttress—“transverse buttress” of Rak (1983)—is described as prominent in *Gorilla*, less so in *Pan*, weak or absent in *Homo*, and variable in *A. afarensis* (Rak, 1983, Kimbel et al, 2004). Based on external morphology alone, these descriptions emphasize the role of relative positioning and size of various facial features (zygoma, snout, anterior pillars, canine fossa, zygomaticoalveolar crest) in determining the appearance of this buttress. The internal morphology of this region remains to be documented using CT scans.

In long mandibles like those of *Alligator* (Zapata et al., 2010) and in long bones of mammals the axis of maximum stiffness is aligned along the long axis of the bone. The limb bones are subjected to compressive stresses along their long axis, so if the pillars exist structurally and they are similarly adapted, we expect the axes of maximum stiffness of pillars to be aligned perpendicular to the occlusal plane at all pillar sites, and parallel to the palate in the buttresses. The best available data on material properties of the human facial skeleton are from studies of fifteen fresh-frozen dentate adult humans reporting cortical thickness, bone density, and elastic properties, including the direction of maximum stiffness, from forty-six sites on the cranium (Figs. 3 and 4; Peterson and Dechow, 2003; Peterson et al., 2006). Of the 46 sites in the facial skeleton sampled, only 17 had a statistically significant axis of maximum stiffness (Fig. 3). Three of these are in the canine-frontal pillar (sites 5, 11, 12), and one is in the pterygoid pillar (9; Fig. 3). Moreover, at these three canine-frontal pillar sites the axis of maximum stiffness is aligned along the axis of the pillar; a similar pattern is observed in rhesus monkeys (Wang and Dechow, 2006). It is tempting to see this as evidence of the existence of pillars, however Peterson and Dechow (2003) and Peterson et al. (2006) also showed that sites 13 and 8, also in pillars, do not have a preferred axis of stiffness, and of the five sites in the zygomatic pillar, only the most inferior site (7), representing the zygomaticoalveolar crest (at the level of alveolar process), has a preferred axis of stiffness. Similarly, of the five sites in horizontal supra- and infraorbital buttresses, only one site 1 has a preferred axis of stiffness, roughly parallel to the occlusal plane. Contrary to predictions for distribution of density in simple axially loaded pillars, sites 11, 12, and 13 in the canine-frontal pillar exhibit increasing density from the bottom to the top of the pillar, as do sites 8 and 9 in the pterygoid pillar (Peterson et al., 2006; see Table 1).

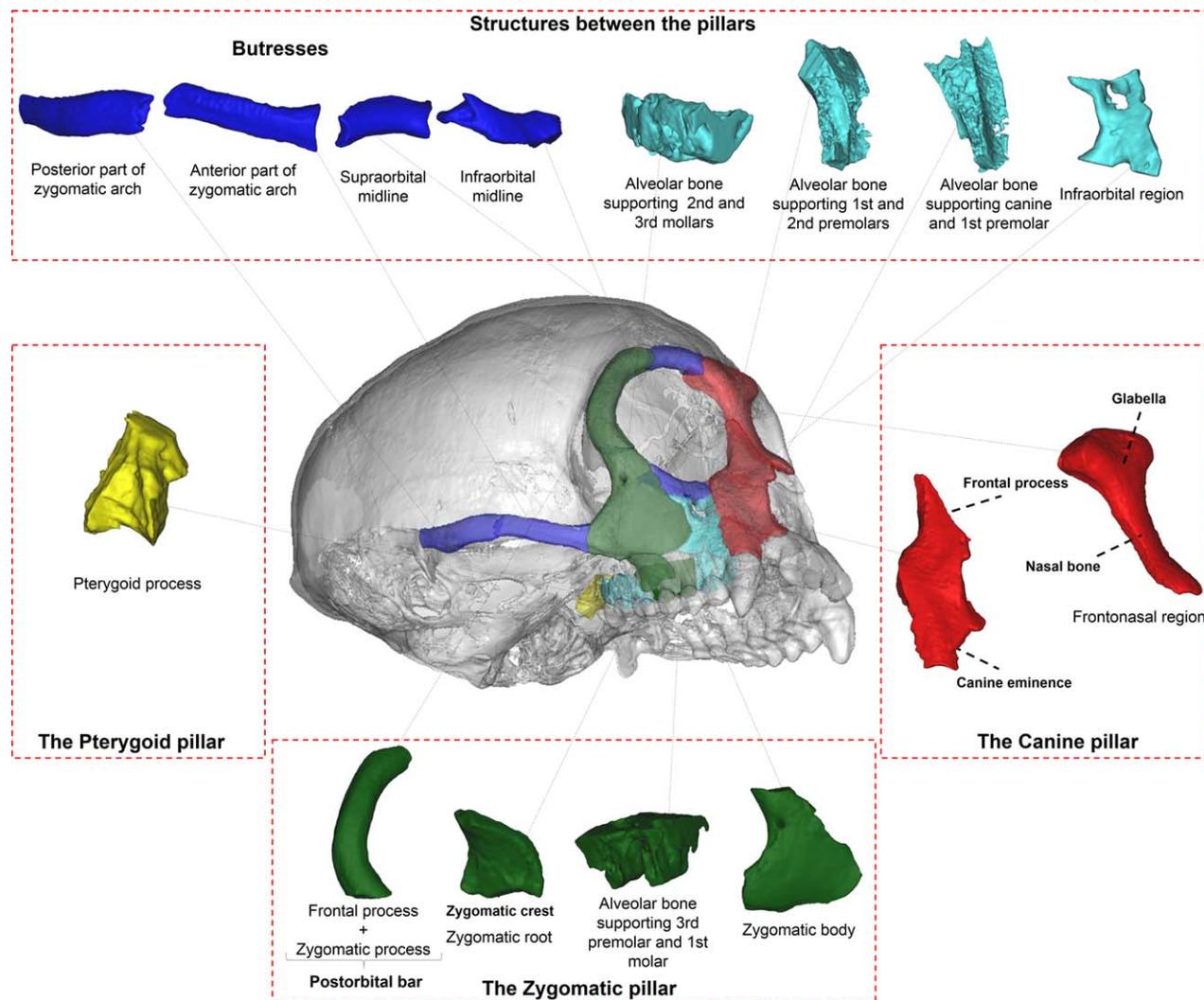


Fig. 5. Regions of *Sapajus* crania in which bone microarchitecture variables were recorded. Three-dimensional surface reconstructions of a volume extracted in Mimics v. 18 software. Microarchitecture data are presented in Figure 6.

The concept of facial pillars and buttresses is also not supported by the data on bone density and cortical thickness (Fig. 4). Bone density is above 1.8 g/cm^3 across the infraorbital buttress and the upper part of the canine-frontal pillar, but is lower everywhere else in the face. Cortical bone thickness is in excess of 1.9 mm at all zygoma pillar sites and supraorbital buttress sites but the canine-frontal pillar only has bone in excess of 1.9 mm at the alveolar site (Peterson and Dechow, 2003; Peterson et al., 2006). Together the available data on bone material properties do not support the hypothesis that pillars and buttresses are distinguished from other areas by cortical bone thickness, orientation of maximum stiffness, or cortical bone density.

METHODS

Here, we present new data on the microarchitecture of the facial pillars and buttresses in *Sapajus apella* using 3-dimensional micro-CT. *S. apella* provides an

interesting test of the pillar-buttress model because, as in humans, the palate is positioned below the orbits and anterior cranial fossa, and these capuchin monkeys engage in powerful biting that might be expected to demand a craniofacial skeletal structure that is biomechanically optimized for resisting the associated forces. Micro-CT of seven skulls of adult *S. apella* were used in this study (4 males and 3 females, aged 7–14 years). The skulls were scanned in a SkyScan 1178 (SkyScan 1178, Bruker) microtomograph at 65 Kv at high resolution ($1024 \times 1024 \times 1024$ pixels), and a pixel size of $80\text{-}\mu\text{m}$. The images obtained were imported into the NRecon software (SkyScan, Belgium) to convert into grayscale and then into DICOM format.

After constructing a 3D model, in each monkey, we quantified the three-dimensional structure of bone in the facial pillars and buttresses in regions of interest (ROI) defined to capture variability within and between pillar and buttress regions. To calculate the morphometric parameters we used CT-Analyzer, developed by the

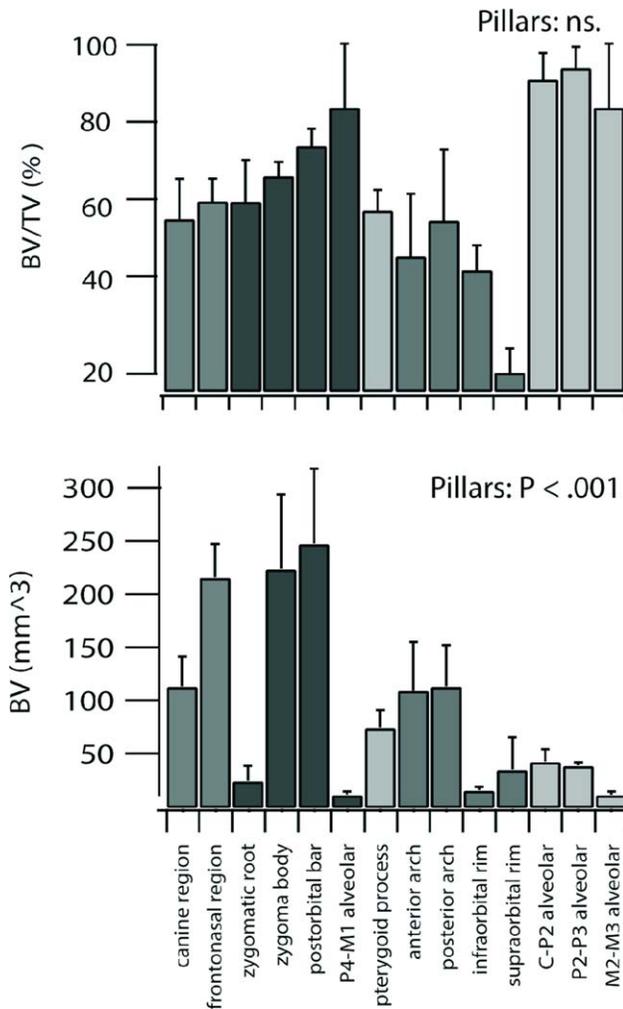


Fig. 6. Bar plots of microarchitecture variables quantified in the regions of the face in Figure 5, categorized into pillars and buttresses. Data from seven *Sapajus apella*. Results of nonparametric comparisons between pillars and non-pillar areas are given. Pillars and buttresses combined differ from all non-pillar/buttruss areas at $P < 0.001$.

microCT manufacturer, SkyScan (Leuven, Belgium). The three-dimensional morphometric analysis was performed automatically using the image sequence plus the gray scale configuration. Using CT-Analyser software the ROIs were defined by manually digitizing, in each slice, a polygon surrounding the regions shown in Figure 5. The method of thresholding was based on the configuration of greyscale values. This scale ranged from 0 (minimum) to 255 (maximum). We assigned bone the range of 20 (minimum) to 150 (maximum). To compare the pillars and buttresses with other areas of the facial skeleton, we selected regions from the canine-frontal, zygomatic, and pterygoid pillars, the supraorbital and horizontal buttresses, and the alveolar process. In each region, we selected a ROI, standardized the grayscale and then standardized the number of slices.

1. Canine-frontal pillar, consisting of: the canine region, including the maxillary cortical bone forming the canine eminence, delimited laterally by a vertical line through the edge of the infraorbital foramen, medially

by the piriform aperture, inferiorly by a transverse plane through the cervix of the canine, and superiorly by the orbital aperture and the nasal bone; the frontonasal region, formed by the nasal bone, and by the glabellar portion of the frontal bone, delimited inferiorly by the nasal bone, laterally by a marked thinning of bone, and superiorly by the transverse plane through the top edge of the frontal sinus.

- Zygomatic pillar: alveolar bone supporting third premolar and first molar; the zygomatic crest and root, cortical bone forming the zygomaticoalveolar crest, delimited mesially and distally by the points where the bone curves out from the alveolar process, and superiorly where the crest becomes continuous with the inferior edge of the zygomatic arch; the zygomatic body, delimited by the zygomaticomaxillary suture inferiorly and medially, the level of the inferior orbital rim superiorly, and laterally, the region of the arch where the upper and lower borders become approximately parallel; the post-orbital bar, delimited by the zygo body region inferiorly and the zygomaticofrontal suture superiorly (excluding the postorbital septum);
- Pterygoid pillar, the pterygoid process of the sphenoid.
- Buttresses: the zygomatic arch, the parts of the zygomatic process of the temporal bone and temporal process of the zygomatic bone anterior to the articular eminence and posterior to where the upper and lower borders are approximately parallel (anterior and posterior zygomatic arches are divided by a vertical plane through the middle of the temporozygomatic suture); the supraorbital margin is delineated superiorly by the superior limit of the frontal sinus, medially by glabella in the frontonasal region laterally by the frontozygomatic suture, and posteriorly by the edge of the thick bone forming the rim (i.e., the thin bone forming the orbital plate of the frontal bone was excluded); and the infraorbital margin delimited by the zygomaticomaxillary suture laterally, the canine-frontal pillar medially, the infraorbital foramen inferiorly, and the thin bone of the orbital floor posteriorly.
- Nonpillar, nonbuttress regions: the alveolar bone supporting the teeth (except for the third premolar and first molar) and the infraorbital region delimited by the canine-frontal and zygomatic pillars.

To illustrate the boundaries of the pillar and nonpillar areas, three-dimensional surface models were formed from the reconstructed micro-CT images using Mimics v.18 software (Materialise, N.V. Leuven, Belgium; Fig. 5).

