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Gross anatomy
and microanatomy

Enigmatic Cranial Superstructures Among Chamorro Ancestors From the Mariana Islands: Gross Anatomy and Microanatomy

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ABSTRACT

This study focuses on the gross anatomy, anatomic relations, microanatomy, and the meaning of three enigmatic, geographically patterned, and quasi-continuous superstructures of the posterior cranium. Collectively known as occipital superstructures (OSSs), these traits are the occipital torus tubercle (TOT), retromastoid process (PR), and posterior supramastoid tubercle (TSP). When present, TOT, PR, and TSP develop at posterior cranial attachment sites of the upper trapezius, superior oblique, and sternocleidomastoid muscles, respectively. Marked expression and co-occurrence of these OSSs are virtually circumscribed within Oceania and reach highest recorded frequencies in protohistoric Chamorros (CHamoru) of the Mariana Islands. Prior to undertaking scanning electron microscopy (SEM) work, our working multifactorial model for OSS development was that early-onset, long-term, and chronic activity-related microtrauma at enthesis sites led to exuberant reactive or reparative responses in a substantial minority of genetically predisposed (and mostly male) individuals. SEM imaging, however, reveals topographic patterning that questions, but does not negate, activity induction of these superstructures. Although OSSs appear macroscopically as relatively large and discrete phenomena, SEM findings reveal a unique, widespread, and seemingly systemic distribution of structures over the occipital surface that have the appearance of OSS microforms. Nevertheless, apparent genetic underpinnings, anatomic relationships with muscle entheses, and positive correlation of OSS development with humeral robusticity continue to suggest that these superstructures have potential to at once bear witness to Chamorro population history and inform osteo-

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biographical constructions of chronic activity patterns in individuals bearing them. Further work is outlined that would illuminate the proximate and ultimate meanings of OSS. *Anat Rec*, 297:1009–1021, 2014. © 2014 Wiley Periodicals, Inc.

Key words: Chamorros; occipital torus tubercle; retromastoid process; posterior supramastoid tubercle; entheses; functional anatomy; SEM survey

INTRODUCTION

Cranial superstructures refer to muscle and tendon markings, such as crests, tubercles, tuberosities, and processes, macroscopically observed on the external surface of the braincase (Weidenreich, 1940). We focus on three superstructures of the posterior cranium: (1) tubercle development on the torus occipitalis (occipital torus tubercle [TOT]), (2) processus retromastoideus (retromastoid process [PR]), and (3) tuberculum supramastoideum posterius (posterior supramastoid tubercle [TSP]), all of which are encountered more frequently among anatomically modern humans indigenous to Oceania (Pacific Islands and Australia) than in non-Oceanic populations. Among the indigenous people of the Mariana Islands (Chamorros or CHamoru), who lived during the overlapping Latte (AD 1000–1700) and Early Historic (AD 1521–1700) Periods (Moore, 2002), these superstructures occur at very highest frequencies and strongest degrees of expression (Heathcote et al., 2012b; Heathcote et al., forthcoming). Few morphological traits of the human skeleton are similarly geographically circumscribed such that they are virtual phenotypic markers of regional populations (Heathcote et al., 1996).

We present a critical and contextualized review of the gross anatomy, anatomical relations, and associated musculature of these superstructures (Fig. 1), together with the results of scanning electron microscope (SEM) imaging of a single ancestral Chamorro cranium that reveal novel topographic patterning of microstructures on the cortical surface. English nomenclature, together with acronyms faithful to the Latin terms, are used for these traits, namely, tubercle on the TOT, PR, and TSP. Collectively, these three are referred to as occipital superstructures (OSSs), notwithstanding the frequent extraoccipital (periasterionic) location of TSP. The primary objective of this study is to provide a foundation for resolving the meaning of these enigmatic OSSs, through consideration of what their functional anatomy and microanatomy suggest about their genesis, development, and patterning.

In more marked degrees of development, OSSs appear abruptly as well-circumscribed superstructures, with surfaces that are smooth yet textured and penetrated by vascular canals. Two of the OSSs (TOT and TSP) may develop along or adjacent to the mendosal suture, whereas one-third (PR) may arise inferior to this suture. The mendosal suture demarcates the junction between the membranous and endochondral developmental parts of the occipital squamous. By the fifth fetal month, these parts begin to fuse (Baker et al., 2005); however, the

suture may persist into adulthood as a hypostotic sutural variant (Ossenberg, 1969, 2013, p 13–14). PR superstructures have an exclusively endochondral origin. TOT develops near the developmental interface marked by the mendosal suture, whereas periasterionic TSP develops in an ossification boundary zone proximal to the lateral-most extensions of the mendosal suture, where the parietals (of intramembranous origin) articulate with the (endochondrally formed) petromastoid portion of the temporals (see Davies and Coupland, 1967).

HISTORICAL BACKGROUND

Our collaboration began in 1989–1990, when three of us (G.M.H., D.B.H., and B.E.A.) exchanged communications about markedly developed OSSs encountered in our independent studies of archaeologically recovered crania from the Mariana Islands (Figs. 2–4). Figure 2 illustrates marked expressions of two of the three traits (TOT and PR) in a 45- to 55-year-old male (Bernice P. Bishop Museum, No. 881) from the Taga Site, Tinian (Heathcote et al., 2012a). The cranium of a middle-aged male from Guam (#B-123), excavated from Gogna-Gun Beach (Anderson, 1992), is shown in Figure 3. The most striking morphological feature of this individual is a set of large, pedunculated TSP located along the parietal–mastoid suture, just anterior from asterion (Fig. 1). Figure 4 shows a 40- to 45-year-old female (Nansay-4), recovered from the Achugao area of Saipan. Although supraorbital development, nuchal crest, and mastoid process size are equivocal with regard to sex, this individual's subpubic angle and sciatic notch are strongly female-like, and femoral and humeral head dimensions are consistent with the latter assessment (Hanson, 1995). Although her periasterionic regions lack superstructure development, Nansay-4 has enormous pedunculated tubercles at the left and right TOT sites and also bears markedly expressed PR, projecting downward bilaterally from lateral continuations of the occipital torus (OT).

