

Bone Bits

Mandibular Fossa of *Homo erectus*: A Response to Durband

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Durband (2002) has criticized our recent analysis of Sambungmacan 3 (Delson et al., 2001) with regard to the implications of the squamotympanic fissure (SQF) and the postglenoid tubercle (PGT) for grouping *Homo erectus* fossils. His criticism is based upon two abstracts and an unpublished masters thesis (Durband 1997, 1998; Durband and Kidder, 2000) and depends on interpretation of the observed morphology as well as the taxonomic “weight” of these characters. Here we take the opportunity to briefly respond to his queries and provide observations that are somewhat more extensive.

Delson et al. (2001: 390–392) wrote:

“Sm 3 also shares with the Ngandong specimens the distinct morphology and relative position of the squamotympanic fissure (Fig. 7). In his description of the Ngandong crania, Weidenreich (1951, p. 273–4) noted both the deep and anteroposteriorly short shape of the mandibular fossa and the course of the squamotympanic fissure (which he mistakenly termed the “Glaserian” fissure; see Márquez and Mowbray, in preparation) as being characteristic for this group. He observed that in the Ngandong specimens and in Sangiran 4 the squamotympanic fissure courses medio-laterally and coincides with the deepest portion of the mandibular fossa, whereas in the Chinese *H. erectus* specimens and in modern humans this fissure is positioned more posteriorly, and the floor of the fossa descends toward the posterior wall before reaching the fissure. In the last fifty years, many additional *H. erectus* crania preserving this region have been recovered. The Indonesian specimens Sangiran 17 and Sm 1 show a morphology which is similar to that preserved in the Ngandong group. The African representatives are divided in the expression of this feature. ER 3733 and 3883 have a flat and anteroposteriorly long mandibular fossa and a squamotympanic fissure that runs posterior to the deepest portion of the fossa.

WT 15000 also shows a flat and long fossa, but the squamotympanic fissure courses in its deepest portion. However, it is noted again that growth has not been completed in this specimen (see above). Finally, OH 9 presents a mandibular fossa that is similar both in its shape and in the position of the squamotympanic fissure to the Ngandong and other Indonesian specimens. It appears that this trait unites the Indonesian *H. erectus* specimens to the exclusion of the other Asian and African ones, with the exception of OH 9 and possibly also WT 15000. . . .”

Durband (2002) essentially argues that within the mandibular fossa, the feature “course of the SQF” must be further atomized into various states in terms of its orientation, depth, and position with respect to contiguous structures, especially the PGT. He further questions the presence of a PGT in a variety of *H. erectus* specimens. In fact, Durband defines a “Ngandong group” (which for him includes the Sambungmacan 1 and 3 and Ngawi fossils) based on the shared possession of character states of the resulting subdivided features. Thus, in his opinion, specimens of the Ngandong group present an SQF which lies entirely in the deepest part of the mandibular fossa but lack a PGT, while in other specimens the lateral end of the fissure curves around the PGT and departs from the deepest portion of the fossa.

Our published text followed Weidenreich (1951, as cited above) in examining only the first of these features. We did not originally make extensive comments, as our goal was to list the presence or absence of characters attributed to