From the resulting binary images, Bone Volume (BV)—number of bone voxels (in mm^3)—and percent Bone Volume (BV/TV)—number of bone voxels/total voxels in the segmented ROI (in %)—were calculated following Parfitt et al. (1987).

To determine whether pillars and buttresses differ from other areas of the face in these variables, we compared pillar and buttress sites with nonpillar and nonbuttress sites using nonparametric Mann-Whitney U-tests (significance set at $P < 0.05$).

RESULTS

Figure 6 shows bar plots of BV and BV/TV quantified in the fourteen regions of the face, categorized into

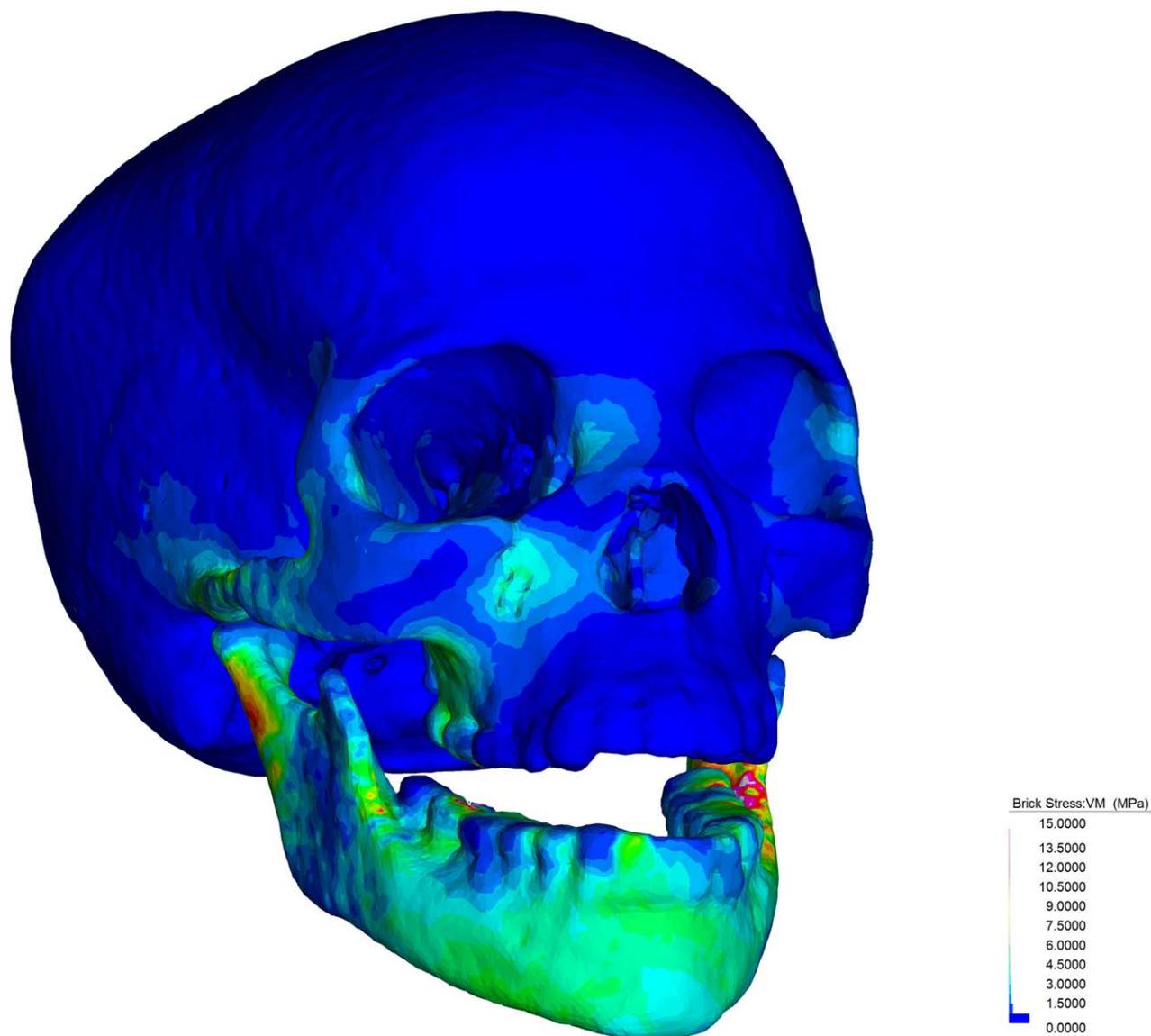


Fig. 7. Von Mises stress distribution in FEM of human skull (courtesy of S. Wroe).

pillars, buttresses, and nonpillar/nonbuttress areas. The color codes match those in Figure 5. An independent samples Kruskal-Wallis test reveals a significant effect on both variables of belonging to the buttress group, pillar group or neither. Pillars and buttresses have a greater BV than nonpillar areas ($P < 0.001$) purely because they are larger proportions of the selected areas. However, in non-pillar/buttress areas bone makes up a greater percentage of the volume of interest than in pillar and buttress areas (BV/TV in % with; $P = 0.5$). Although these results do not speak directly to the question of the structural existence of pillars and buttresses in humans, they do suggest that microarchitecture variables can provide precise, objective quantitative measures of differences between pillars, buttresses and other areas of the craniofacial skeleton. Pillars do not have more bone

overall than non-buttress areas in *Sapajus*. It will be important to determine whether these features also characterize “pillars” in human crania.

In sum, the evidence for pillars and buttresses in the facial skeletons of humans and their close relatives is scant. The external morphology of the facial skeleton suggests that robust canine-frontal pillars can only be confirmed in *A. africanus* and *A. robustus*. They are not found in *Homo*. The diversity and complexity of the morphology of the zygomatic complex makes it difficult to evaluate the presence of a zygomatic pillar on the basis of external morphology alone. A transverse infraorbital buttress is similarly only variably present in humans, and is otherwise most pronounced in great apes and *A. africanus*. Again, however, the internal morphology of this “buttress” has yet to be documented. Available data

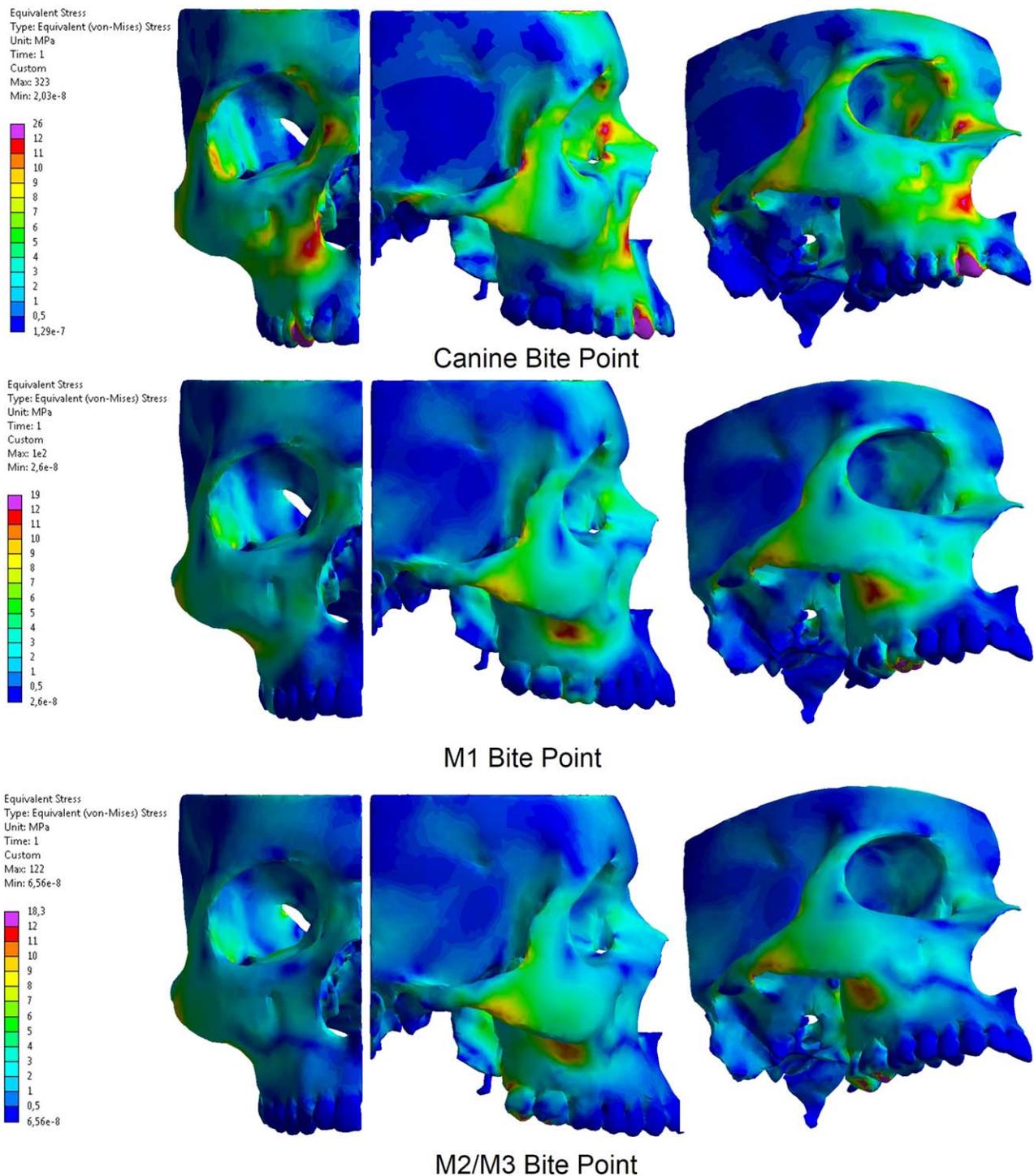


Fig. 8. Equivalent von Mises stress distribution in the human facial skeleton during simulated biting at the canine, M¹, and M²⁻³ molar bite points. The color scale was adjusted to highlight the compressive stress.

on the distributions of bone material properties across the human facial skeleton do not support the hypothesis that pillars and buttresses exist. Our new data on *Sapajus apella* do not support the notion that there is reality

to the pillars and buttresses in this species: collection of microarchitecture data from CT scans of human crania will be important in addressing these questions in the future.

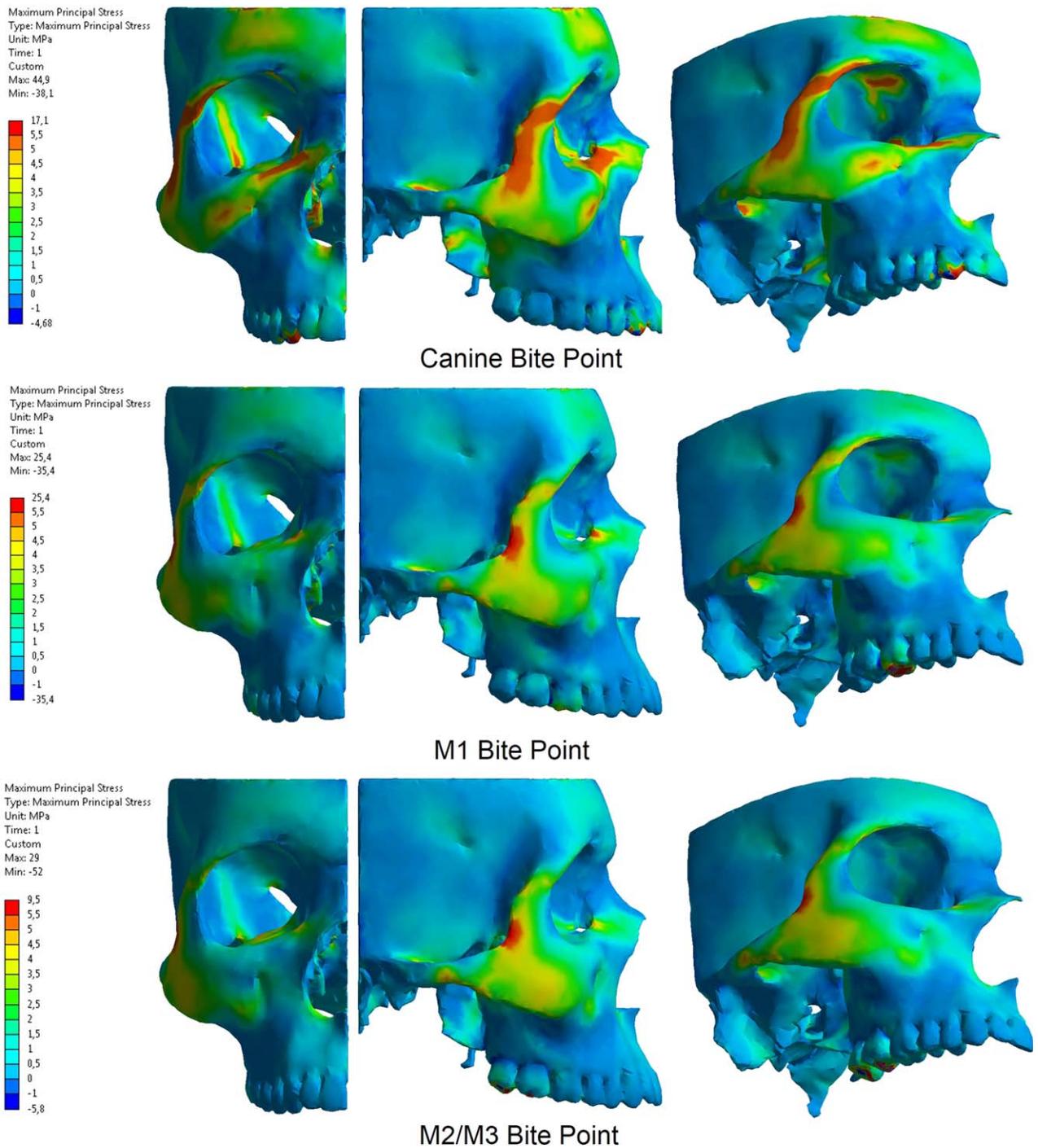


Fig. 9. Maximum principal (tensile) stress distribution in the human facial skeleton during simulated biting at the canine, M¹, and M²⁻³ molar bite points. The color scale was adjusted to highlight the tensile stress distribution.