Our initial (and false) impression that these superstructures had received little attention from previous researchers, beyond nonspecific remarks about occipital rugosity in some Oceanic crania, was based on the feedback during conference presentations (e.g., Anderson, 1992; Hanson, 1992; Heathcote et al., 1992), correspondences with colleagues, and examination of numerous human anatomy texts and atlases, including those known for coverage of morphological variation and anomalies (Anson, 1963; Trotter and Peterson, 1966; Anderson, 1983), as well as two compendia on human

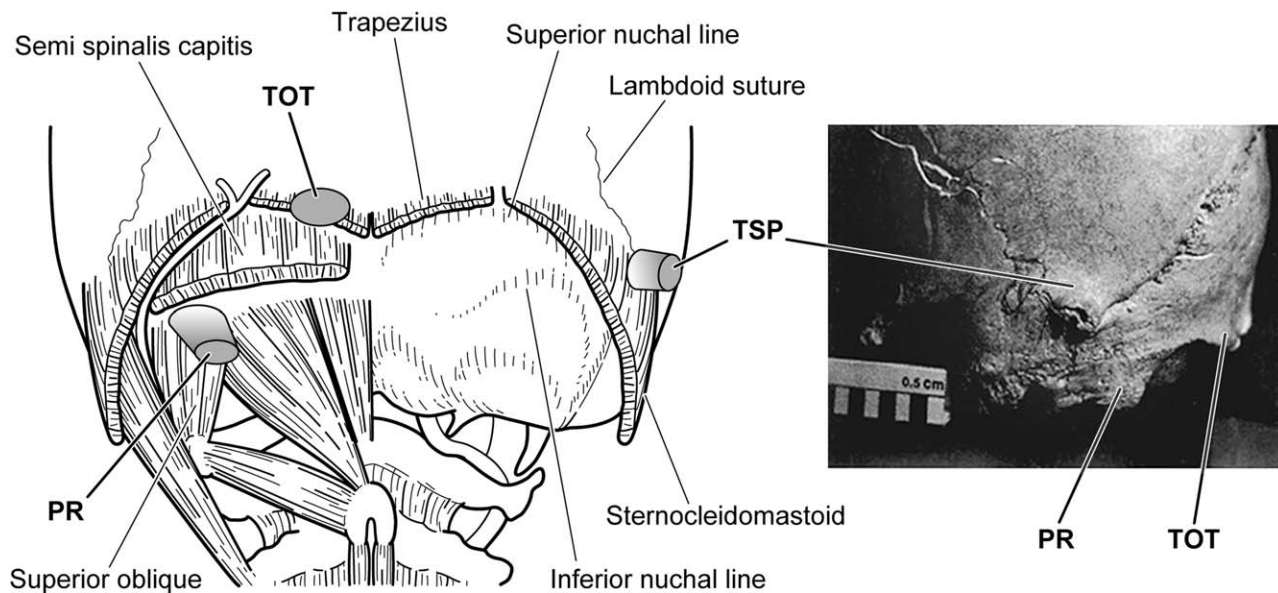


Fig. 1. Schematic drawing on left shows locations of three posterior cranial superstructures in relation to muscle attachment sites and anatomic features discussed in text (after Fig. 12.14 in Aiello and Dean, 1990; used with the permission of Leslie Aiello). TOT, tubercles on the

occipital torus; PR, retromastoid process; TSP, posterior supramastoid tubercle. Illustration at right shows these superstructures on the posterior cranium of a 40- to 50-year-old male from the Gogna-Gun Beach site, Guam (Burial No. 123).



Fig. 2. Skull, right lateral view, of a 40- to 50-year-old male from the Taga Site, Tinian (Bernice Pauahi Bishop Museum, No. 881). Superstructure scores are TOT = 3, PR = 4, and TSP = 2 (see Heathcote et al., 1996).

anatomic variation (Bergman et al., 1988; Tountas and Bergman, 1993). Furthermore, Kennedy's (1989) wide-ranging review of purported skeletal markers of occupational stress made no mention of activity-induced changes to the posterior cranium, and a comprehensive work on epigenetic traits of the human skull made no mention of TOT, only passing mention of TSP, and although a weakly developed PR is illustrated (Hauser and De Stefano, 1989, p 108), we failed initially to

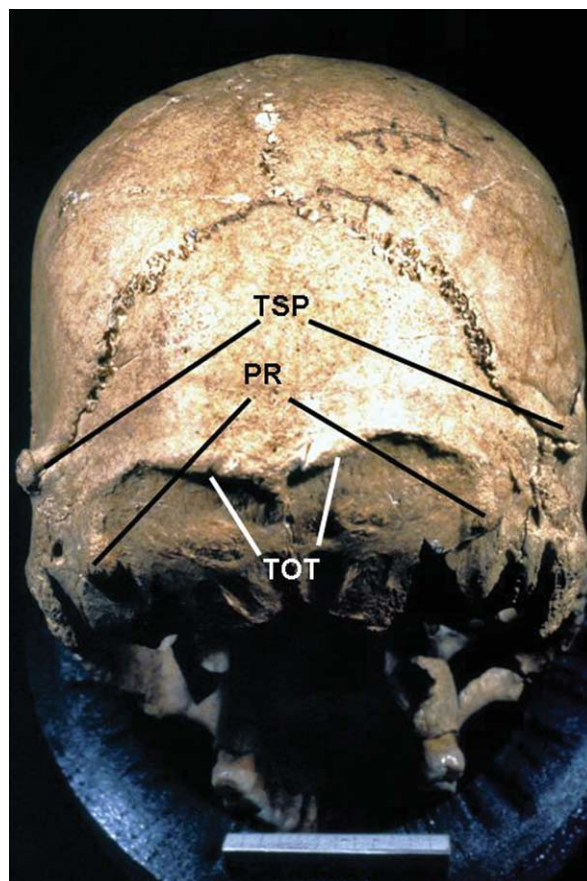


Fig. 3. Cranium, baso-occipital view, of same individual illustrated in Fig. 1. Left and right side superstructure scores are TOT = 2/2, PR = 2/2, and TSP = 4/4.