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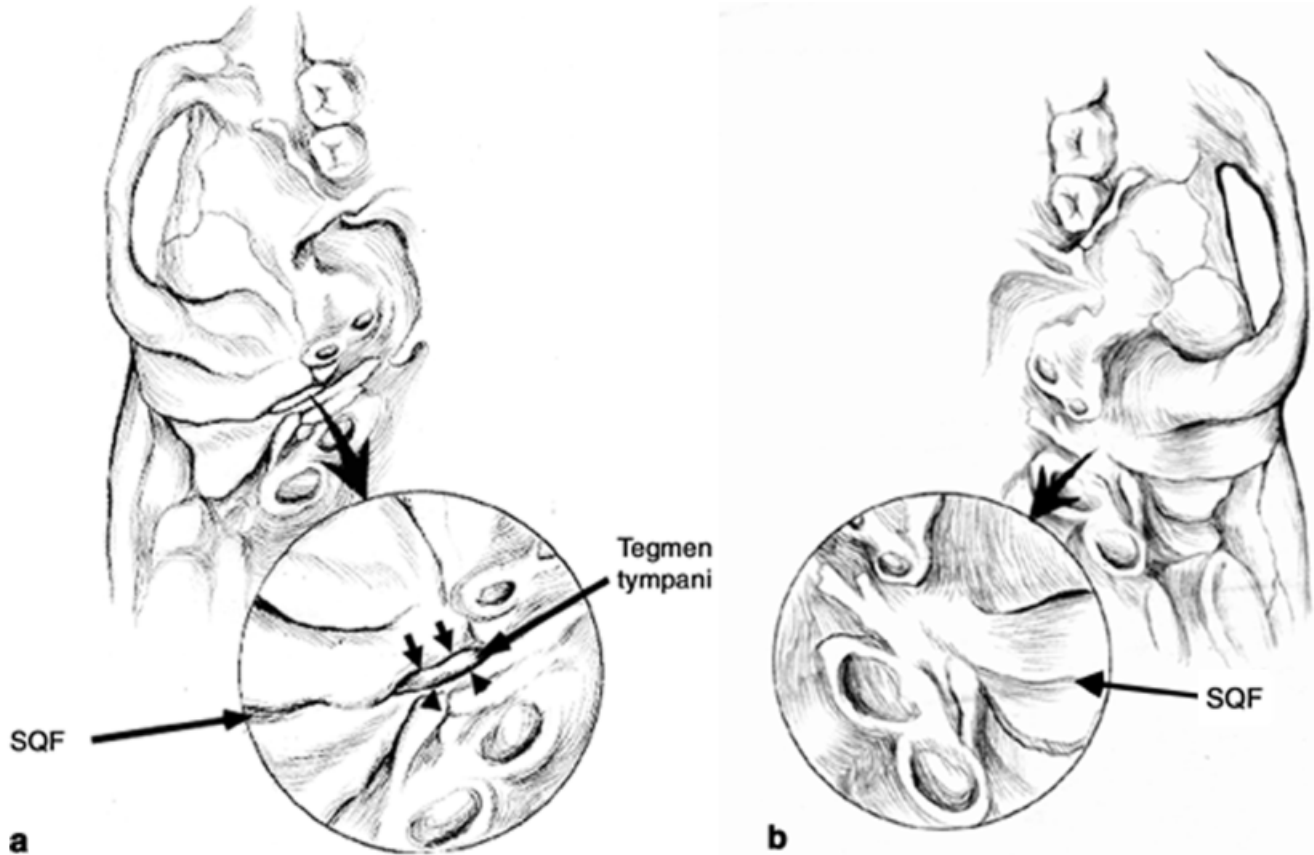


Fig. 1. **a:** Right mandibular fossa in basal view. Note the division of the SQF medially into the petrotympanic fissure posteriorly (arrowheads) and petrosquamous fissure anteriorly (arrows), caused by the encroachment of the tegmen tympani into the mandibular fossa. **b:** Left mandibular fossa in basal view. Note the bilateral difference in the course of the SQF. © Mowbray and Márquez.

H. erectus (*s.l.*¹) by a number of sources, present it in tabular form, and attempt to relate Sm 3 to other specimens. Our aim was to extend Weidenreich's data by examining casts of specimens unknown in the 1940s and briefly report our assessments. Moreover, we offered no new information on Sangiran (Sgr) 4 in the quoted excerpt but merely cited Weidenreich's observation, a point Durband apparently misunderstood.

MANDIBULAR FOSSA

In order to respond to Durband's assessment of features within the mandibular fossa, we find it is necessary to accurately describe the ontogeny of this basicranial portion in anatomical position as a baseline for understanding the topography involved in the course of the SQF.