DO PILLARS AND BUTTRESSES EXIST FUNCTIONALLY?

Do pillars and buttresses exist functionally? Here we evaluate this question by asking whether pillar and buttress areas experience stress and strain magnitudes higher than other parts of the craniofacial haft.

Hypotheses

We hypothesize that if the pillars and buttresses exist functionally

- they must experience higher stresses and strains than neighboring regions;

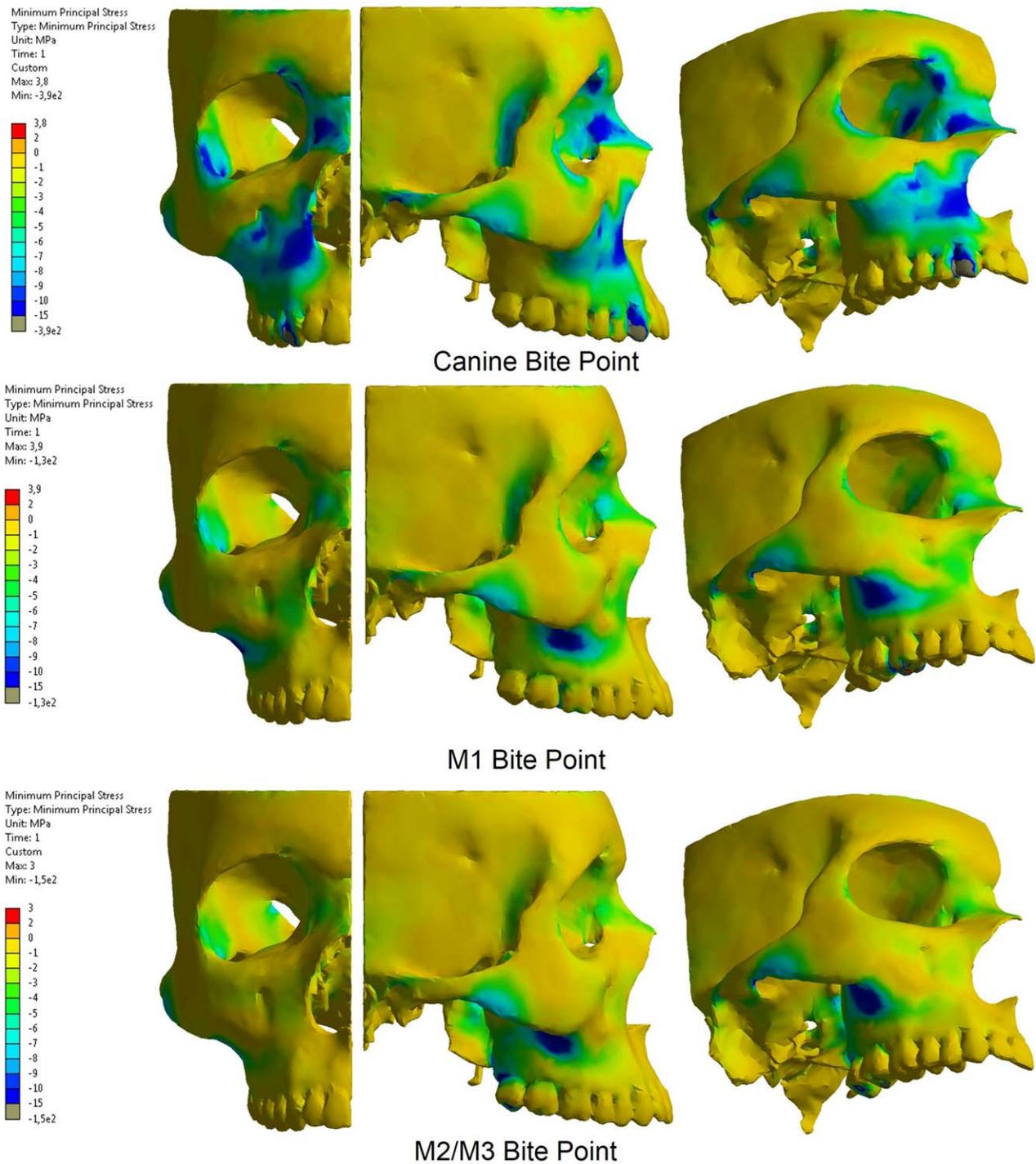


Fig. 10. Minimum principal (compressive) stress distribution in the human facial skeleton during simulated biting at the canine, M^1 , and M^{2-3} molar bite points. The color scale was adjusted to highlight the compressive stress.

- the pillars should resist primarily axial, compressive loads and stresses.

Other than the criterion that they prevent buckling of the pillars, we are agnostic as to the patterns of stress

and strain in the buttresses. Buttresses could resist pillar buckling through compression or tension along their axes, but because they are curved, as Endo (1966) demonstrated, high magnitudes of bending and shear are to be expected. Here we evaluate these hypotheses by

reviewing the recent literature on finite element modeling (FEM) of the human and non-human primate facial skeleton,

- What do *in vivo* and *in silico* studies tell us about patterns of stress, strain, and deformation in the zygomatic complex?

FEM of the human cranium. Wroe et al. (2010) used FEA to compare the abilities of hominid crania to resist bite forces (Fig. 7). Separate models were run to simulate unilateral bites at the canine, second premolar and second molar, and VM stresses were used as the measure of mechanical performance. Their results suggest that some parts of the human zygomatic complex, such as the zygomaticoalveolar crest (~ 6.17 Mpa) are more highly stressed than others, such as the lateral orbital rim (~ 1.76 Mpa). Moreover, rather than exhibiting strips of high von Mises stress aligned with the canine and zygomatic pillars, their results from molar loading reveal a strip of high Von Mises stress extending from the bite point obliquely upward and medial towards the interorbital region. Other concentrations of high stress are seen at the medial orbital margin and the inferolateral corner of the orbital aperture. Although the authors do not report principal stress patterns, these results are markedly similar to those reported by other authors, below.

Prado et al. used a FEM of an adult male human facial skeleton to evaluate the distribution of Von Mises and principal stresses in the zygomatic (Prado et al., 2013), canine (Freire et al., 2014), and pterygoid “pillars” (Figs. 8–10. See animations in Video 1: <http://bcove.me/2mla49wp>, Video 2: <http://bcove.me/39ip9imm>, Video 3: <http://bcove.me/e0rpa5s4>). Applying muscle forces at the origins of the jaw elevator muscles and constraints at either the occlusal surfaces of M^1 , M^{2-3} , or the canines, they found nonuniform stress distributions in both zygomatic and canine pillars. Some parts of the zygomatic pillar, such as the zygomaticoalveolar crest and the temporal process of the zygomatic bone experience high Von Mises stresses (7–12 MPa), whereas stresses in the zygomatic body and frontal process of the zygomatic bone are lower (3–4 MPa). High tensile stresses are evident at the junction of the top of the zygomatic arch with the postorbital bar, and high compressive stresses are seen in the zygomaticoalveolar crest. In the canine pillar, high Von Mises stresses are seen in the inferolateral corner of the piriform aperture and inferomedial corner of the orbit, where principal stresses are compressive. Thus, as with the study by Wroe et al. (2010), these results do not support the hypothesis of stress/strain concentrations in the canine and zygomatic pillars. Rather, high tensile stresses are seen in a band running across the lower border of the orbit, and a strip of compressive stress extends from the bite point obliquely upward and medial toward the interorbital region. Concentrations of high compressive stress at the medial orbital margin and the inferolateral corner of the orbital aperture are similar to the Von Mises stress distributions reported by Wroe et al. (2010). Rather than being indicative of axial compression of a pillar, these results are suggestive of bending of the facial skeleton in the manner suggested by Endo (1966) and confirmed by Ross et al. (2011) in catarrhines.

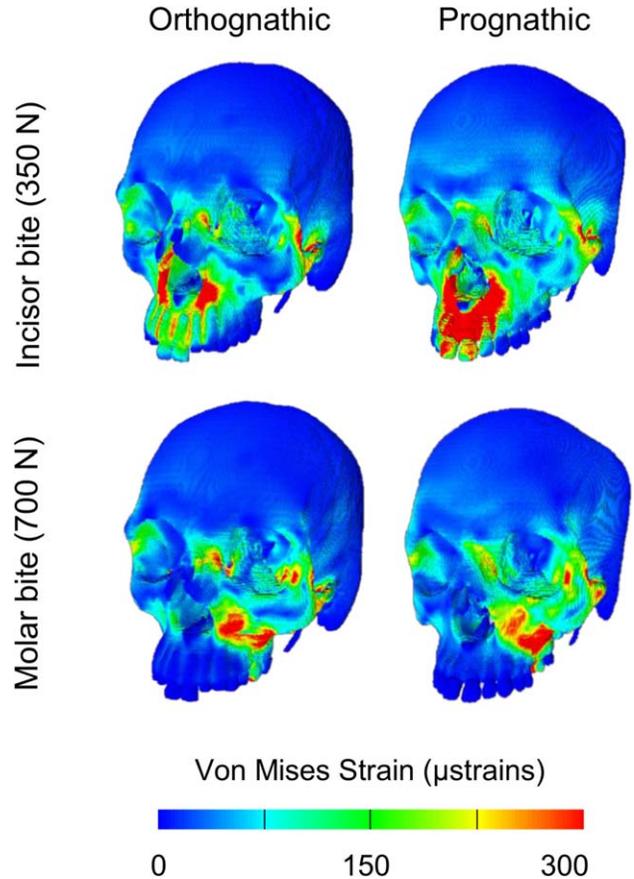


Fig. 11. Von Mises stress distribution in the human facial skeleton cortical bone during simulated clenching (Reprinted with permission from Janovic et al. 2015. Occlusal load distribution through the cortical and trabecular bone of the human mid-facial skeleton in natural dentition: a three-dimensional finite element study. *Ann Anat* 197:16–23.).

Janovic et al. (2014, 2015) used micro-computed tomography scans (micro-CT) of an adult male skull to develop a FEM of the human cranium including homogeneous, isotropic, and linear elastic properties for bone and teeth, but with elastic moduli of 9.1 GPa for cortical bone, 4.5 GPa for trabecular bone, and 20 GPa for teeth. In modeling both cortical and trabecular bone, their model represents an improvement over that of Prado et al. (2013). They simulated the action of jaw-closing muscles, and applied static vertical forces of 840 N to the tooththrow on one side, with 400 N on the molars, 280 N on the premolars, and 160 N on the anterior teeth. To fix the model in static equilibrium they constrained the cranium at the occipital condyles. Although this is an unnatural situation for biting, the constraints are far enough from the zygomatic and canine pillar areas to allow comparison with the model of Prado et al. The distributions of stresses are very similar across the two models, with the pillars and buttresses exhibiting heterogeneous stress magnitudes. Similar to the model of Prado et al. (2013), the model of Janovic et al. (2014) exhibits two strips of compressive stress, one running obliquely from the inferolateral corner of the piriform aperture to the zygomaticoalveolar crest, and a second

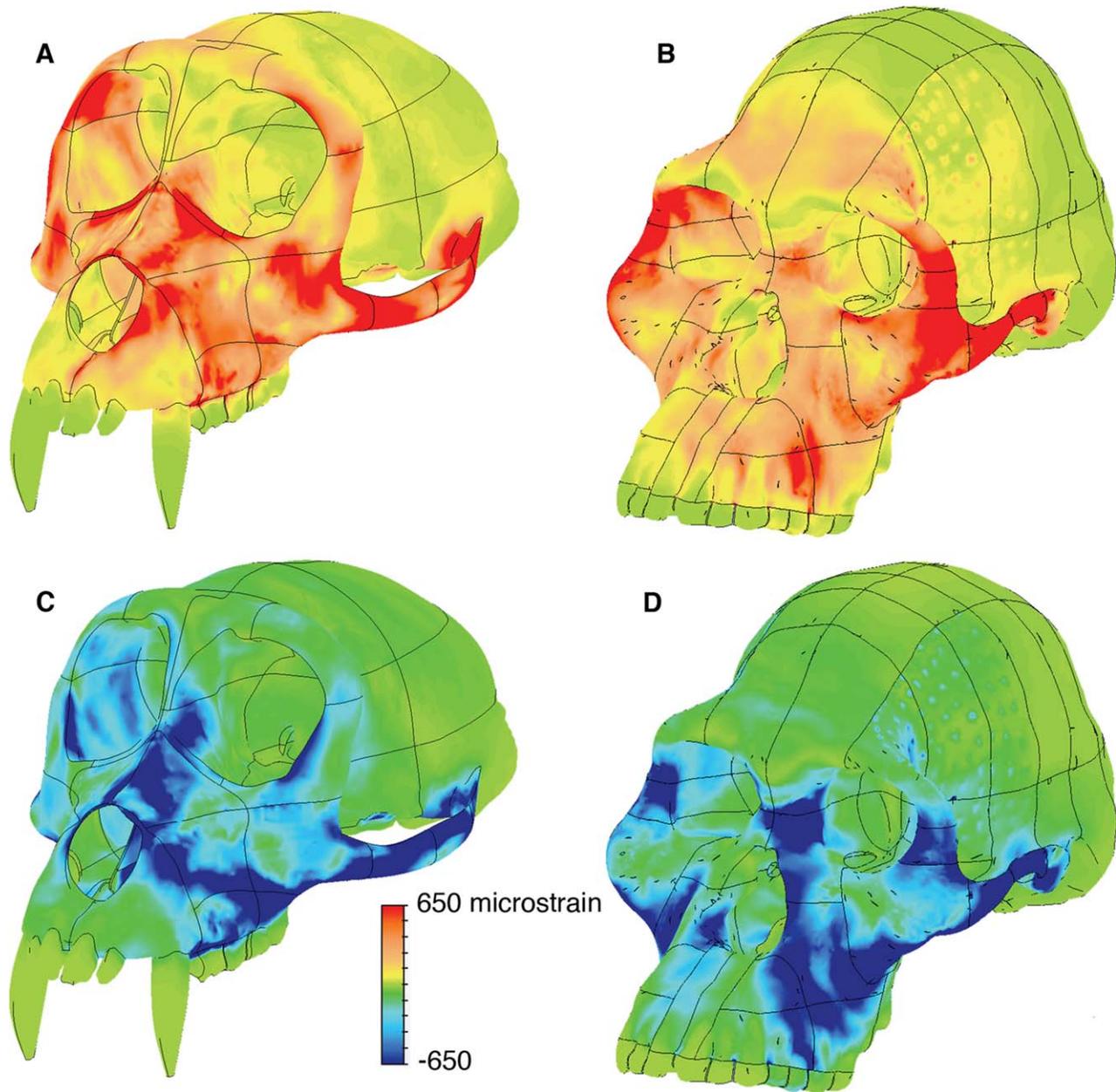


Fig. 13. From Strait et al. (2009) (From, The feeding biomechanics and dietary ecology of *Australopithecus africanus*. Proc Natl Acad Sci U S A 106: 2124-2129. Published with permission from PNAS.) Principal strains in FEM of *Macaca fascicularis* and *Australopithecus africanus* models during premolar biting. Maximum principal strain (A and B) representing tension and minimum principal strain (C and D) representing compression in *M. fascicularis* (A and C) and *A. africanus* (B and D).

extending from the medial edge of the orbital aperture to nasal bones near the frontonasal sutures.