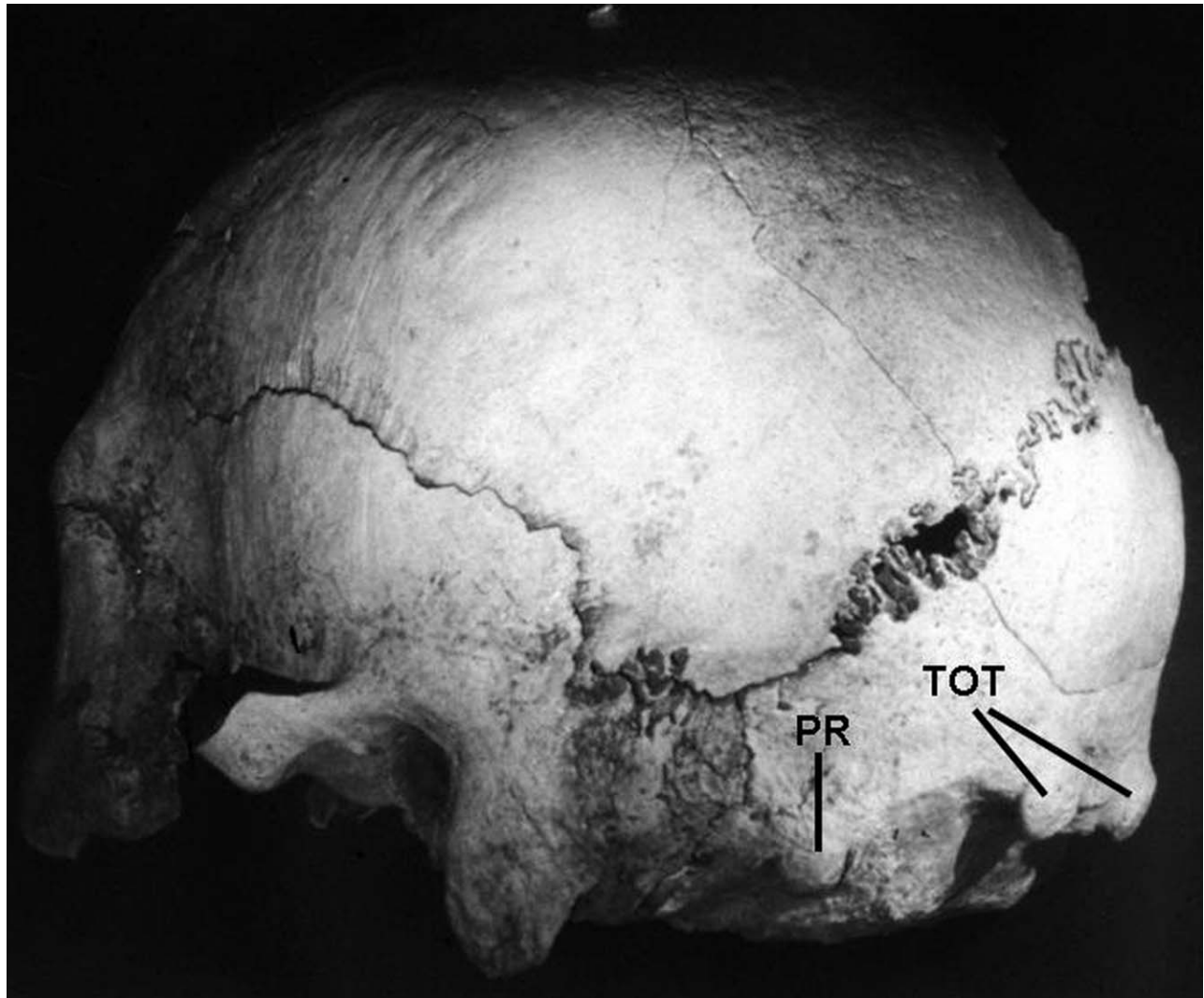


Fig. 4. Cranium, left occipito-lateral view, of a 40- to 45-year-old female from Achuago, Saipan (Nansay-4). Left and right superstructure scores for TOT = 4/4. Left side PR = 3, and TSP = 0.

appreciate its homology with much larger processes observed on Mariana Islander crania.

Subsequent bibliographic research into primary literature revealed a number of pertinent studies, mostly in non-English language publications from the mid to late 19th and early 20th centuries (e.g., Schaaffhausen, 1858; Joseph, 1873; Ecker, 1878; Hagen, 1880; Waldeyer, 1880, 1909, 1910; Le Double and Dubreuil-Chambardel, 1905; Matiegka, 1906; Schlaginhaufen, 1906; Michelsson, 1911; Passow, 1924; Hori, 1925; Hasebe, 1935), as well as recent publications and reports (Jacob, 1967; Arai, 1970; Hublin, 1978a; Pietrusewsky, 1990; Underwood, n.d.). Of these, Hasebe (1935) and Arai (1970) are of greatest interest, given their attention to all three OSSs and description and illustration of TOT, TSP, and PR in Micronesian (including Mariana Islander) skulls. The study of Hasebe included illustrations showing the appearance of marked expressions of TOT and PR in living Micronesian men from Merir (Palau outlier), Ebon (Ralik Chain of the Marshalls), "Guajelen" (Kwajalein in

the Marshalls), Pohnpei (Mokil), and Jaluit (Ralik Chain of the Marshalls).

PREVIOUS STUDIES OF POSTERIOR CRANIAL SUPERSTRUCTURES

Earlier literature on the morphology of the posterior cranium, mostly written in German, features fairly consistent nomenclature for OSSs in modern humans; however, recent studies introduced a proliferation of terminology. Concordances for older and newer nomenclature are provided below in discussions about the gross morphology and anatomic relations of OSSs. We adapted the scheme of Waldeyer (1880, 1909), who recognized four OSSs as the most commonly encountered in modern humans: OT; TSA and TSP; and PR. Studies that have adopted our nomenclature and/or OSS scoring protocol (Heathcote et al., 1996) include Douglas et al. (1997), Pietrusewsky et al. (1997), Capasso et al. (1999),

Valentin et al. (2005), Littleton and Kinaston (2008), Weiss (2010), and Matisoo-Smith (2011).

Occipital Torus and Tubercles on the Occipital Torus

Various aspects of the OT, including its morphology, size variation, placement, and proposed homologies with occipital crests in nonhuman primates, are discussed in the older literature (e.g., Schaaffhausen, 1858; Joseph, 1873; Ecker, 1878; Hagen, 1880; Waldeyer, 1880, 1909; Matiegka, 1906; Hori, 1925; Hasebe, 1935; Arai, 1970). The OT is a marked transverse ridge on the squamous part that, in sublime expression, characterizes *Homo erectus* (*sensu lato*), and in structurally reduced form is variably encountered in modern *H. sapiens* (Trotter and Peterson, 1966; Lahr, 1994). It is considered present when a plateau of bone, located between the superior nuchal line (SNL) and highest nuchal line (HNL), forms a transverse ridge across the posterior-most portion of the occipital bone (Ecker, 1878; Waldeyer, 1880; Weidenreich, 1940).

TOT appear to represent focalized secondary superstructural developments on top of the OT. Perhaps the first to publish on TOT was Ecker (1878), who noted that bilateral tubercles were sometimes present on the OT. These were named “supranuchal tubercles” by Hasebe (1935), and this term is used by Hublin (1978a), whereas Lahr (1995) prefers “Tubercle of Hasebe.” We do not adopt these terms, because the former (and, by extension, the latter) is a misnomer, for nonmarked TOT developments occur at (not above) the level of the SNL (Fig. 1). Although marked expressions of TOT extend somewhat superior to the SNL, the term “supranuchal” does not describe the full range of TOT morphological expression.

Retromastoid Process

Early works on the PR include Le Double and Dubreuil-Chambardel (1905), Schlaginhaufen (1906), Waldeyer (1909), Hori (1925), and Hasebe (1935). The PR (Fig. 1) appears as a variably raised tuberosity or process at the insertion site of the m. obliquus capitis superior (superior oblique muscle), where the superior branch of the inferior nuchal line (INL) converges with the lateral portion of the SNL. A variant expression of the PR is a ridge of bone that extends from the most inferior point of the PR and runs parallel to the occipito-mastoid suture (Waldeyer, 1909). The PR should not be confused with weak bumps that may be present along the INL, such as the tuberculum crurium, at the bifurcation of the INL (Michelsson, 1911). Likewise, the PR should not be confused with protuberances that can develop higher along the crista asteriaca inferior (inferior asterial crest), as thickenings of the lateral portions of the highest and superior nuchal lines, above the insertion site of the superior oblique muscle (Matiegka, 1906).