In humans, the mandibular fossa derives from two mesenchymal condensations—a glenoid blastema associated with the temporal bone, and a condylar blastema associated with the mandible—that slowly fuse together around the 7th to 12th week in utero. At 23 weeks, the petrous portion and tympanic ring begin synostosis, producing the petrotympanic fissure through which pass the chorda tympani nerve and residual tissue of the malleolar disc ligament (Sperber, 2001). At birth, the tympanic ring fuses with the squamous part of the temporal bone, forming the SQF. The tympanic ring continues to grow laterally (in response to the lateral direction of growth of the neurocranium) forming the tympanic plate. Often, the thinned anterior surface of the petrous portion of the temporal bone—or the roof of the tympanic cavity (i.e., the tegmen tympani), encroaches into the SQF and later ossifies, thus further dividing this region into the petrotympanic fissure posteriorly and the petrosquamous fissure anteriorly (Fig. 1a).

As the mandibular fossa develops, it increases in size and changes in shape due to epigenetic constraints (e.g., strain generated during chewing episodes). For example, in living humans the fossa is generally flat and wide anteroposteriorly, as it is in chimpanzees, gorillas, australopiths, and early *Homo*. In *H. erectus* (*s.l.*), however, the mandibular fossa is typically much narrower anteroposte-

¹Some authors have placed these and other African fossils in *H. ergaster* (Tattersall, 1995; Wood, 1991) or even *H. leakeyi* (Clarke, 1990), but for the present we retain a broad definition of *H. erectus*, which subsumes all of these specimens. We note that at least one (D 2282) of the recently described crania from Dmanisi, Georgia, which have been suggested to be most similar to African "*H. ergaster*" (Gabunia et al., 2000; Balter and Gibbons, 2000), in fact has facial features strongly reminiscent of Sgr 17.

riorly and higher from the base of the tympanum to the roof. In some circumstances, it can appear cone-shaped, as seen in Sm 3 and Ng 11.

As the fossa increases in size ontogenetically, the posterolateral edge of the mandibular roof (the anterior edge of the SQF) may develop an eminence that is generally called either a postglenoid process or a PGT. The PGT is simply a build-up of bone anterior to the tympanic plate that serves as an attachment site for ligaments of the superior lamina—a band of elastic fibers that allows the disc between the temporal bone and the mandibular condyle to translate forward. The area of temporal bone where a PGT has the potential to develop also marks the most lateral margin of the mandibular joint capsule. The size and shape of the resulting eminence will determine its descriptive epithet. Unfortunately, there is no clear distinction among the use of such terms as “postglenoid process” and “tubercle” since much of the description of the PGT is highly subjective and somewhat arbitrary due to its overall continuously varying morphology. Nonetheless, if present, the PGT (or process or spine) can develop in modern humans as early as the first year of life (Scheuer and Black, 2001) and can become extensively altered as a function of age, joint disease processes, or mechanical malocclusions.

Course of the SQF

In living humans and extinct hominids, the SQF marks the division between the mandibular fossa and the tympanic plate. The SQF generally courses along the same trajectory followed by the petrous portion of the temporal bone, roughly 40°–60° to the coronal plane. Since the PGT only develops from osteogenic activity on the lateral edge of the posterior portion of the mandibular fossa and not the tympanic plate, the SQF will *always* course posterior to the PGT, if one is present. Furthermore, when this region is described in correct anatomical position the mandibular fossa is actually a roof, not a floor; therefore, the SQF cannot run along its *deepest* portion. Instead, the SQF should be described as coursing along the *highest* part of the mandibular fossa roof, if that is the case. In our original brief discussion, we followed Weidenreich (1951) among others in using the looser terminology based on the position in which the cranium is usually held for examination, but to avoid confusion in this more precise discussion, we stress the correct version. Durband's (2002) conflation of the two conflicting systems of nomenclature in a single sentence (when he writes of the deepest portion and the roof of the fossa as equivalent) highlights the need for greater clarity. For example, it is hard to decipher the statement that “it is clear that while the deepest portion of the *articular* area of the mandibular fossa always lies anterior to the squamotympanic fissure, only in Ngandong does the roof of the fossa continue to slope superiorly to the fissure, thus containing the entire course of the fissure along its deepest extent.”