Although Janovic et al. (2014) did not explicitly compare pillar and buttress areas with nonpillar and nonbuttress areas, they did compare cortical and trabecular bone microarchitecture between high and low Von Mises stress areas. They found no significant differences between cortical bone microarchitecture with mean Von Mises stress level, but they did find that trabecular bone in high Von Mises stress areas exhibited greater BV

fraction, total BV density, and trabecular thickness than in low stress areas. It would be of interest to know whether these variables also characterized trabecular bone in buttress and pillar versus nonbuttress and pillar areas of the facial skeleton.

Janovic et al. (2015) more explicitly addressed the question of the functional existence of pillars and buttresses. Although the authors suggest that occlusal forces are distributed along five vertical pillars and two horizontal buttresses, we would argue that their data do

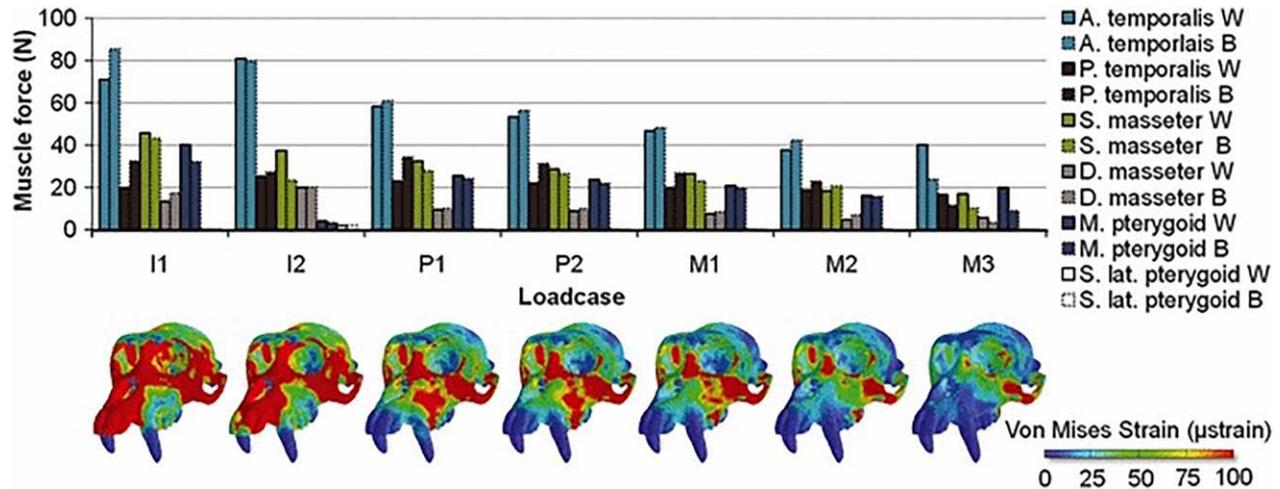


Fig. 14. Figure 2 from Fitton et al. (2012). The bar graphs indicate the muscle forces for each muscle group, keyed on the right. These were calculated at each bite point using multi-body dynamics analysis. The images below show the distribution of Von Mises strain in the facial skeleton associated with each loading regime. (Published with permission from Wiley).

not support this conclusion. The areas of high Von Mises and principal stresses are oblique or transverse to the classical pillars, and, as they note, high stresses are actually found between the pillars in the anterior wall of the maxillary sinus (Fig. 11). Janovic et al. also note that stresses in the posterior maxillary wall are not concentrated in a vertical pillar, a result confirmed by Prado et al. (2013). Moreover, their statement that “[s]tudies of bone strain in the supraorbital and infraorbital region in both human and nonhuman primate skulls were consistent with suggestions that the two buttresses participate in the transfer of occlusal forces” is not correct. The low strain magnitudes in the supraorbital region reported *in vivo* and *in silico* do not support the hypothesis that this region is important in dissipating feeding forces (Hylander et al., 1991; Ross et al., 2011). Rather than providing partial support for the “classical theory of buttresses,” we argue that Janovic et al. results argue strongly against it.

Toro-Ibacache et al. (2016) presented two FEMs from the orthognathic and prognathic extremes of normal human cranial morphological variation. Their models reveal marked differences in strain patterns in the premaxillary regions of the two models during incisor biting, but only subtle differences between them during molar biting. Moreover, the patterns of Von Mises strains in the models closely resemble those reported by Wroe et al., Prado et al., and Janovic et al., that is, molar biting is accompanied by a strip of high von Mises strain running obliquely across the maxilla from the molar bite point to the lateral margin of the piriform aperture, a second strip in the inferolateral corner of the orbital aperture, and another in the medial orbital wall and interorbital region. Although principal strain values are not presented, the strain patterns resemble those of Prado et al. and Janovic et al.

Most recently, Ledogar et al. (in press) analyzed feeding biomechanics in FEMs of six crania lying at the extremes of human variation, as well as one specimen that conformed most closely to the average shape (see

Fig. 12). Similar to previous analyses, simulations of molar biting generated high concentrations of compressive strain at the zygomatic root (zygomaticoalveolar crest), along a strip running obliquely from the crest toward the interorbital region, as well as the lateral and medial orbital margins (Fig. 12). Although orientations of compressive strain are roughly aligned with the zygomatic pillar, at least in the zygoma, high levels of compression are not seen along the zygomatic pillar itself. Instead, high levels of tension are found, particularly in the zygoma, under the inferiorly directed pull of the masseter muscle. During premolar biting, compressive strain orientations along the nasal margin are aligned with the canine pillar. However, rather than being concentrated along the canine pillar, high compressive strains extend laterally across the maxilla, as well as into the nasoalveolar region. Further, premolar biting generates high levels of tension near the inferior aspect of the nasal margin, indicating intense shearing of the lower maxilla.

Together, the available results for FEM modeling of humans are similar enough to suggest that there is general agreement on the pattern of deformation in the human cranium. These studies do not support the hypothesis that the pillars and buttresses exist functionally in humans. In the Videos (Video 1: <http://bcove.me/2mla49wp>, Video 2: <http://bcove.me/39ip9imm>, Video 3: <http://bcove.me/e0rpa5s4>) we present 18 animations, combined into 3 videos, of the patterns of deformation in the FEM of the human cranium created by Prado et al. Six animations are presented for each of three simulated bite points: canine, M¹, and M²⁻³. We present results for E1 stress (maximum principal tension), E3 stress (maximum principal compression), and Von Mises stress in frontal and lateral views. Several points should be noted for comparison with stress, strain, and deformation patterns in nonhuman primates discussed below.

- The zygomatic arch is bent downwards and rotated inwards; the orbital aperture is deformed by being

compressed superoinferiorly, producing compressive stresses at the inferolateral corner of the orbit and at the medial orbital wall, and tensile stresses at the superolateral and inferomedial margins. A strip of compressive stress is also seen across the anterolateral face of the maxilla, above the alveolar process, and across the interorbital region.

- Stress distributions are very similar across different bite points, but stress magnitudes are higher for more anterior (canine) bites than more posterior (molar) bites.
- Compressive stresses do not concentrate in any of the pillars under any loading regime. Rather, the canine-frontal and zygomatic pillars are always subjected to bending, as suggested by alternating strips of tensile and compressive stress concentrations across the “pillars”. Although not clearly seen in these views, the same is also true for the pterygoid “pillar”.

***In Vivo* and *In Silico* Studies of the Nonhuman Primate Zygomatic Complex**

The weakness of FEM studies of humans is that they are difficult to validate with *in vivo* strain gage data. In this respect, FEM studies of nonhuman primates are of particular interest (Strait et al., 2005; Ross et al., 2011). FEMs of the crania of fossil and living hominid relatives of *Homo sapiens* are also of interest because they allow us to evaluate the extent to which strain, stress and deformation regimes (*sensu* Ross et al., 2011) are related to variation in the morphology of the “pillars” and “buttresses” in humans and their close relatives.

Strait et al. (2009) used FEMs to estimate the distribution of strain energy density, Von Mises strains and principal strains in the crania of *Australopithecus africanus* and *Macaca fascicularis* during biting. They applied loads to the models using forces from the eight major masticatory muscles estimated from electromyography and physiological cross-sectional area, constrained the FEMs at articular eminences and, depending on the bite point being modeled, also constrained the left premolars, molars, or all of the postcanine teeth (molars and premolars). The models of both *M. fascicularis* and *A. africanus* exhibited high levels of principal strains in the zygomatic “pillar” (postorbital bar, anterior root of the zygoma, zygomatic arch) during biting anywhere along the postcanine tooth row; however, the strains and stresses are not purely compressive, as predicted by the pillar model. Rather, the patterns of tensile and compressive strains and stresses and the overall deformation patterns suggest that bending is the most important loading regime in the zygomatic “pillar”: the lateral orbital wall is bent in frontal planes and the zygomatic arch is bent in sagittal planes and twisted about its long axis. Moreover, the supraorbital region, one of the putative “buttresses” of the face, does not experience high strains and stresses during biting anywhere along the toothrow in either *Macaca* or *A. africanus*. This does not mean that complete removal of this bone would not be associated with weakening of the facial skeleton, but it does mean that the shape and amount of bone in that region could probably be considerably altered without significant consequences for the strength of the facial skeleton during feeding.

The strains and stresses in the canine-frontal “pillar” are of particular interest because many *A. africanus* specimens exhibit a ridge of bone extending from the canine root, up the lateral margin of the piriform aperture to the interorbital region (Rak, 1983, Villmoare and Kimbel, 2011), and the functional significance of this anterior pillar (Rak, 1983) may provide insight into diet or feeding behavior of our fossil relatives. Strait et al.’s modeling revealed that during simulations of premolar biting, the *A. africanus* cranium exhibits high levels of compressive stress and strain all along the canine pillar, from the premolar toothrow to the interorbital region (Fig. 13). In contrast, under the same loading regime in *M. fascicularis* the area corresponding to the “canine-frontal pillar” (which does not exist structurally in *Macaca*) experiences both tensile and compressive stresses and strains, suggestive of the importance of both shear and bending deformation regimes. It would appear, then that this region of the face functions as a strut under compression in the hominin, but not the macaque. One caveat is that compressive strains in *A. africanus* appear (Fig. 13) to not be concentrated only along the nasal margin but rather are widely distributed across the maxilla, which might imply that the pillar is not disproportionately carrying occlusal load. However, this is an artifact of the scale used to produce the image in Strait et al. (2009). Elsewhere in this issue, Ledogar et al. (in review) show, using a different scale, that Von Mises strain is concentrated in the canine (anterior) pillar in *A. africanus* whereas the adjoining infraorbital regions exhibit less strain. When the pillar is removed virtually as a modeling experiment, high strain areas expand across the maxilla (Ledogar et al., in review). This demonstrates that the pillar in *A. africanus* concentrates stress and acts as a compression-resisting element. However, this is the only example of a functional pillar in the two models. Thus, the results of Strait et al. (2009) and of Ledogar et al. (this issue) provide support for the functional existence of a canine-frontal pillar in *Australopithecus africanus*, which may be functioning as a compression resisting element during premolar biting.