Waldeyer (1909) was skeptical about a functional interpretation for PR, as he did not understand how the small muscle that inserts at its location could produce a large process. He illustrated dissections of deep and superficial neck and shoulder muscles showing a set of rather small PR anchoring small superior oblique muscles and appears not to have considered muscular

correlates of larger PRs. Waldeyer pondered a cultural modification explanation for PR development, mentioning use of a wooden neck support/pillow by mid-19th-century Fijians, and how it allegedly produced a “scirrhus lump, (often) as large as a goose egg” on the nape of the neck (Wilkes, 1845 in Waldeyer, 1909, p 15), but did not pursue this association further, as Felix von Luschan advised him that people who use wooden neck supports generally rest with the side of their head, not their neck, on such supports (Waldeyer, 1909, p 15).

Supramastoid Tubercles (TSA and TSP)

Waldeyer (1909, 1910) described two distinct round or oblong tubercles, TSA and TSP, which may occur from the region of the supramastoid crest and parietal notch to the area surrounding asterion (see Planche V and Figs. 1 and 3 in Hublin, 1978a). This region includes the attachment sites of m. sternocleidomastoideus (sternocleidomastoid muscle [SCM]) and m. splenius capitis (splenius capitis) and extends anteriorly to the posterior and inferior-most point of attachment of the temporalis muscle. The TSA is located at the posterior-most portion of the supramastoid crest on the temporal bone. The descriptive morphology of TSA is covered in the study by Matiegka (1906), whereas the study by Jacob (1967) discusses variations. In developing our scoring system for supramastoid tubercles (see Heathcote et al., 1996, p 287, 294), a much greater range of phenotypic expression was noted for TSP than for TSA. As a result of this empirical finding, and in view of there being more published research on TSP, TSA was dropped from our protocol.

The TSP is found in the vicinity of the parietal-mastoid suture and can be encountered on the temporal or parietal bone, or both, and may involve a small portion of the occipital at asterion (Fig. 1). We sometimes use the term “periasterionic tubercles” as a descriptor (cf. nomen) to refer to topographic variants of the TSP that develop in proximity to asterion. Protuberant developments along the inferior asterial crest, situated inferior to asterion on the occipital bone, are likely not occipital variants of the TSP, as the former are thought to be associated with aponeurotic attachments that mark the SNL and highest nuchal lines (Matiegka, 1906, p 411). When restricted to the parietal bone, the TSP is located immediately anterior and superior to asterion, which is why Haferland (1905) referred to this variation as the processus asteriacus (asterionic process [AP]).

We agree with researchers who have considered the AP to be a variation of the TSP (Matiegka, 1906; Schlaginhaufen, 1906; Passow, 1924; Hasebe, 1935). In contrast, Jacob (1967) and Arai (1970) maintained that the TSP occurs on the temporal bone, and Hauser and De Stefano (1989, p 107) stated that its location is limited to the base of the mastoid process of the temporal, anterior to the occipito-mastoid suture. The claim that TSP can be found at the midportion and posterior edge of the mastoid process (Waldeyer, 1909, 1910) is doubtful. Such (more inferiorly located) tubercles may be localized swellings along the crista mastoidea (mastoid crest), a trait not systematically scored by us, although we noted that strong mastoid crest markings are regularly associated with markedly developed TSP in crania from the Marianas. Mastoid crests are associated with the SCM muscle and

are characteristically well developed in *Homo erectus* (*sensu lato*; Aiello and Dean, 1990). An anterior swelling along the mastoid crest, the tuberculum mastoideum anterius, has been identified as one of the four apomorphic characteristics of European Neanderthal skulls (Hublin, 1978b) and is not homologous with the TSP.

Some authors have alleged that the AP is homologous with the angular (or temporal) torus of the parietal. The angular torus (AT), best known from the studies of archaic hominins, is a ridged portion of the posterior superior temporal line marking the attachment of the posterior fibers of hypertrophied temporalis muscles and their fascial covering (see Aiello and Dean, 1990, p 66–67). In some Asian *H. erectus*, including crania from Ngandong, Java (Wolpoff, 1999), the AT is located at the mastoid angle of the parietal, superior to asterion (Weidenreich, 1943, 1951). Matiegka (1906), Waldeyer (1909), and Hasebe (1935) considered the AP to be a variation of the AT. However, we disagree, for we (G.M.H. and V.J.S.) have examined modern Pacific crania with weakly developed AT that co-occur with AP (*viz.* periasterionic TSP). In these cases, the AT is located well anterior of asterion, owing to the more forward placement of the posterior fibers of the temporalis muscle in modern humans versus archaic hominins (see Aiello and Dean, 1990, p 65).

ASSOCIATED MUSCULATURE

This section is informed by Davies and Coupland (1967), Trotter and Peterson (1966), Crouch (1985), Shipman et al. (1985), O’Rahilly (1986), Romanes (1986), Cartmill et al. (1987), Aiello and Dean (1990), Kreighbaum and Barthels (1990), and Rosse and Gaddum-Rosse (1997). For the most part, these sources are in essential agreement about origins, insertions, and actions of muscles associated with TOT, PR, and TSP. The studies that dispute or qualify the anatomical canon are cited below.

Muscles Associated With the TOT Site

The semispinalis capitis muscle inserts between the inferior and superior nuchal lines on the occipital bone in a noncircumscribed region of the planum nuchae just inferior to the TOT site. However, it appears that TOT superstructures are not associated with the semispinalis capitis in a functional sense. Flethy fibers of this muscle attach directly onto the periosteum, and such entheses produce a smooth underlying bone surface with boundaries not well defined (Hems and Tillman, 2000; Benjamin et al., 2002).

In contrast, the entheses for the origin of the upper part of the trapezius muscle appears to be related functionally to TOT genesis and development. The bilateral origin sites are located parasagittally along the SNL and, if TOT is markedly expressed, on top of an OT (Fig. 1). The upper trapezius assists in the extension and hyperextension of the neck, bends the neck toward the same side, and draws the clavicle backward, in actions such as pulling and rowing. Although often stated that the trapezius has a direct role in elevating the scapula, a dissection study of the fascicular anatomy of the trapezius disputes this. Johnson et al. (1994) demonstrated a transverse orientation of the upper and middle trapezius

fibers, which is not consistent with a scapular elevation function. Their study revealed that the nuchal portion of the upper trapezius draws the clavicle backward or medially and thus plays only an indirect role in moving the scapula through the acromioclavicular joint. An overlooked action of the upper trapezius, involving the fascicle that attaches at the SNL (TOT site), is support for the lateral clavicle and acromion of the scapula, for example, when heavy weights are held by the hands, with the arms down at the side (Luttgens and Wells, 1989). Although the fibers of the upper trapezius are among the smallest and weakest of the trapezius fascicles, their oblique orientation give them the capacity to exert compressive loads on the neck (Johnson et al., 1994) when weights are so carried in the hands.