As we mentioned above, character state expressions of the SQF feature can be highly variable. For example, there are instances when the SQF is not always a continuous fissure. When this occurs, a small portion of the posterior border of the mandibular fossa fuses to the tympanic plate, creating a bridge of bone between the lateral edge of the tympanum and the medial end of the SQF. It is our experience that idiosyncratic states of SQF expression alone make it extremely difficult to describe a single pattern of growth within and between populations be-

cause of age differences, sexual dimorphism, and morphological variability generated through differences in diet. Moreover, the SQF is often bilaterally dissimilar within individuals (compare Fig. 1a and b), especially in sedentary modern populations that tend to exhibit malocclusion disorders and periodontal disease.

When dealing with fossil humans, it is rare to find bilaterally well-preserved (i.e., unbroken) mandibular fossae, which adds to the confusion of describing this region at such an atomized level of inspection. In addition, the highest point of the mandibular fossa can change depending on the orientation of the skull in the sagittal plane. One might consider orienting in the three-point plane configuration of the Frankfurt Horizontal (FH), but since many of the fossil specimens lack faces, the FH is difficult to accurately establish. Considering these cautionary notes, we now address the specific comments offered by Durband (2002) concerning the feature “course of the SQF.”

In the Indonesian fossils, we found that Sgr 17, Sm 1, and Sm 3 all are similar to the Ngandong series in that their SQF lies in the highest portion of the mandibular fossa. We do not agree that Durband's Figure 1 (modified after Wood, 1991, by the addition of the position of the SQF) is an appropriate or convincing illustration of his argument: in such a lateral view of the temporal region, the structures under examination are hidden.

On the casts themselves, Sgr 4 and 17 exhibit morphology that is nearly identical to that seen on some Ngandong specimens, such as Ng 7 (= Solo VI), in which the SQF begins posterior to the broken postglenoid process and courses anteroposteriorly to the highest portion of the mandibular roof. It then turns posteriorly as it continues in a medial trajectory until it reaches the petrotympanic fissure. The mandibular fossa in Ng 7 and most other Asian fossil hominids is convex in shape, ranging in degree from very little (Sgr 17) to marked (Sm 3 and Ng 11). Since the highest portion of the convex mandibular roof is oriented in the transverse plane and its lateral and medial walls are oriented in the sagittal plane, it seems unlikely that the SQF can ever course entirely along the highest portion of the roof, simply due to its overall shape and design.

Of perhaps greater importance is our observation that several African members of the *H. erectus* (*s.l.*) group, such as NMT OH 9 and KNM-WT 15000, exhibit an SQF aligned similarly to those of the Indonesian fossils. Durband argues that the SQF in NMT OH 9 is unlike that in Sgr 4 and 17 because it does not follow the highest point of the roof throughout the entire fossa. Close examination of a cast of NMT OH 9 reveals that the SQF does run in the highest portion of the mandibular fossa roof. Tracking it from its medial border, the SQF runs along the highest part of the roof and continues laterally demarcating the posterior edge of the temporally-derived portion of the glenoid fossa, which has become slightly lower at its most lateral roof edge.

Examination of the Nariokotome *H. erectus* (KNM-WT 15000) right mandibular fossa unmistakably indicates the presence of an SQF that runs for its entire length along the highest portion of the roof. The damaged left side is more difficult to assess because it was recovered fractured at the point of the fissure. Although Durband is correct in stating that the SQF runs posterior to the glenoid joint surface in WT 15000, we are unsure why he states that “it does not traverse the roof surface.” Durband may be confusing “roof surface” with “articular surface,” which is a very different anatomical landmark. The roof surface refers to the entire surface of the mandibular fossa where

the malleolar disk is attached. The articular surface, on the other hand, refers only to the portions of temporal bone with which the condyle of the mandible articulates (however slightly): the articular eminence and the posterior area of bone that sometimes generates a PGT.

PGT

The presence of a PGT is the second feature that Durband emphasizes. As with the course of the SQF, the expression of the “PGT” feature can be described in various characters and states, including: 1) presence or absence, and 2) size and shape (it can be big or small, rounded or pointed, 10.1 mm in height, etc.).