In contrast, there is no support for the hypothesis that the zygomatic complex functions as a compression-resisting pillar in our fossil relatives, or in macaques. The validity of the FEM of *Macaca fascicularis* was evaluated by Ross et al. (2011) by comparing patterns of strain in the model with this recorded *in vivo*. Agreement between *in vivo* and *in silico* strain data was highest in the anterior root of the zygoma and zygomatic arch. Because the body of the zygoma links the zygomaticoalveolar crest with the frontal process of the zygomatic bone, it is a central component of the zygomatic “pillar” of Sicher and Tandler. Ross et al.’s results suggest that the inferior border of the anterior root of the zygoma experiences concentrations of both high tensile and high compressive strains, suggestive of the presence of high shear strains resulting from inferiorly directed components of masseter muscle force acting laterally, and superiorly directed components of bite force acting medially. In addition, as the zygomatic arch is twisted and pulled inferiorly by the masseter muscle, the anterior root of the zygoma is subjected to significant bending in frontal planes. The fact that the zygomatic body experiences primarily bending and shear stresses and strains, rather than compression, effectively invalidates

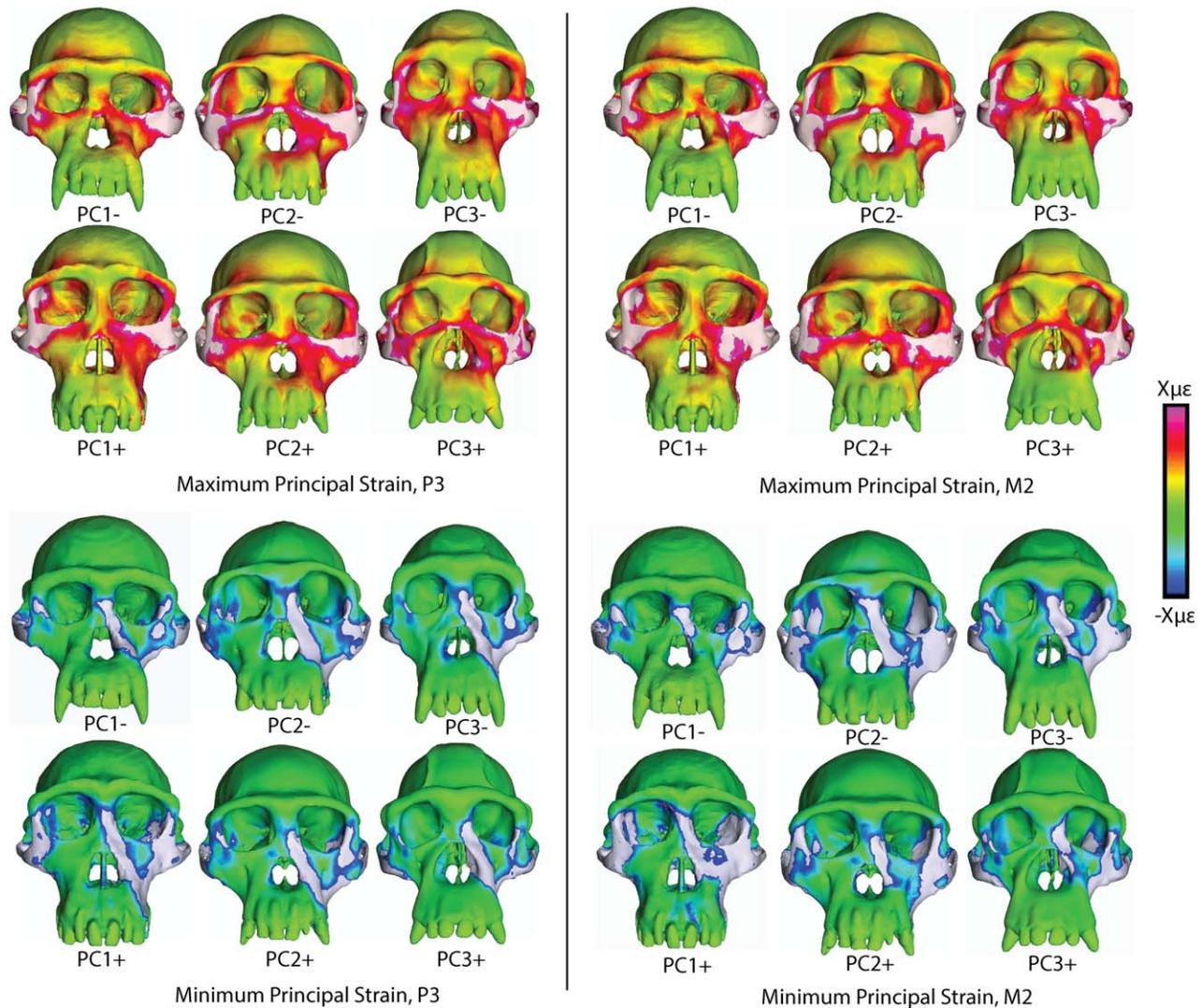


Fig. 15. Figure 4 from Smith et al. (2015a,b) illustrating principal strain distributions in FEM of the crania of *Pan troglodytes* during simulated biting on the mesial premolar (P^3) and mesial molar (M^1). Note the thin strip of compressive strain corresponding to the location of the canine-frontal pillar during premolar biting, which is not present during molar biting. Strain regimes in the zygoma vary little with bite point. (Published with permission from Wiley).

the concept of a zygomatic “pillar.” Nor is the concept of a zygomatic pillar supported by patterns of stress and strain in the lateral orbital wall, the upper part of the zygomatic “pillar.” Ross et al.’s model (2011) suggests that inferiorly directed forces at “the lateral ends of the supraorbital torus bend the supraorbital region in the frontal plane” resulting in laterally directed tensile strains in the dorsal interorbital region. Thus, Ross et al.’s (2011) results confirm that, rather than being subjected primarily to compression, the facial skeleton, including the zygomatic “pillar” is primarily subjected to bending, shear and twisting (Endo, 1966; Rak, 1983; Hylander et al., 1991; Hylander and Johnson, 1997).

An independent study of cranial deformation in a *Macaca fascicularis* cranium by Fitton et al. (2012, 2015) yielded similar results, but provides additional details on the effects of variation in muscle loads, bite

points, material properties, and model simplification. Figure 14 illustrates the results of their analysis of the effects of variation in bite point, with a target bite force of 100 N, and muscle forces estimated using multibody dynamics analysis. Incisor biting results in high Von Mises strains along the dorsum of the rostrum, the interorbital region, the lateral orbital wall, zygoma, and zygomatic arch. These strains are necessarily high because, with the bite force target set at 100 N across all bite points, the muscle forces need to be higher at anterior bite points. As found by Strait et al. (2009), pre-molar biting produces a strip of high Von Mises strains extending from the bite point up the side of the rostrum to the interorbital region. However, as Strait et al. found, this high strain region is not confined to a “pillar,” but is spread across the side of the rostrum. At all bite points (incisor through molar) strain values in

the supraorbital region (a buttress area) are lower than in the lateral orbital wall (pillar), which itself is lower than that recorded from the zygomatic arch.

Chimpanzees are more closely related to humans than any other extant primates and their crania resemble those of *A. africanus* and *A. afarensis* in important respects, making FE modeling of their crania of particular interest. Moreover, because they are well represented in museum collections, it is possible to evaluate intraspecific variation in cranial stress, strain, and deformation patterns. Smith et al. (2015a, 2015b) compared patterns of strain (Fig. 15) in the crania of six *Pan troglodytes* (common chimpanzee) representing the extremes of the principal components of shape variation in the species while holding cranial size, external forces, and loading conditions constant. The best evidence for the functional existence of pillars is found in this study, but only during modeling of premolar biting. In all six FEMs, a thin strip of high compressive strains extends from the premolar bite point up the lateral margin of the piriform aperture to the interorbital region. This strip is continuous across the alveolar process of the maxilla to a second strip of compressive strain extending up the zygomaticoalveolar crest to the inferior edge of the zygoma and, in some individuals, onto the orbital side of the postorbital bar. Yet, the regions in the zygomatic exhibiting high compressive strains also experience high tensile strains, indicating that the overall deformation regime in those locations is one of shear. In contrast, the canine pillar experiences notably higher compressive than tensile strains during premolar biting.

Smith et al. (2015a,b) also examined strain distributions in the facial skeleton of the OH5 specimen of *Paranthropus boisei*, a fossil hominin with a massively inflated and anteriorly placed anterior zygoma, and *Australopithecus africanus*. When loading was applied at the left third premolar, there was variation in Von Mises' strain values in both non-pillar and pillar regions, zygomatic arch and the zygomatic root across the FEMs. The FEM of the *P. boisei* revealed much lower strain magnitudes in the zygoma compared to the other hominins.

Summary of zygomatic complex deformation, stress, and strain regimes during biting. The studies presented here reveal common patterns of deformation, stress, and strain and in the zygomatic region, which we argue require that the notion of a zygomatic "pillar" be abandoned. As Ross et al. (2011) state, "the FEM, including its specific geometry and material properties, and the resulting loading, stress and deformation regimes" is the best hypothesis regarding behavior of the cranium during loading" (Ross et al., 2011; see also Chalk et al., 2011). Geometric morphometric approaches currently being developed and implemented provide more rigorous tools for comparing FEMs than the verbal descriptions presented here (e.g., Fitton et al., 2015) and we look forward to their implementation for the problems discussed in this paper. Nevertheless, we believe a valid, written, qualitative summary of the deformation patterns of the zygomatic complex can be presented as follows.

During all feeding behaviors so far modeled the zygomatic arches are subjected to the deformation regimes

suggested by Hylander and Johnson (1997): masseter muscle forces bend and shear the zygomatic arches in sagittal planes and twist them about their long axes. This results in: coronal bending and shear stresses and strains (i.e., bending and shear stresses/strains in coronal planes) acting on the infraorbital plate and anterior zygoma root; and twisting of the working side mid-facial skeleton about the bite point such that the lateral orbital margin is pulled inferolaterally, subjecting it to tensile stresses/strains and bending of the lateral orbital wall. This bending, combined with other deformations of the orbital walls, deforms the orbital aperture so that it becomes longer along a superomedial-inferolateral axis and shorter along orthogonal axes. This deformation of the orbital aperture is accompanied by tensile strain concentrations in the superolateral and inferomedial corners and compressive strains in the inferolateral and superomedial corners of the orbits. On the biting/working side of the cranium, which also has superiorly directed bite forces acting on the molar toothrow, coronal shear stresses/strains in the anterior root of the zygoma and infraorbital plate are accentuated.

This deformation regime is found in: FEM of macaques, validated by *in vivo* and *in vitro* strain gage data (Kupczik et al., 2007; Ross et al., 2011; Fitton et al., 2012, 2015); frame models of the human and gorilla facial skeletons validated by *in vitro* strain gage data (Endo, 1966); FEMs of the human facial skeleton developed independently by Wroe et al. (2010), Prado et al. (2013), Freire et al. (2014), Janovic et al. (2014, 2015), Toro-Ibacache et al. (2016), and Ledogar et al. (in press); and frame models (Rak, 1983) and FEMs of the crania of human fossil relatives, *A. africanus* (Strait et al., 2009) and *A. sediba* (Ledogar et al., 2016).

These deformation regimes do not result in the axial compression implicit and explicit in Sicher and Tandler's (1928) pillar model of the human facial skeleton. Rather, the lateral orbital wall portion of the zygomatic "pillar" extending from and including the anterior zygoma root to the cranium is, because of its geometry and the nature of its external forces, subjected primarily to bending and shear stresses/strains, as originally suggested by Endo (1966). Moreover, the zygomatic arch itself, also a component of Sicher and Tandler's (1928) zygomatic pillar, is also mainly subjected to bending, twisting, and shear (Hylander and Johnson, 1997), not compression. In fact, the only part of the zygomatic "pillar" that primarily experiences compression during chewing is the zygomaticoalveolar crest extending from the toothrow to the anterior root of the zygoma. However, in contrast with a "pillar" concept, during molar biting and chewing this compressive zone is not a thin strip, but extends to the entire alveolar process of the maxilla and often much of the wall of the maxillary sinus as well.

During premolar biting, when the canine pillar is subjected to the highest compressive stresses, chimpanzee and *A. africanus* crania show the best evidence for the existence of a functional pillar, with a thin zone of compressive stress/strain extending from the premolar region, up the lateral margin of the piriform aperture to the interorbital region. High compressive strains within this strip contrast markedly with the low compressive strains in the adjacent infraorbital region. However, in macaques and humans, compressive stress is distributed across a broader region of the snout, and is not confined