Muscle Associated With the PR Site

The superior oblique muscle is one of the four sets of short suboccipital muscles, situated deeply at the base of the neck. This muscle originates from tendinous fibers on the upper surface of the transverse process of the atlas and inserts onto the PR site on the occipital bone, between the SNL and INL, lateral to the semispinalis capitis and overlapping the insertion of the rectus capitis posterior major (Fig. 1). Schlaginhaufen (1906) thought that PR marked the site of a “fallen” splenius capitis insertion; however, he was mistaken, as shown by Waldeyer (1909), who dissected and illustrated the superior oblique muscle inserting at the PR site. The actions of the superior oblique, together with the splenius capitis, are bending the neck backward (when both act together) and rotating it to the same side (when one acts alone). Together with the rectus capitis posterior major and minor, it serves as a postural muscle.

Although more superficial fascicles of the muscle may insert directly at the PR site, a microdissection study has shown that a “hidden” internal tendon (aponeurosis) runs the course of the superior oblique (Kamibayashi and Richmond, 1998). Thus, the insertion entheses would be at least partially fibrocartilagenous.

Muscles Associated With the TSP Site

Two muscles converge on the TSP site, the SCM, sometimes referred to as the sternomastoid, and the occipital part of the m. occipitofrontalis (OPO). The OPO, one of the two scalp muscle groups, consists of four bellies, two occipital and two frontal. The occipital OPO originates from the HNL in the region of the mastoid angle of the parietal. Insertion is into the epicranial aponeurosis, and its action is to pull the scalp backward. As to whether the OPO could transmit sufficient loads to have a role in the genesis of TSP superstructures, it is pertinent that Bromage (unpublished data) has examined macaque brow ridge histology and has seen evidence of substantial connections of the OPO frontal aponeurosis to the brow ridges; enough, he feels, to strain the brow ridge considerably. Notwithstanding a possible role of the OPO in TSP development, this superstructure appears to be primarily related to SCM activity, however.

Acting together, the SCM muscles draw the neck forward and raise it when the body is supine, and if the neck is fixed, the SCM assists in raising the thorax in

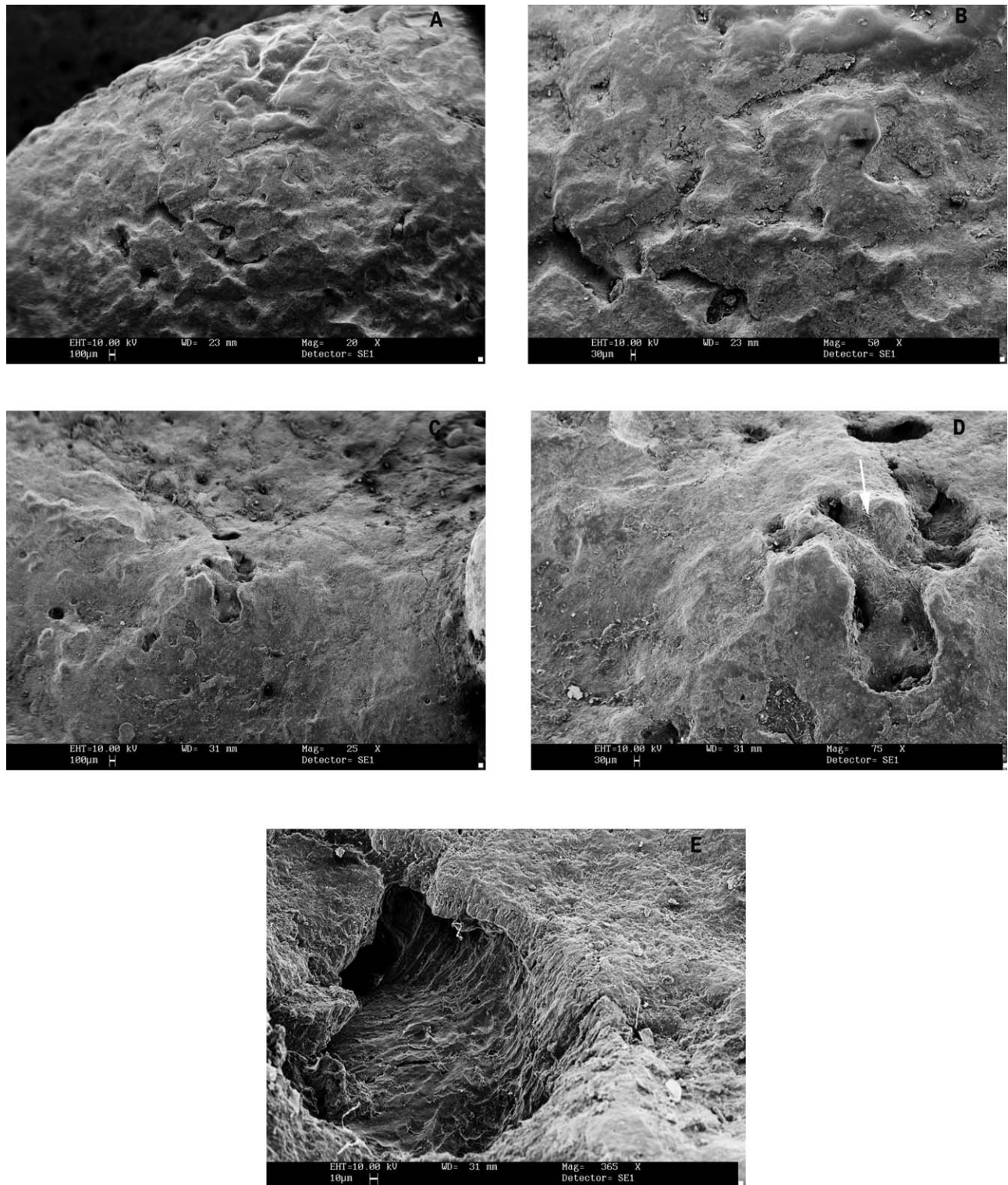


Fig. 5. SEM scans of Nansay-4, on the surface of a TOT and immediately adjacent to its base. **A:** Vermiculate morphology of the TOT surface; such morphology suggests that the TOT surface may have been covered with a fibrocartilagenous cap. **B:** A closer look at the same surface reveals that the vermiculate pattern results from a series of irregular-shaped ridges. **C:** A low-lying ridge and processes lie adjacent to the base of the TOT superstructure, shown at right, and an

apparent incipient superstructure is shown in the center of this scan. **D:** A closer look at this apparent microform shows a series of eminences rising up around foramina thought to be vascular canals. A wall to a definitive vascular groove is shown (arrow). **E:** At greater magnification, anisotropic resorption bays are revealed along the wall and on the floor of the vascular groove.

