



JEFFREY H. SCHWARTZ, IAN TATTERSALL

TOWARD DISTINGUISHING *HOMO NEANDERTHALENSIS* FROM *HOMO SAPIENS*, AND VICE VERSA

ABSTRACT: Here, we 1) point out that one of the major features used to distinguish Neanderthals from modern humans (the prominence of the occipitomastoid crest) is not valid, 2) provide comparative data indicating that *Homo sapiens* (not Neanderthals) possesses the derived character states of the vaginal and styloid processes, 3) demonstrate that Neanderthals have a novel configuration of the anterior squamosal, while *H. sapiens* is autapomorphic in lacking distinction between infratemporal and temporal fossae, and 4) argue that synapomorphy between Neanderthals and *H. sapiens* exists in the presence in juveniles of a prominent, domed arcuate eminence. The nature of similarity and difference between mid-late Pleistocene and recent hominids still needs clarification.

KEY WORDS: Neanderthal – *Homo sapiens* – Squamosal – Alisphenoid – Infratemporal and temporal fossae – Petrosal – Vaginal – Styloid and mastoid processes – Styломastoid foramen

INTRODUCTION

In the more than one hundred years since the discovery of the first Neanderthal specimen – the adult cranium of Gibraltar 1 (Forbe's Quarry) – there has been a virtually unbroken stream of publications on the novel morphologies of this hominid. Interestingly, this outpouring of description has been inexplicably unaffected by the existence of competing theories on the taxonomy and phylogenetic relationships within the genus, *Homo*, of Neanderthals. Although some of the details of these debates have changed over time, the essence of the dichotomy has remained essentially the same: Do the fossils represent the remains of an extinct species of the genus, *Homo*? Or do they represent individuals whose morphology can be incorporated into the domain of variation within our own species, *H. sapiens*?

The list of features that can now be generated by which Neanderthals are distinguished from so-called anatomically

modern *H. sapiens* is long and includes the following: cranial and postcranial bone thicker; cranial vault long and low; face relatively large and puffy; nasal bones markedly projecting; snout and jaws anteriorly displaced (indicated in the mandible by a retromolar space between M3 and the ascending ramus); supraorbital torus double-arched and arcuately continuous across glabella; frontal sinuses expanded laterally throughout the supraorbital torus; nasal aperture extraordinarily large and nasal cavity expansive; chin poorly developed or lacking altogether; occipital torus uniformly thick (not segmented or medially elevated), horizontally oriented, and well-delineated above and below; suprainiac depression pitted and circumscribed by a raised margin; occipitomastoid crest at least as prominent as mastoid process; anterior mastoid tubercle present; vaginal and mastoid processes not in contact; styloid process medially emplaced; long bones rounder in cross-section; hand and foot bones massive; superior pubic ramus elongate and thin and pubic symphysis platelike (e.g.

TABLE 1. Mid-late Pleistocene hominid specimens studied.

Abri Pataud cranium
Biache partial cranium
Crô-Magnon 1, 2, 3 crania, pelves
Engis adult & child crania
Fontchevade frontal, callosities
Gibraltar 1 & 2 (child) crania
Kabwe cranium, palate
La Chapelle-aux-Saints cranium, postcranium
La Ferrassie 1 & 2 crania, 2 pelves, 4BIS & 5 newborns
La Quina 5 cranium
Neanderthal calvaria and partial skeleton
Pech de l'Azé (child) cranium
Reilingen calvaria
Roc de Marsal infant
Saint-Césaire partial cranium & skeleton
Sima de los Huesos partial crania and postcrania of multiple individuals
Skhul II, V, VI, VII, VIII, IX crania, mandibles, & postcrania
Spy 1 & 2 partial skeletons
Steinheim cranium
Tabun C1 (cranium) & 1 (maxilla, teeth)
Zafarraya mandible and femur

Howells 1973a, b, Hublin 1978, Santa Luca 1978, Stringer, Andrews 1988, Stringer *et al.* 1984, Vandermeersch 1978).