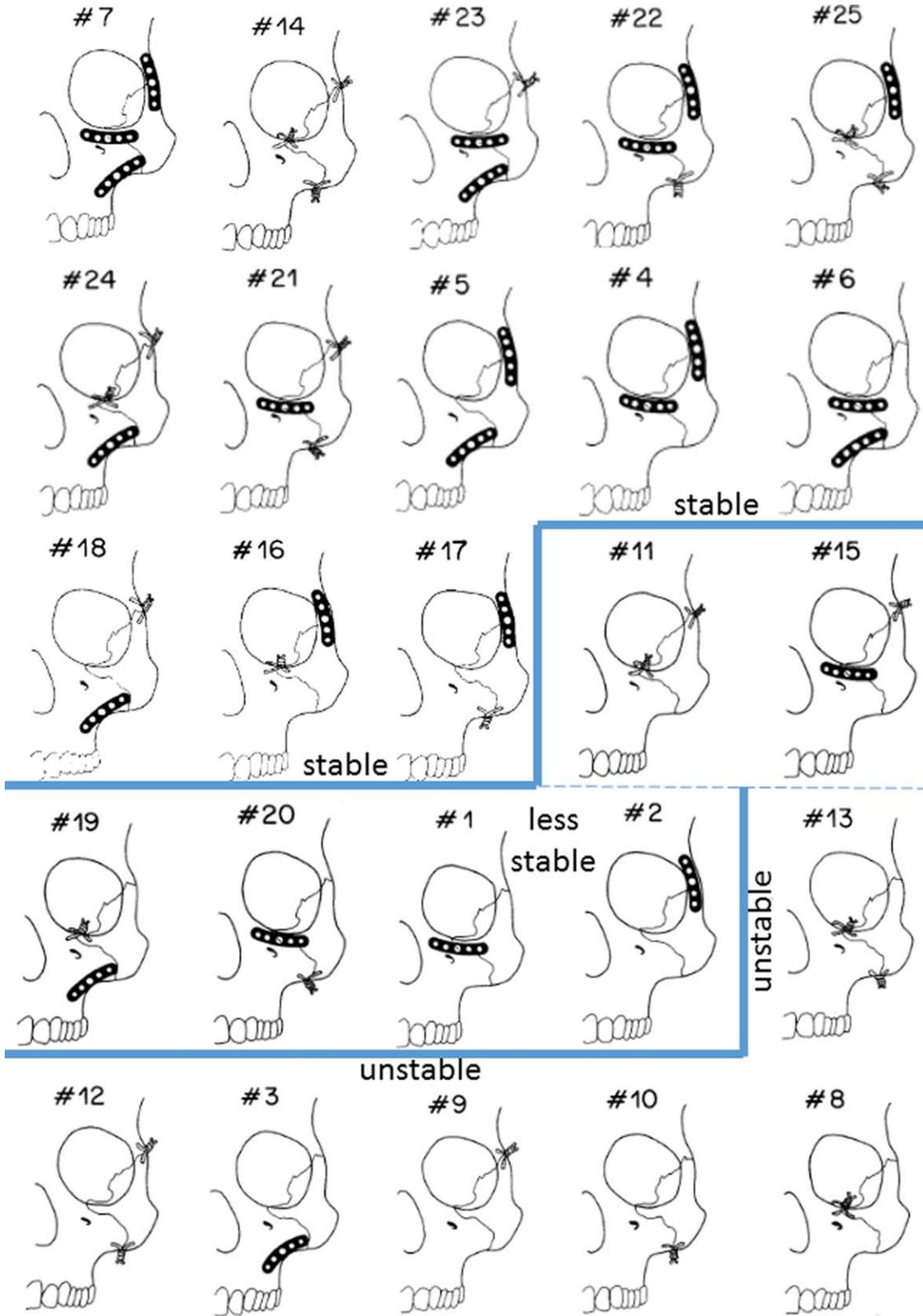


Fig. 16. Figures 5–7 from Davidson et al. (1990) reproduced combined. Configurations of zygomatic fracture repair techniques from most stable (top left) to least stable (bottom right). Davidson et al. (1990) classified #7–#17 as stable, #11–#2 as acceptable, and #13–#8 as unstable. (Reprinted from Davidson J, Nickerson D, Nickerson B. 1990. Zygomatic fractures: comparison of methods of internal fixation. *Plast Reconstr Surg* 86: 25-32, with permission from Elsevier).

to the region of the classic “pillar.” Thus, the concept of vertical pillars resisting and distributing bite forces primarily as compressive forces and stresses through narrow specialized regions of the facial skeleton is not supported by the evidence.

One area of future research that deserves more attention is the role of the temporalis fascia in modulation of deformation, stress, and strain regimes in the zygomatic arch and anterior zygoma root. This is of some clinical significance in humans because the Gilles approach to tripod fracture repairs compromises this fascia. A role for the temporalis fascia in support of the zygomatic arch is supported by Brodie’s (1952) comparative observations that animals such as moles, shrews, hedgehogs, anteaters and sloths present incomplete zygomatic arches but still have well-developed masseter muscles. Experimental evidence in support of this hypothesis came from Eisenberg and Brodie’s (1965) experiments with *Cebus*, and FEM analyses arguing for a role for the temporalis fascia in supporting the arch in macaques (Kupczik et al., 2007) chimpanzees, gorillas, and humans (Witzel et al., 2004). Curtis et al. (2011) addressed this issue, but their analysis did not actually model the fascia, but applied superiorly directed forces to the arch estimated to be similar to those imposed by the fascia. Future *in vivo* measurements of 3D muscle architecture and temporalis fascia dynamics during feeding promise to inform this debate.

HOW USEFUL IS THE PILLAR-BUTTRESS CONCEPT CLINICALLY AND CAN A NEW CONCEPT ADVANCE CLINICAL PRACTICE?

Although the biological reality of the “pillars and buttresses” of the facial skeleton is debatable, they still serve as important concepts in discussions of fracture reduction and repair, and are accepted anchor points for plates, screws, and other implants (Manson et al., 1980; Gruss and Mackinnon, 1986; Yamamoto et al., 1998; Nagasao et al., 2005; Andrades et al., 2008; Rodriguez et al., 2008; Bluebond-Langner and Rodriguez, 2009; Olynik et al., 2013; Roumeliotis et al., 2015; Hurrell et al., 2016; Litschel and Suárez, 2015). The zygomatic complex is especially important because it is the strongest and most easily accessible of the vertical facial “pillars,” the zygoma serves as an important anchor point for zygomatic implants (Fernández et al., 2014), and zygomatic complex fractures due to motor vehicle accidents and interpersonal violence are the most common facial fractures treated by maxillofacial surgeons. As with early approaches to mandible repair (Ruderman and Mullen, 1992), good practical results have been achieved without accurate and precise knowledge of the patterns of stress, strain, and deformation of the zygomatic complex during normal functioning, post-stabilization, and healing. Why, then, are the biomechanics of the facial skeleton clinically relevant? There are several important answers to this question.

The most general answer is that there is room for improvement in techniques and technology used in craniofacial fracture repair, orthognathic surgery, and dental implantology. Although current techniques for fracture immobilization and dental implant fixation are successful in the majority of cases, they are not completely free of morbidity. Titanium miniplates and

screws often need to be removed in adult patients due to infection, pain, esthetics, or exposure of the plates in the oral cavity, and some clinics remove them routinely (Francel et al., 1992; Rallis et al., 2006; O’Connell et al., 2009). Moreover, long term use of titanium implants is not without concerns about particle shedding, inflammatory responses, and alterations to the peri-implant bone that can endanger the implant (Kim et al., 1997; Langford and Frame, 2002; Haïat et al., 2014). Use of titanium hardware in children is thought to be even more problematic due to drift during growth, and when they are used, it is argued that they should be removed after 3–4 months (Eppley et al., 2005). Resorbable plates offer one possible solution, but the ideal combination of resorbable and titanium plates in adults is still being evaluated (Hanemann et al., 2005) and to our knowledge there are no randomized controlled studies of their long term sequelae in children (Boyette, 2014). Decreasing the number of plates provides another route to decreased morbidity, and the early agreement on the advisability of using at least two mini-plates in zygomatic fracture repair (Rinehart et al., 1989; Davidson et al., 1990) is being questioned by advocates of single plate implants (Balakrishnan et al., 2015).

What then are the specific implications of our review of *in vivo* and *in silico* data on the biomechanics of the zygomatic complex for procedures used to produce functionally and cosmetically optimal restorations of the craniofacial skeleton after zygomatic complex fracture? Clearly, control of patterns of strain and deformation in the fractured, repaired, and healing facial skeleton is relevant to the design and deployment of bony implants, as reflected in several decades of biomechanical research into fixation methods for zygomatic complex fractures. After open fracture reduction (surgical repositioning of bones to a near normal position), repair of zygomatic complex fractures involves stabilization and rehabilitation. Different degrees of stabilization are associated with different kinds of bone healing (Egol et al., 2004): absolute stabilization (immobilization), when fracture gap (L) strain is less than two percent (i.e., $\Delta L/L < 2\%$), is associated with primary bone healing—endosteal healing involving direct osteonal formation without callus formation; relative stabilization, ($2\% < \Delta L/L < 10\%$) is associated with secondary bone healing—callus formation, followed by extensive modeling and remodeling; and $\Delta L/L > 10\%$ is too high for healing because it is associated with tissue rupture (Perren, 2002; Egol et al., 2004).

Davidson et al. (1990) simulated fracture of the zygomatic complex in human crania with osteotomies (although apparently leaving the zygomatic arch intact, see their Fig. 1), applied mechanical loads to mimic superficial masseter muscle forces, and evaluated the rigidity of 25 combinations of miniplate x wire fixation methods across a zygomaticofrontal osteotomy near the eponymous suture, a zygomaticomaxillary osteotomy on the inferior orbital margin, and along the zygomaticoalveolar crest (Fig. 16). They divide their results into stable ($< 2^\circ$ zygoma rotation about any axis), acceptable ($< 5^\circ$), and unstable ($> 5^\circ$) fixation, but because Davidson et al. helpfully provide a rank order of all configurations, we can parse their results in a way that links them to our modeling results (Fig. 16). The stable combinations include: three-point fixation using any combination of

miniplates or wires; all combinations of two miniplates with or without a wire; and three combinations of one miniplate and one wire (#18, 16, and 17). These latter three combinations are noteworthy in either having the miniplate across the zygomaticofrontal osteotomy, or a wire across the zygomaticofrontal and the miniplate on the zygomaticoalveolar crest. It is illustrative to group these stable configurations with the two most stable configurations in the “acceptable fixation” category (#11 and 15)—those that have wire fixation at the zygomaticofrontal osteotomy, and either a wire or a miniplate across the zygomaticomaxillary site—assigning the remainder of the configurations to a “less stable and unstable” group. In this latter group we find all of the single-point fixation methods (#3–#8; Fig. 16, bottom row), most combinations without zygomaticofrontal fixation, and the two-wire combinations that include a wire at the zygomaticoalveolar crest. The only stable fixation method without zygomaticofrontal fixation includes two miniplates at the other two osteotomies, and the most stable two-wire fixation method consists of one at the zygomaticofrontal and one at the zygomaticomaxillary osteotomy.

Rudderman and Mullen (1992) have already explained how three-point fixation prevents translation along and rotation about all three orthogonal Cartesian axes, and how certain one-plate + one-wire combinations can achieve the same results. Encouraging the reader to study Rudderman and Mullen (1992), we limit our discussion here to the relationship between Davidson et al.’s results and the pattern of circumorbital deformation that we hypothesize is common among catarrhine primates, including humans. First, note that the locations of the wires in the most stable two-wire configuration (#11, Fig. 16) are those areas subjected to high maximum principal (tensile) strain values: the regions of the zygomaticofrontal and the zygomaticomaxillary sutures. Some component of the tensile strain in these areas is due to deformation of the orbital margins in bending (best seen in the animations in Video 1: <http://bcove.me/2mla49wp>, Video 2: <http://bcove.me/39ip9imm>, and Video 3: <http://bcove.me/e0rpa5s4>) as suggested by Endo (1966), Rak (1983), and Ross et al. (2011), a deformation and strain regime that can only occur when these regions are solidly connected, that is, unfractured/uncut. However, some of this tensile strain is also caused by the inferomedially directed masseter muscle force rotating the zygomatic complex about an anteroposterior axis passing through or near the zone of compression at the top of the zygomaticoalveolar crest (cf. Deveci et al., 2004). Because wire fixation can resist tension across fractures, they perform adequately at these locations to stabilize the zygomatic complex against masseter muscle forces. Further examples emphasize this point. Combinations #18 and #16 from Davidson et al. are both equally stable. #18 has a wire appropriately resisting tensile strain at the frontozygomatic site and a plate appropriately resisting compression at the zygomaticoalveolar crest location, whereas in combination #16 a miniplate resists tension and rotation about an AP axis at the frontozygomatic site, relieving strain on the zygomaticoalveolar crest, while the wire is appropriately located to resist tension across the zygomaticomaxillary osteotomy. The least stable of the “stable” configurations (#17) has a wire at a location subjected to compression, for which it is not as well designed. The point here is

not to argue for the implementation of wire fixation, rarely used today (Zachariades et al., 1998), but to highlight how the patterns of deformation in FEM inform appropriate implant design (match of form to function), decreasing the implant load, and hence, morbidity. Here we have retrospectively explained the suitability of certain fixation techniques, but this process can equally well be used for design of implants in the future (Nagasao et al., 2005; Aquilina et al., 2014).

After reduction and fixation, successful healing depends on adaptation (remodeling and modeling) of the craniofacial bone to the new loading conditions. FEM of facial bones provides information on bone deformation, stress, and strain relevant to design of implant techniques in three important ways. First, it is important to create the optimal strain environment for bone healing. Prior knowledge of the strain and deformation environment into which an implant is being placed is of great value. In some situations absolute stability and primary bone healing may be most beneficial, whereas in others relative stability and secondary bone healing might be more appropriate. Implants that are too stiff can create stress shielding, possibly inducing bone resorption, whereas implants that are not stiff enough can result in too much strain across the fracture zone. We are not aware of studies that ask whether the healing environment of a bone should be optimized to the bone’s original strain environment. Does bone in high strained areas such as the zygoma heal faster when subjected to high strains during healing? Does bone in low strained areas such as the supraorbital torus heal faster when subjected to low strains during healing? We do know that the bones of the facial skeleton are exposed to widely varying peak and routine strain magnitudes during normal physiological behaviors, such as feeding (Hylander et al., 1991; Ross, 2001; Ross and Metzger, 2004; Ross et al., 2011). Some bone in the face, such as the floor, roof, and medial wall of the orbit, probably never experience even 100 $\mu\epsilon$, meaning that their threshold for bone resorption is likely seldom reached.