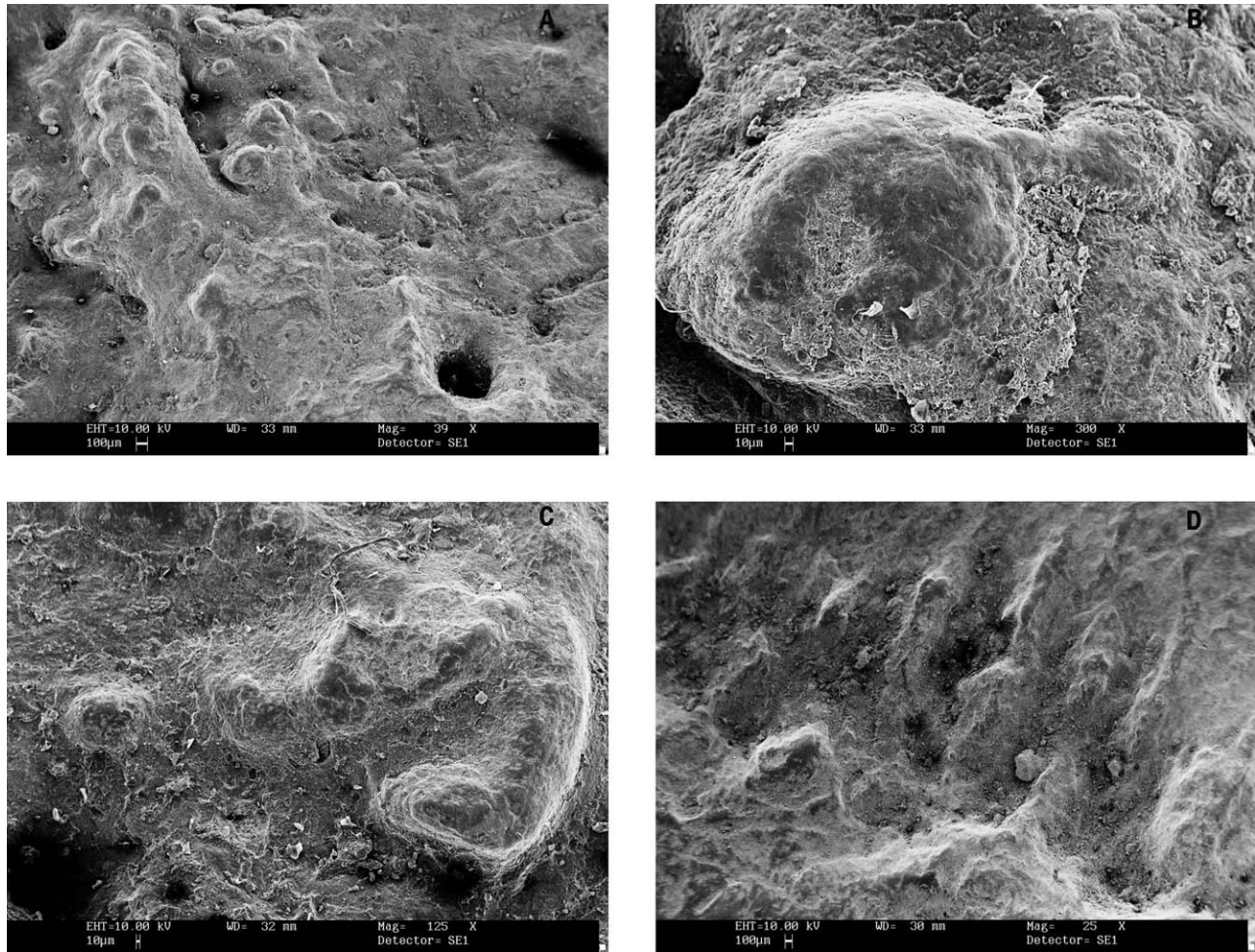


Fig. 6. SEM scans on the occipital squamous surface of Nansay-4. **A:** A representative low-magnification scan shows the very beginnings of the vermiculate pattern observed on the TOT superstructures. Apparent microforms of superstructures “rise up” in low-lying ridges, particularly around presumed vascular canals. See this complex structure at the upper left corner. **B:** One of these microforms at greater magnification, appearing as a semicircular formation with a trailing

ridge. To its left, a groove partially undercuts it and continues on to penetrate the bone. **C:** A less magnified look at the squamous surface shows the pattern observed in (B) to be quite widespread, practically everywhere on the surface of the occipital of Nansay-4. **D:** Low-magnification scans show that linear arrays of ridges are also consistently observed. These ridges presumably relate to inserting collagen fiber bundles from muscles and tendons.

forced respiration. When one SCM acts, it tilts the neck toward the shoulder on the same side, and the face is rotated to the opposite side. The SCM originates from the front of the manubrium, below the clavicular notch, and from the superior border of the medial third of the clavicle. Most anatomy texts agree that the SCM inserts via a thin aponeurosis onto the anterior border of the mastoid process and the lateral portion of the SNL; however, Clemente (1985, p 457) dissented stating that the SCM “inserts by a strong tendon into the lateral surface of the mastoid process, and by a thin aponeurosis into the lateral half of the superior nuchal line of the occipital bone.” Kamibayashi and Richmond (1998) documented that the sternomastoid portion of the SCM is relatively thick, providing support for Clemente’s revision. By extension, this part of the SCM would not insert at the TSP site via a thin aponeurosis.

MICROANATOMY

A SEM imaging survey of the Nansay-4 OSS occipital (Fig. 4) was conducted by T.G.B. All surfaces were coated with gold to make them electrically conductive and observed in secondary electron emission mode by a LEO S440 SEM (Cambridge, UK) under conditions of high vacuum, 10 kV accelerating voltage, 100 pA filament current, and relatively long-working distances to permit enhanced fields of view. Observations of the larger of the superstructures, the TOT, reveal a vermiculate-like surface morphology (Fig. 5A). Normally, such a surface would characterize underlying and relatively rapidly forming compacted cancellous bone. There is no preferred orientation on the surface, which would be expected if there had been muscular or tendinous collagenous insertions there. Thus, such a surface may

have been covered with a fibrocartilagenous cap; however, in the absence of histological examination, we can only speculate. A closer look at the same field illustrated in Fig. 5A reveals the vermiculate pattern as a series of irregular-shaped ridges (Fig. 5B). The smooth surfaces are likely an artifact of abrasion exerted during diagenesis, preparation, and handling since deposition. The foramina at the far lower left are vascular canals.

Frequently, low-lying ridges and processes emanate from the base of the TOT (Fig. 5C). Along these ridges are found incipient superstructures (OSS microforms?) that give us a clue as to their formation. A closer look reveals a series of eminences rising up around foramina that, in this case, are vascular canals (Fig. 5D), on which one can observe a resorptive wall on one of the vascular floors (arrow). This occurs when vessels are drifting, during growth, relative to the surrounding bone. A yet closer look at the groove on the right reveals resorption, as characterized by anisotropic resorption bays, along the wall and partly down to the floor of the groove (Fig. 5E). This is a very common observation around the occipital, for example, on the TOT, adjacent to the TOT, and elsewhere on the squamous occipital.