His argument suffers from his conflation of the concepts “tubercle” and “process”—for example, when he uses both terms to describe the structure in Sgr 4. Then he claims that Sgr 4 is unlike the Ngandong specimens in that it has “a large PGT,” but if we are not sure how he defines a tubercle, it is difficult to objectively assess his taxonomic conclusion. This is illustrated by his finding that there is “little evidence of true postglenoid tubercles in the Ngandong specimens. Any postglenoid structures in these hominids are vestigial at best and appear as low ridges, while true tubercles are present in virtually every other specimen of *H. erectus* found to date. Each of the specimens noted by Delson et al. (2001) as being similar to the Ngandong fossils in this area possesses a large postglenoid tubercle. . . .”

Durband’s use of terms such as “true” PGTs (as opposed to false PGTs?) or “vestigial” (implying developmental reduction, when all that should really be said is “small”) is problematic. Close examination of casts of Ng 7 and Ng 10 clarifies any confusion regarding the presence of PGTs in the “Ngandong group.” In contrast to Durband’s assertion that no Ngandong specimens present PGTs, Ng 7 and Ng 10 both have prominent bony projections at the posterolateral edge of the right mandibular fossa. Sm 1 also exhibits a PGT, whereas the right postglenoid region on Sm 3 is slightly damaged, but appears most similar to that of Ng 11 where no eminence is discernable. We disagree with Durband’s assertion that the PGT areas in Sgr 4 and 17 are similar: our cast of Sgr 17 indicates that it does not possess a large tubercle as does Sgr 4, but rather has a smaller, blunted process that appears to be eroded. On the other hand, the PGTs of Sgr 4 and NMT OH 9 are remarkably similar in overall morphology.

CONCLUSIONS

Weidenreich (1951) suggested that the position of the SQF in the floor (actually the roof) of the mandibular fossa separated then-known Indonesian from Chinese *H. erectus*. We (Delson et al., 2001) extended this observation to note that some more recently recovered Indonesian (Sgr 17 and Sm 1) and African (OH 9 and WT 15000) specimens shared the pattern Weidenreich described for Ngandong and Sgr 4. Durband (2002) questions this finding, arguing that the character must be modified to reflect the presence or absence of a PGT, which if present would cause the SQF to curve laterally and depart from the highest portion of the fossa roof. He suggests that such morphology characterizes the known Ngandong, Sumbingmacan, and Ngawi specimens to the exclusion of Sangiran and African fossils. In addition to misunderstanding our simple citation of Weidenreich’s views, Durband conflates terminology in two areas: the correct description of the mandibular fossa as a roof vs. its more common “shorthand” view as a basin, and the distinction between a PGT and process.

Moreover, we contend that overstressing minor variations in the SQF is meaningless because it often differs bilaterally in modern individuals. This becomes problematic when assessing morphological variation in fossils, especially when one side is often damaged. We maintain our view that both OH 9 and Sgr 17, as well as Sgr 4, share the essential state of the SQF traversing the highest portion of the mandibular fossa roof, similar to what we see in Sm 3 and in the Ngandong specimens discussed in our original work (Delson et al., 2001). Furthermore, we find a PGT (or variant) present in some Ngandong fossils (e.g., 7 and 10) but absent in others as described by Weidenreich; OH 9 and Sgr 4 both have well developed PGTs, while Sgr 17 and Sm 1 have smaller, less developed ones.

After reexamination of the Indonesian and African *H. erectus* (*s.l.*), we conclude that atomizing the morphology of the mandibular fossa and SQF in these groups does not aid in clarifying phylogenetic relationships. We applaud Durband’s efforts in attempting to fine-tune the pattern of preserved morphology in the Indonesian sample, but we doubt that this noble goal can be attained solely by focusing on a bony region that is developmentally constrained by epigenetic factors. Much as we might agree with Durband’s apparent rejection of the Ngandong population as a possible ancestor for some modern humans of Sunda and Sahul, we cannot accede to his use of an invalid character analysis as supporting evidence.

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