Regardless of whether there is a single or multiple optimal strain environments for bone healing, controlling those environments in biological structures characterized by steep strain gradients and complex deformation regimes is a challenge. Part of this challenge is to understand how patterns of bone deformation and strain impact the bone-screw interfaces on which implant stability relies. Screw pull-out forces and stresses due to screw torsion and tilting vary with implant plate length, stiffness, and deformation magnitude (Perren, 2002; Egol et al., 2004), so implants should be designed to match their deformation environments. The strain and deformation environment at the zygomaticofrontal suture is important because stabilization of this region is seen as fundamental for success of zygomatic complex fracture repairs (Rinehart et al., 1989; Davidson et al., 1990; Kasrai et al., 1999; Deveci et al., 2004; Hanemann et al., 2005). The strain and deformation regimes along the inferior orbital rim are also of interest in light of Hanemann et al.’s (2005) finding that when zygomatic complex fractures are repaired using combinations of titanium and resorbable plates, high magnitude loading rarely broke or stretched plates at the zygomaticoalveolar crest (their zygomaticomaxillary buttress), but plates in the zygomaticofrontal region

were stretched and broken, and screws in the inferior orbital rim location experienced pullout and fracture at the screw head-shaft interface. The results reviewed here reveal that both the zygomaticofrontal and inferior orbital rim regions of the orbital margin are subjected to high maximum principal (tensile) strains and deformation due to bending, whereas the “zygomaticomaxillary buttress” area is subjected to high magnitudes of compressive stress and strain. A more detailed understanding of the exact nature of the stress, strain, and deformation regimes in the areas of implant failure would clearly be of value.

Finally, it is equally important to preserve normal strain and deformation environments in bone distant from fracture and implant sites to minimize potentially maladaptive bone remodeling and modeling at these secondary sites. The high connectivity and rigidity of the bones of the facial skeleton means that changes in shape in one area can alter strain and deformation patterns in other areas (Strait et al., 2008). Implant designs should create the best environment for healing at the fracture without compromising bone quality elsewhere.

CONCLUSIONS

Review of the available morphological data and *in vivo* and FEM data on stress, strain and deformation regimes in the facial skeletons of humans and nonhuman primates suggest that the concept of pillars and buttresses does not accurately describe the biomechanical behavior of the human facial skeleton during biting. During molar biting in particular, stress, strain and deformation regimes do not support the idea that the canine-frontal and zygomatic and pillars are loaded in compression. Instead, on the basis of the results of four independent research groups, during molar biting the human zygomatic complex is primarily loaded in bending and shear. These patterns resemble those reported previously for *Macaca*, and hypothesized by Endo for *Gorilla* and *Homo*. Thus, the concept of a zygomatic pillar receives no support in the human or nonhuman primate literature. In contrast, studies of our close relatives, both extant and fossil, suggest that the canine-frontal pillar has some structural and functional reality. In humans however, this pillar does not seem to exist. The bone material properties data do not support its existence and the strain and deformation patterns do not support its existence. It would appear therefore that a canine-frontal pillar may have characterized human close relatives, or even ancestors, but is not present in extant humans. However, until detailed studies of bone microarchitecture, like those presented here for *Sapajus*, are performed on humans, the possibility of bone microarchitecture corroborating the existence of a canine-frontal pillar should not be discounted.

ACKNOWLEDGMENTS

This project was funded by grants from the National Science Foundation Physical Anthropology HOMINID program (NSF BCS 0725219, 0725183, 0725147, 0725141, 0725136, 0725126, 0725122, 0725078). FBP worked on this article while at University of Chicago supported by CNPq, National Council for Scientific and Technological Development, Brazil.

LITERATURE CITED

- Alexandridis C, Thanos CE, Caputo AA. 1981. Distribution of stress patterns in the human zygomatic arch and bone. *J Oral Rehabil* 8:495–505.
- Andrades P, Rosenthal EL, Carroll WR, Baranano CF, Peters GE. 2008. Zygomaticomaxillary buttress reconstruction of midface defects with the osteocutaneous radial forearm free flap. *Head Neck* 30:1295–1302.
- Aquilina P, Parr WC, Chamoli U, Wroe S, Clausen P. 2014. A Biomechanical Comparison of Three 1.5-mm Plate and Screw Configurations and a Single 2.0-mm Plate for Internal Fixation of a Mandibular Condylar Fracture. *Craniofacial Trauma Reconstr* 7:218–223.
- Balakrishnan K, Ebenezer V, Dakir A, Kumar S, Prakash D. 2015. Management of tripod fractures (zygomaticomaxillary complex) 1 point and 2 point fixations: A 5-year review. *J Pharm Bioallied Sci* 7(Suppl 1):S242–S247.
- Ballenger JJ, Wackym PA, Snow JB. 2009. Ballenger's Otorhinolaryngology: Head and Neck Surgery. 17th ed. Hamilton, Ontario: PMPH USA.
- Benninghoff A. 1925. Spaltlinien am Knochen, eine Methode zur Ermittlung der Architektur platter Knochen. *Verh Anat Ges* 34: 189–206.
- Black EH, Nesi FA, Gladstone G, Levine MR, Calvano CJ. 2012. Smith and Nesi's Ophthalmic Plastic and Reconstructive Surgery. Berlin: Springer.
- Bluebond-Langner R, Rodriguez ED. 2009. Application of skeletal buttress analogy in composite facial reconstruction. *Craniofacial Trauma Reconstr* 2:19–25.
- Bluntschli H. 1926. Rückwirkuneg des Kieferapparatus auf den Gesamyschädel. *Z Zahnärzte Orthoped* 18:71–85.
- Boyette JR. 2014. Facial fractures in children. *Otolaryngol Clin North Am* 47:747–761.
- Brodie GA. 1952. Consideration of musculature in diagnosis, treatment and retention. *Am J Ortho* 38:823–835.
- Brunet M, Guy F, Pilbeam D, Mackaye HT, Likius A, Ahounta D, Beauvilain A, Blondel C, Bocherens H, Boisserie JR, et al. 2002. A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* 418:145–151. Erratum in: *Nature*. 2002. 418: 801.
- Cattaneo PM, Dalstra M, Melsen B. 2003. The transfer of occlusal forces through the maxillary molars: a finite element study. *Am J Orthod Dentofacial Orthop* 123:367–373.
- Chalk J, Richmond BG, Ross CF, Strait DS, Wright BW, Spencer MA, Wang Q, Dechow PC. 2011. A finite element analysis of masticatory stress hypotheses. *Am J Phys Anthropol* 145:1–10.
- Couly G. 1976. La statique osseuse de la face. *Rev Belge Stomatol* 77:420–426.
- Cryer MH. 1916. *The Internal Anatomy of the Face*. Philadelphia: Lea & Febiger.
- Curtis N, Witzel U, Fitton L, O'Higgins P, Fagan M. 2011. The mechanical significance of the temporal fasciae in *Macaca fascicularis*: an investigation using finite element analysis. *Anat Rec (Hoboken)* 294:1178–1190.
- Davidson J, Nickerson D, Nickerson B. 1990. Zygomatic fractures: comparison of methods of internal fixation. *Plast Reconstr Surg* 86:25–32.
- Dechow PC, Wang Q, Peterson J. 2010. Edentulation alters material properties of cortical bone in the human craniofacial skeleton: functional implications for craniofacial structure in primate evolution. *Anat Rec (Hoboken)* 293:618–629.
- Deveci M, Eski M, Gurses S, Selmanpakoglu N, Akkas N. 2004. Biomechanical analysis of the rigid fixation of zygoma fractures: an experimental study. *J Craniofac Surg* 5:595–602.
- Eisenberg NA, Brodie AG. 1965. Antagonism of temporal fascia to masseteric contraction. *Anat Rec* 152:185–192.
- Egol KA, Kubiak EN, Fulkerson E, Kummer FJ, Koval KJ. 2004. Biomechanics of locked plates and screws. *J Orthop Trauma* 18: 488–493.
- Ellis E. 1991. Fractures of the zygomatic complex and arch. In Fonseca RJ, Walker RV, editors. *Oral and Maxillofacial Trauma*, vol 1. Philadelphia: PA Saunders. p 435.

- Ellis E, El-Attar A, Moos KI 1985. An analysis of 2,067 cases of zygomatic-orbital fracture. *J Oral Maxillofac Surg* 43:417–428.
- Endo B. 1966. Experimental studies on the mechanical significance of the form of the human facial skeleton. *J Fac Sci* 1–106.
- Eppley BL, Pietrzak WS, Blanton MW. 2005. Allograft and alloplastic bone substitutes: a review of science and technology for the craniomaxillofacial surgeon. *J Craniofac Surg* 16:981–989.
- Fernández H, Gómez-Delgado A, Trujillo-Saldarriaga S, Varón-Cardona D, Castro-Núñez J. 2014. Zygomatic implants for the management of the severely atrophied maxilla: a retrospective analysis of 244 implants. *J Oral Maxillofac Surg* 72:887–891.
- Fitton LC, PrôA M, Rowland C, Toro-Ibacache V, O'higgins P. 2015. The impact of simplifications on the performance of a finite element model of a *Macaca fascicularis* cranium. *Anat Rec (Hoboken)* 298:107–121.
- Fitton LC, Shi JF, Fagan MJ, O'Higgins P. 2012. Masticatory loadings and cranial deformation in *Macaca fascicularis*: a finite element analysis sensitivity study. *J Anat* 221:55–68.
- Francel TJ, Birely BC, Ringelman PR, Manson PN. 1992. The fate of plates and screws after facial fracture reconstruction. *Plast Reconstr Surg* 90:568–573.
- Freire AR, Prado FB, Rossi AC, Noritomi PY, Haiter Neto FH, Caria PHF. 2014. Biomechanics of the human canine pillar based on its geometry using finite element analysis. *Int J Morphol* 32:214–220.
- Furst IM, Austin P, Pharoah M, Mahoney J. 2001. The use of computed tomography to define zygomatic complex position. *J Oral Maxillofac Surg* 59:647–654.
- Görke O. 1904. Beitrag zur funktionellen Gestaltung des Schädels bei den Anthropomorphen und Menschen durch Untersuchung mit Röntgenstrahlen. *Arch Anthropol* 1:91–108.
- Gross MD, Arbel G, Hershkovitz I. 2001. Three-dimensional finite element analysis of the facial skeleton on simulated occlusal loading. *J Oral Rehabil* 28:684–694.
- Gross JS, Mackinnon SE. 1986. Complex maxillary fractures: role of buttress reconstruction and immediate bone grafts. *Plast Reconstr Surg* 78:9–22.
- Haiat G, Wang HL, Brunski J. 2014. Effects of biomechanical properties of the bone-implant interface on dental implant stability: from *in silico* approaches to the patient's Mouth. *Annu Rev Biomed Eng* 16:187–213.
- Hanemann M, Jr, Simmons O, Jain S, Baratta R, Guerra AB, Metzinger SE. 2005. A comparison of combinations of titanium and resorbable plating systems for repair of isolated zygomatic fractures in the adult: a quantitative biomechanical study. *Ann Plast Surg* 54:402–408.
- Hardt N, Kuttnerberger J. 2010. Chapter 1, Anatomy of the Craniofacial Region, in *Craniofacial Trauma: Diagnosis and Management*. 1st ed. Berlin: Springer. p 3–13.
- Herman H, Bucksch H. 2014. *Dictionary Geotechnical Engineering/Wörterbuch GeoTechnik*. 1st ed. Berlin: Springer. p 179–179.
- Hilloowala R, Kanth H. 2007. The transmission of masticatory forces and nasal septum: structural comparison of the human skull and Gothic cathedral. *Cranio* 25:166–171.
- Hurrell MJ, Borgna S, David MC, Batstone MD. 2016. A multi-outcome analysis of the effects of treatment timing in the management of zygomatic fractures. *Int J Oral Maxillofac Surg* 45:51–56.
- Hylander WL. 1979. An experimental analysis of temporomandibular joint reaction force in macaques. *Am J Phys Anthropol* 51:433–456.
- Hylander WL, Johnson KR. 1997. *In vivo* bone strain patterns in the zygomatic arch of macaques and the significance of these patterns for functional interpretations of craniofacial form. *Am J Phys Anthropol* 102:203–232.
- Hylander WL, Picq PG, Johnson KR. 1991. Masticatory-stress hypotheses and the supraorbital region of primates. *Am J Phys Anthropol* 86:1–36.
- Janovic A, Milovanovic P, Saveljic I, Nikolic D, Hahn M, Rakocevic Z, Filipovic N, Amling M, Busse B, Djuric M. 2014. Microstructural properties of the mid-facial bones in relation to the distribution of occlusal loading. *Bone* 68:108–114.
- Janovic A, Saveljic I, Vukicevic A, Nikolic D, Rakocevic Z, Jovicic G, Filipovic N, Djuric M. 2015. Occlusal load distribution through the cortical and trabecular bone of the human mid-facial skeleton in natural dentition: a three-dimensional finite element study. *Ann Anat* 197:16–23.
- Karlan MS, Cassisi NJ. 1979. Fractures of the zygoma: A geometric, biomechanical, and surgical analysis. *Arch Otolaryngol* 105:320–327.
- Kasrai L, Hearn T, Gur E, Forrest CR. 1999. A biomechanical analysis of the orbitozygomatic complex in human cadavers: examination of load sharing and failure patterns following fixation with titanium and bioresorbable plating systems. *J Craniofac Surg* 10:237–243.
- Kim YK, Yeo HH, Lim SC. 1997. Tissue response to titanium plates: a transmitted electron microscopic study. *J Oral Maxillofac Surg* 55:322–326.
- Kimbel WH, Rak Y, Johanson DC. 2004. *The skull of Australopithecus afarensis*. Oxford: Oxford University Press.
- Kupczik K, Dobson KA, Fagan MJ, Crompton RH, Oxnard CE, O'Higgins P. 2007. Assessing mechanical function of the zygomatic region in macaques: validation and sensitivity testing of finite element models. *J Anat* 210:41–53.
- Langford RJ, Frame JW. 2002. Surface analysis of titanium maxillofacial plates and screws retrieved from patients. *Int J Oral Maxillofac Surg* 31:511–518.
- Le Fort R. 1901. Etude expérimentale sur les fractures de la mâchoire supérieure. *Rev Chir Paris* 23:208–227.
- Ledogar JA. 2015. Human feeding biomechanics: intraspecific variation and evolution. Ph.D dissertation, University at Albany.
- Ledogar JA, Benazzi S, Smith AL, Weber GW, Carlson KB, Dechow PC, Grosse IR, Ross CF, Richmond BG, Wright BW, et al. The biomechanics of bony facial “buttresses” in South African australopithecids: an experimental study using finite element analysis. *Anat Rec* (in review).
- Ledogar JA, Dechow PC, Wang Q, Gharpure P, Gordon AD, Baab KL, Smith AL, Weber GW, Grosse IR, Ross CF, et al. Human feeding biomechanics: performance, variation, and functional constraints. *PeerJ* (in press).
- Ledogar JA, Smith AL, Benazzi S, Weber GW, Spencer MA, Carlson KB, McNulty KP, Dechow PC, Grosse IR, Ross CF, et al. 2016. Mechanical evidence that *Australopithecus sediba* was limited in its ability to eat hard foods. *Nat Commun* 8:7:10596.
- Linnau KF, Stanley RB, Jr, Hallam DK, Gross JA, Mann FA. 2003. Imaging of high-energy midfacial trauma: what the surgeon needs to know. *Eur J Radiol* 48:17–32.
- Litschel R, Suárez GA. 2015. Management of zygomatic fractures: bone and Arch. *Facial Plast Surg* 31:368–375.
- Manson PN, Hoopes JE, Su CT. 1980. Structural pillars of the facial skeleton: an approach to the management of Le Fort fractures. *Plast Reconstr Surg* 66:54–62.
- Nagasao T, Nakajima T, Kimura A, Kaneko T, Jin H, Tamaki T. 2005. The dynamic role of buttress reconstruction after maxillectomy. *Plast Reconstr Surg* 115:1328–1340.
- O'Connell J, Murphy C, Ikeagwuani O, Adley C, Kearns G. 2009. The fate of titanium miniplates and screws used in maxillofacial surgery: a 10 year retrospective study. *Int J Oral Maxillofac Surg* 38:731–735.
- Olynik CR, Gray A, Sinada GG. 2013. Dentoalveolar trauma. *Otolaryngol Clin North Am* 46:807–823.
- Oyen OJ, Tsay TP. 1991. A biomechanical analysis of craniofacial form and bite force. *Am J Orthod Dentofacial Orthop* 99:298–309.
- Parfitt AM, Drezner MK, Glorieux FH, Kanis JA, Malluche H, Meunier PJ, Ott SM, Recker RR. 1987. Bone Histomorphometry: standardization of nomenclature, symbols and units. *J Bone Min Res* 2:595–610.
- Perren SM. 2002. Evolution of the internal fixation of long bone fractures. The scientific basis of biological internal fixation: choosing a new balance between stability and biology. *J Bone Joint Surg Br* 84:1093–1110.
- Peterson J, Dechow PC. 2003. Material properties of the human cranial vault and zygoma. *Anat Rec A Discov Mol Cell Evol Biol* 274:785–797.