Evident remodeling around blood vessel canals is an indication that vessels have changed their relative position during growth of the apparent microforms and/or the growth of the individual. The latter possibility raises the issue that these microscopic superstructures may start to develop in juveniles. We cannot address this question adequately, as we have not yet examined many subadults. To date, the youngest individual for whom we have recorded a moderate development of PR is a 15- to 16-year-old male (likely) Chamorro from Guam (Camp Watkins Road Project, Burial No. 6B) of uncertain dating (PHRI, n.d.). The youngest individual we have seen with moderate degrees of development for both TOT and TSP is an approximately 18-year-old Chamorro male from Guam (Gogna-Gun Beach, Burial No. B117), who likely dates from the 10th to 15th centuries (Anderson, 1992).

Remarkably, SEM surveys of the occipital squamous surface—beyond the boundaries of the TOT—reveal the very beginnings of the vermiculate pattern (so readily observed on the TOT surface), practically everywhere (Fig. 6A). At their most incipient stage, small protrusions rise up and around low-lying ridges, particularly around vascular canals, as mentioned above. A closer look at one of these structures reveals a bleb of vermiculate bone, appearing as a semicircular mass with a trailing ridge (Fig. 6B). To the left of this mass, one can see a vascular groove, which partially undercuts the edge, traversing into the interior, and finally penetrating the bone. This pattern can be found practically everywhere on the squamous surface of the occipital bone (Fig. 6C). Linear arrays of ridges are also consistently observed on the surface, presumably in relation to inserting collagen fiber bundles from muscles and tendinous sheaths (Fig. 6D). In these cases, from the least to the most developed, it appears as if bone formation is concentrated between bundles.

In summary, the analysis of SEM images of the Nansay-4 occipital bone reveals a systemic effect on all periosteal surfaces thus far examined. Vermiculate ridges and mounds of bone matrix were formed and mineralized in association with the vasculature of this cra-

nial bone. Rapid bone formation is typically associated with a bone surface saturated with capillary vessels (Bromage, 1984); however, the vessels associated with the vermiculate ridges are substantially larger than capillaries, indicating that the rate of bone formation was deliberate and slow. The vermiculate bone formation seems to not have been particularly related to specific muscle or tendon insertions; however, because much of the surface of this bone is covered in muscle and nuchal ligament, the effect of numerous collagenous insertions from the periosteum—too small to be observed by conventional SEM—cannot be ruled out as a mediator of mechanical stress conduction to the bone. However, as the associations of these peculiar bone structures are with the vasculature passing through the bone cortex, the microanatomical evidence suggests a systemic cause, affecting the entire bone surface.

DISCUSSION

In over 30 years of conducting SEM surveys on human and other primate crania, T.G.B. has never before encountered such surface patterning. Such novel and unexpected microanatomy, pointing to a systemic effect in the expression of OSS, compounds their enigma, given that their relationship to musculoskeletal stress remains apparent at the macroscopic level. Activity induction finds support from the spatial association of OSSs with entheses sites for the SCM, upper trapezius, and superior oblique muscles and from recent investigations of OSS expression in relation to humeral robusticity, serving as a proxy for musculoskeletal exertion and strength (Heathcote et al., 2012b, p 56). Heathcote et al. (2012b) reported a significant positive correlation ($r = 0.70$; $P < 0.003$) between cumulative scores for OSS development and indices of humeral robusticity in protohistoric Chamorros, whereas Weiss (2010) found a significant correlation ($r = 0.29$; $P < 0.05$) between lesser expressions of the same cranial muscle markers and cross-sectional robusticity of humeri in California Amerinds.

In our earlier OSS studies (see Capasso et al., 1999, p 11–12), TOT, PR, and TSP were conceptualized, more straightforwardly than now, as cranially expressed musculoskeletal stress markers (MSMs; Hawkey and Merbs, 1995; Hawkey, 1998; Steen and Lane, 1998). MSMs are thought to have potential for yielding interpretations of chronic activity patterns, given the generally accepted view that differential muscular activity leads to differential marking of bone at entheses (osteotendinous junction) sites (Weiss, 2009; cf. Mariotti et al., 2004; Schlecht, 2012; Foster et al., in press). Later, D.B.H. took a lead role in our development of a more refined multifactorial model of OSS activity induction (e.g., Heathcote et al., 2012b), according to which muscle movement and consequent strain were viewed as proximate triggers of new fibrocartilage calcification at entheses sites, with differential genetic predisposition, interacting with strain and trauma, conceptualized as the ultimate cause of OSS development.

Virtually all MSM studies have focused on the infracranial skeleton (cf. Weiss, 2010) and have been informed by histological studies of long bones. Pioneer studies of the latter (e.g., Benjamin et al., 1986) established two basic kinds of entheses, fibrous and

fibrocartilagenous (Benjamin et al., 1986), and although this dichotomy is now considered an oversimplification (Benjamin et al., 2006; Villotte and Knüsel, 2013), the following distinctions remain generally valid for the infracranial skeleton: fibrous entheses, associated with bone that ossifies intramembranously, are characterized by direct attachment of fibrous connective tissue onto bone or periosteum where cortical bone is relatively thick, whereas fibrocartilagenous entheses, situated near bone of endochondral origin, are associated with thin cortices (Claudepierre and Voisin, 2005; Jurmain and Villotte, 2010; Schlecht, 2012).

In more extreme degrees of expression, MSMs are regarded as enthesopathies (Niepel and Sit'aj, 1979; Mariotti et al., 2007), that is, lesions at tendon–bone (or muscle–bone or ligament–bone) junctions. These lesions manifest as “irregularities, rough patches, and bone projections or osteophytes” and are interpreted as developing in response to prolonged and excessive muscular activity (Larsen, 1997, p 188). Knüsel (2000, p 387) speaks of “enthesis activity-related change” that manifests either in bone deposition or resorption, the former producing crests or spicules and the latter producing sulcus-like excavations in cortical bone. The formulations of Larsen and Knüsel are consistent with the classification of MSMs by Hawkey and Merbs (1995) into (1) robusticity markers, (2) stress lesions, and (3) ossification exostoses. Robusticity markers range in the expression from faint rugosities to sharp ridges or crests of bone and are thought to reflect habitual muscle usage connected with daily motor activities. Stress lesions are considered to be the result of overactivity of muscles, resulting in continuous microtrauma to attachment sites, and are defined by pitting or furrowing into the cortex, appearing as lytic lesions. They occur only at insertion sites and are considered part of an activity-related continuum, along with robusticity markers, as evidenced by strong robusticity scores co-occurring with weak stress lesion scores. In contrast, ossification exostoses are interpreted as being due to a macrotraumatic episode, resulting in ligaments or muscle becoming ossified into new bone.

In our work with ancestral Chamorros, we have encountered a few exuberantly developed OSSs that have the appearance of robusticity markers grading into stress lesions, but such changes could be the result of normal surface remodeling related to the growth of the OSSs. We have observed very few OSSs that manifest as irregular, projecting osteophytes, thus a generalized macrotraumatic origin of OSSs can be dismissed. Alternatively, conceptualizing an OSS as an MSM of the robusticity marker variety is not without problems, given that many OSSs do not look like they should, if most anatomy texts are correct about the morphology of soft tissue attachments at TOT, PR, and TSP sites (Heathcote et al., 1995). There is reason to question standard reference sources concerning normative morphology, however, as the factual bases of standard anatomy texts and atlases derive from dissection studies of biogeographically biased (and non-Oceanic) cadaver collections and such sources often ignore or give little attention to within- and between-population morphological variation.

Given our focus, the most problematic statements in the standard literature are that the SCM inserts at the

TSP site and that the upper trapezius originates from the TOT site, both by way of thin aponeuroses. It is highly unlikely that such muscle–bone interfaces could have been present in individuals whose skulls bear markedly developed TSP and TOT superstructures. Kamibayashi and Richmond's (1998) microdissection study is pertinent here, as they reported substantial interindividual differences in the dimensions and cross-sectional areas of human neck muscles, countering the standard view that SCM necessarily attaches via thin aponeuroses at the TSP region. Such findings, in the grand tradition of 19th century studies on variations and anomalies of human myology (e.g., Wood, 1868, 1870; Macalister, 1875; cf. Greiner et al., 2004), hardly surprise us, for as biological anthropologists we expect to find intragroup and intergroup diversity in anatomic structures with complex etiologies.

Conceptualizing OSSs as developing at fibrocartilagenous entheses sites presents further appearance difficulties; however, this may be because what we think we know of the osteological markings of such entheses is derived from studies of the infracranial skeleton, almost exclusively. Although the osteological signature of normal fibrocartilage entheses, located on thin-walled long bone epiphyses or apophyses, is typically well circumscribed, smooth and avascular (Benjamin et al., 1986) OSSs, situated on thick cranial cortex, have a different topography. Although markedly expressed TOT, PR, and TSP have an abrupt, well-defined morphology (Figs. 1–4), their surfaces are penetrated by vascular canals and, while generally smooth, are textured. What could explain this contrast? One pertinent observation is that subtendinous bursae may be found at fibrocartilagenous entheses insertion sites and these are commonly associated with synovium. As synovium is proinflammatory and highly vascular (Benjamin et al., 2002; Benjamin and McGonagle, 2009), implications for osteological appearance are apparent. In addition, entheses at OSS sites could be “mixed,” as was found for the masseter muscle insertion, where fibrocartilagenous junctions appeared alongside periosteal and bony fibrous attachments (Hems and Tillmann, 2000). Furthermore, as blood vessel growth is stimulated when tissue damage occurs at fibrocartilagenous entheses (Benjamin et al., 2007), and excessive biomechanical stress may hasten vascularization of fibrocartilage, as well as calcification and ossification of soft tissues at entheses sites (Villotte and Knüsel, 2013), these factors could well account for the vascularity and textured surfaces of OSS at predominantly fibrocartilagenous entheses sites.

Finally, we have considered a number of alternative hypotheses on OSS development and meaning, unrelated to mechanical induction, and will discuss them at length in another paper. The most deserving of these are hereditary multiple exostoses (HMEs; Brannon and Fowler, 2001; Stieber and Dormans, 2005), benign fibro-osseous lesion (BFOL; Lam et al., 2008; Sia et al., 2010), and Ehlers-Danlos syndrome, Subtype IX (EDNINE; Sartoris and Resnick, 1987; Yeowell and Pinnell, 1993). Consideration of such alternative etiologies has failed to find a compelling candidate to account for the development and patterning of OSSs; however, evaluation suffers from a lack of SEM work carried out on bone lesions attributed to HME, BFOL, EDNINE, or any other inherited connective tissue or bone matrix formation disorder. Indeed,

SEM investigations of bone pathology, in general, are rare (Schultz, 2001; cf. Sela, 1977).

CONCLUSIONS

Our review and novel SEM findings provide an improved anatomical foundation for addressing the etiological, developmental, functional, and osteobiographical meanings of OSSs in ancestral Chamorros and other Oceanic peoples. At the gross anatomical level, the abrupt and well-defined appearance of these superstructures (in marked expressions), coupled with vascularity and smooth but textured surfaces, suggest that OSSs develop at essentially fibrocartilagenous (but perhaps "mixed") entheses sites, undergoing degenerative changes in response to biomechanical stress. Covariation of OSS expression and humeral robusticity is consistent with upper body activity induction being a proximate cause of these superstructures in genetically predisposed individuals.

However, although our SEM work is based on a single cranium and must be considered preliminary, unexpected findings demand questioning of, and amendments to, any activity-induction model of OSS development. The most interesting of the microanatomical findings is that what we have been assuming to be discrete structures (the OSSs) appear to be relatively large components of a more generalized and systemic phenomenon. There is a widespread distribution over the occipital surface of small structures (with a small size range) that appear as microforms of OSSs (Figs. 6A–C). Further evidence in support of a systemic effect is that these apparent microforms are associated with vascular canals, both on the surface of the OSS macrostructures (Fig. 5D) and on the surrounding squamous surface (Fig. 6A).

Further SEM survey work is needed to reconcile competing interpretations of OSS etiology. A key issue bearing on activity-induction model is this: if microtrauma to entheses sites was involved in inducing TOT formation, would the TOT surface observed under SEM look different than it does? At present, we cannot address this question, for our preliminary SEM work cannot distinguish OSS development as a natural consequence of sustained or persistent muscular function or fibrillar microtrauma at the entheses. An obstacle to such resolution is that there is a profound lack of knowledge about tendon attachment morphology, namely, the microanatomy of collagenous insertions (Sharpey fibers) into hard tissues. This deficiency needs to be resolved before future research can determine whether the macroscopic appearance of OSS sites relates significantly to prominent collagen fiber bundle insertions.

Future SEM studies should look elsewhere on other OSS-bearing skulls, especially those with associated infracranial skeletons, to examine the patterning of such incipient outgrowths more comprehensively. In addition, histological examinations should be carried out, as SEM is most useful in combination with methods that reveal the microstructure of bone underlying the surface (Schultz, 2001). As such work is invasive, and permission to conduct it may not be granted, future studies could use nondestructive means of visualizing subsurface microanatomy, such as confocal scanning optical microscopy (Bromage et al., 2009). Further needs, in testing the multifactorial mechanical induction model,

include ancient DNA analysis of cultural peers who both bear and do not bear markedly developed OSSs, as well as conducting systematic macroscopic studies of the relationships among OSS and MSM expressions on the infracranial skeleton. Individuals should be sampled across a diachronic range inclusive of archaeological assemblages that represent cultures with differing group behavioral practices that may have literally embodied different modalities of motor activity patterns. The full dimensions of OSS meaning in late Pre-Contact and Early Historic Chamorros, as well as in other Oceanic populations, remain elusive; however, this work provides a solid foundation on which to build further investigations.

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