- Peterson J, Wang Q, Dechow PC. 2006. Material properties of the dentate maxilla. *Anat Rec A Discov Mol Cell Evol Biol* 288:962–972.
- Pollock RA. 2012. *Cranio-maxillofacial Buttresses—Anatomy and Operative Repair*. 1st ed. New York: Thieme.
- Prado FB, Freire AR, Rossi AC, Caria PHF. 2012. Finite element analysis of the three support pillars in human craniofacial skeleton. *J Biomech* 45:179.
- Prado FB, Noritomi PY, Freire AR, Rossi AC, Neto FH, Caria PHF. 2013. Stress distribution in human zygomatic pillar using three-dimensional finite element analysis. *Int J Morphol* 31:1386–1392.
- Rak Y. 1983. *The Australopithecine Face*. 1st ed. New York: Academic Press.
- Rallis G, Mourouzis C, Papakosta V, Papanastasiou G, Zachariades N. 2006. Reasons for miniplate removal following maxillofacial trauma: a 4-year study. *J Cranio-maxillofac Surg* 34:435–439.
- Rath MK, Sharma R. 2015. Optimal osteosynthesis in zygomatic complex fractures. *J Craniofac Surg* 26:e605–e606.
- Ravosa MJ. 1988. Browridge development in Cercopithecidae: a test of two models. *Am J Phys Anthropol* 76:535–555.
- Ravosa MJ. 1991. Interspecific perspective on mechanical and non-mechanical models of primate circumorbital morphology. *Am J Phys Anthropol* 86:369–396.
- Ravosa MJ, Johnson KR, Hylander WL. 2000. Strain in the galago facial skull. *J Morphol* 245:51–66.
- Richmond BG, Wright BW, Grosse I, Dechow PC, Ross CF, Spencer MA, Strait DS. 2005. Finite element analysis in functional morphology. *Anat Rec A* 283A:259–274.
- Richter W. 1920. Der Obergesichtschädel des Menschen als Gebisturm, ein statische Kunstwerk. *Dtsch Mschr Zahnheilk* 38:49–68.
- Rinehart GC, Marsh JL, Hemmer KM, Bresina S. 1989. Internal fixation of malar fractures: An exponent biophysical study. *J Plast Reconstr Surg* 84:21–25.
- Roberts D, Tattersall I. 1974. Skull form and the mechanics of mandibular elevation in mammals. *Am Mus Novit* 2536:1–9.
- Rodriguez ED, Bluebond-Langner R, Park JE, Manson PN. 2008. Preservation of contour in periorbital and midfacial craniofacial microsurgery: reconstruction of the soft-tissue elements and skeletal buttresses. *Plast Reconstr Surg* 121:1738–1747.
- Rohner D, Tay A, Meng CS, Hutmacher DW, Hammer B. 2002. The sphenozygomatic suture as a key site for osteosynthesis of the orbitozygomatic complex in panfacial fractures: a biomechanical study in human cadavers based on clinical practice. *Plast Reconstr Surg* 110:1463–1471.
- Ross CF. 2001. *In vivo* function of the craniofacial haft: the interorbital pillar. *Am J Phys Anthropol* 116:108–139.
- Ross CF. 2005. Finite element analysis in vertebrate biomechanics. *Anat Rec A Discov Mol Cell Evol Biol* 283:253–258.
- Ross CF. 2013. Complexity, modularity, and integration in the human head. The evolution of the human head. *J Hum Evol* 64:56–67.
- Ross CF, Berthaume MA, Dechow PC, Iriarte-Diaz J, Porro LB, Richmond BG, Spencer M, Strait D. 2011. *In vivo* bone strain and finite-element modeling of the craniofacial haft in catarrhine primates. *J Anat* 218:112–141.
- Ross CF, Hylander WL. 1996. *In vivo* and *in vitro* bone strain in the owl monkey circumorbital region and the function of the postorbital septum. *Am J Phys Anthropol* 101:183–215.
- Ross CF, Metzger KA. 2004. Bone strain gradients and optimization in vertebrate skulls. *Ann Anat* 186:387–396.
- Ross CF, Patel BA, Slice DE, Strait DS, Dechow PC, Richmond BG, Spencer MA. 2005. Modeling masticatory muscle force in finite-element analysis: sensitivity analysis using principal coordinates analysis. *Anat Rec* 283A:288–299.
- Roumeliotis G, Ahluwalia R, Jenkyn T, Yazdani A. 2015. The Le Fort system revisited: Trauma velocity predicts the path of Le Fort I fractures through the lateral buttress. *Plast Surg (Oakv)* 23:40–42.
- Rowe NL, Williams JL. 1985. *Maxillofacial injuries*. Vol. I. 1st ed. Edinburgh: Churchill Livingstone.
- Rudderman RH, Mullen RL. 1992. Biomechanics of the facial skeleton. *Clin Plast Surg* 19:11–29.
- Russell MD, Brown T, Garn SM, Giris F, Turkel S, İşcan YM, Oyen OJ, Jacobshagen B, Pietruszewsky M, Rightmire GP, et al. 1985. The Supraorbital Torus: “A most remarkable peculiarity” [and Comments and Replies]. *Curr Anthropol* 26:337–360.
- Schwartz-Dabney CL, Dechow PC. 2003. Variations in cortical material properties through the human dentate mandible. *Am J Phys Anthropol* 120:252–277.
- Sicher H. 1963. *Oral Anatomy*. St. Louis: CV Mosby.
- Sicher H, Du Brul EL. 1970. *Oral Anatomy*. 5th ed. St. Louis: CV Mosby.
- Sicher H, Tandler J. 1928. *Anatomie Fur Zahnartzte*. Berlin: Springer.
- Smith AL, Benazzi S, Ledogar JA, Tamvada K, Pryor Smith LC, Weber GW, Spencer MA, Dechow PC, Grosse IR, Ross CF, et al. 2015a. Biomechanical implications of intraspecific shape variation in chimpanzee crania: moving toward an integration of geometric morphometrics and finite element analysis. *Anat Rec (Hoboken)* 298:122–144.
- Smith AL, Benazzi S, Ledogar JA, Tamvada K, Pryor Smith LC, Weber GW, Spencer MA, Lucas PW, Michael S, Shekeban A, et al. 2015b. The feeding biomechanics and dietary ecology of *Paranthropus boisei*. *Anat Rec (Hoboken)* 298:145–167.
- Southard KA, Southard TE, Schlechte JA, Meis PA. 2000. The relationship between the density of the alveolar processes and that of post-cranial bone. *J Dent Res* 79:964–969.
- Strait DS, Wang O, Dechow PC, Ross CF, Richmond BG, Spencer MA, Patel BA. 2005. Modeling elastic properties in finite-element analysis: how much precision is needed to produce an accurate model? *Anat Rec* 283A:275–287.
- Strait DS, Weber GW, Neubauer S, Chalk J, Richmond BG, Lucas PW, Spencer MA, Schrein C, Dechow PC, Ross CF, et al. 2009. The feeding biomechanics and dietary ecology of *Australopithecus africanus*. *Proc Natl Acad Sci U S A* 106:2124–2129.
- Strait DS, Wright BW, Richmond BG, Ross CF, Dechow PC, Spencer MA, Wang Q. 2008. Craniofacial strain patterns during premolar loading: implications for human evolution. In: Vinyard CJ, Ravosa MJ, Wall CE, editors. *Primate craniofacial function and biology*. New York: Springer. p 173–198.
- Swift JQ. 1993. Isolated zygoma fractures. *Atlas Oral Maxillofac Surg Clin North Am* 1:71–83.
- Testut JL. 1911. *Traite d'Anatomie Humaine*. 2nd ed. Paris: Doin.
- Testut JL. 1943. *Anatomica Humana*. 3rd ed. Torino: Doin.
- Testut JL, Jacob O. 1914. *Traite d'Anatomie topographique avec applications medico-chirurgicales*. Vol. 1 and 2. Paris: Doin & Fils.
- Toro-Ibacache V, Zapata Muñoz V, O'Higgins P. 2016. The relationship between skull morphology, masticatory muscle force and cranial skeletal deformation during biting. *Ann Anat* 203:59–68.
- Villmoare BA, Kimbel WH. 2011. CT-based study of internal structure of the anterior pillar in extinct hominins and its implications for the phylogeny of robust *Australopithecus*. *Proc Natl Acad Sci USA* 108:16200–16205.
- Wang Q, Dechow PC. 2004. Variations in cortical material properties of baboon mandibles. *Am J Phys Anthropol* 38:203.
- Wang Q, Dechow PC. 2006. Elastic properties of external cortical bone in the craniofacial skeleton of the rhesus monkey. *Am J Phys Anthropol* 131:402–415.
- Wang Q, Dechow PC, Wright BW, Ross CF, Strait DS, Richmond BG, Spencer MA. 2006. Surface strain on bone and sutures in a monkey facial skeleton: an *in vitro* method and its relevance to finite element analysis. In: Vinyard CJ, Ravosa MJ, Wall CE, editors. *Primate craniofacial function and biology*. New York: Springer.
- Wang Q, Strait DS, Dechow PC. 2006. A comparison of cortical elastic properties in the craniofacial skeletons of three primate species and its relevance to the study of human evolution. *J Hum Evol* 51:375–382.
- Ward SC, Molnar S. 1980. Experimental stress analysis of topographic diversity in early hominid gnathic morphology. *Am J Phys Anthropol* 53:383–395.

- Wetzel G. 1930. Lehrbuch der Anatomie für Zahnärzte und Studierende der Zahnheilkunde. Jena: Verlag von Gustav Fischer.
- Witzel U, Preuschoft H, Sick H. 2004. The role of the zygomatic arch in the statics of the skull and its adaptive shape. *Folia Primatol (Basel)* 75:202–218.
- Wood SA, Strait DS, Dumont ER, Ross CF, Grosse IR. 2011. The effects of modeling simplifications on craniofacial finite element models: the alveoli (tooth sockets) and periodontal ligaments. *J Biomech* 44:1831–1838.
- Wroe S, Ferrara TL, McHenry CR, Curnoe D, Chamoli U. 2010. The craniomandibular mechanics of being human. *Proc Biol Sci* 277:3579–3586.
- Yamaguchi M, Inami T, Ito K, Kasai K, Tanimoto Y. 2012. Mini-implants in the anchorage armamentarium: new paradigms in the orthodontics. *Int J Biomater* 2012:394121.
- Yamamoto Y, Minakawa H, Kawashima K, et al. 1998. Role of buttress reconstruction in zygomaticomaxillary skeletal defects. *Plast Reconstr Surg* 101:943–950.
- Zachariades N, Mezitis M, Anagnostopoulos D. 1998. Changing trends in the treatment of zygomaticomaxillary complex fractures: a 12-year evaluation of methods used. *J Oral Maxillofac Surg* 56:1152–1156.
- Zapata U, Metzger K, Wang Q, Elsey RM, Ross CF, Dechow PC. 2010. Material properties of mandibular cortical bone in the American alligator, *Alligator mississippiensis*. *Bone* 46:860–867.