In spite of recognizing these distinctions, these authors (with the notable exception of Santa Luca) have been reluctant to equate derivedness with species difference. Rather, if interpreted as being apomorphic, the features that distinguish Neanderthals from "anatomically modern" humans are relegated in taxonomic importance only to the level of the subspecies. Other researchers have interpreted Neanderthal morphology as primitive relative to the "anatomically modern" character states seen in *H. sapiens* (e.g. Smith 1994, Smith *et al.* 1989, Thorne, Wolpoff 1981, Wolpoff 1985, Wolpoff *et al.* 1984, Wolpoff *et al.* 1981). This interpretation relies not on determining character state polarity in the context of a broad comparative sample, but, rather, on the premise that fossil hominids, being ancient, possess the primitive or "archaic" character states, whereas humans, being anatomically modern by definition, possess the transformed or derived morphological states.

During our study of mid-late Pleistocene fossil hominids, we found that some of the features cited as distinguishing Neanderthals from *H. sapiens* do not reflect the morphology adequately, while others are not consistently expressed from one specimen to the next. Here, we shall discuss the occipitomastoid region. In addition to clarifying details of morphology, we also discovered a diversity of features that further distinguish Neanderthals from *H. sapiens*, and vice versa. Here, we shall discuss the alisphenoid, squamosal, and petrosal regions. Finally, because our approach is broadly comparative among anthropoid primates, we can address the question of the polarity – primitiveness versus derivedness – of various

features cited in the literature as distinguishing Neanderthals from *Homo sapiens*. Here, we shall discuss the styloid and vaginal processes.

METHODS AND MATERIALS

The fossils studied are listed in *Table 1*. Our interpretation of the derivedness (i.e. relative uniqueness) versus primitiveness (i.e. relative commonality) of a particular feature is grounded in a broad comparative craniodental study of a large sample of recent *H. sapiens* (N = 500) and non-human anthropoid primates (N = 300) (Schwartz, in prep.), as well as our review of the literature and assessment of casts of most fossil *Homo*.

RESULTS

The squamous portion of the temporal and the greater wing of the sphenoid (alisphenoid)

a) Description: The distinctly configured temporal bone of Gibraltar 1, La Chapelle-aux-Saints, and La Ferrassie 1 and 2 (the Neanderthal specimens in which the region is best preserved) is remarkable in two features (*Figure 1*). First, the anterior portion of the low-lying squamosal is flexed medially, being more or less at a right angle to the laterally oriented plane of the rest of the bone. Consequently, the juncture of these two planes is "cornered," forming a blunt edge that delineates from behind the moderately deep, but anteroposteriorly relatively narrow, temporal fossa. Second, the portion of the squamosal parallel but slightly inferior to the zygomatic process is strongly flexed medially, thus forming a horizontal shelf that lies more or less at a right angle to the vertical portion of the squamosal; the border between these two planes is delineated by a crisply defined margin. This inferior, crisply marginate, horizontal shelf extends anteriorly onto the greater wing of the sphenoid. Thus, the inferomedial flexure of the squamosal and alisphenoid bones together delineates a true infratemporal fossa from a temporal fossa above it.

The Roc de Marsal specimen preserves the anterior margin of the squamosal, which is slightly puffed out; however, the transition between the regions of the temporal and infratemporal fossa is smoothly curved, not yet angled. There thus appears to be an ontogenetic alteration in Neanderthals of the inferior portion of the squamosal (from arcuate in the juvenile, to angular in the adult), as well as an exaggeration of the flexure of the anterior portion of the squamosal.

b) Comment: In most extant primates – prosimians and anthropoids – the squamosal is often short (i.e. low-lying) and anteroposteriorly long (i.e. the often straight superior portion of the squamosal suture is situated low on the side of the cranial vault); *H. sapiens* stands out as having the

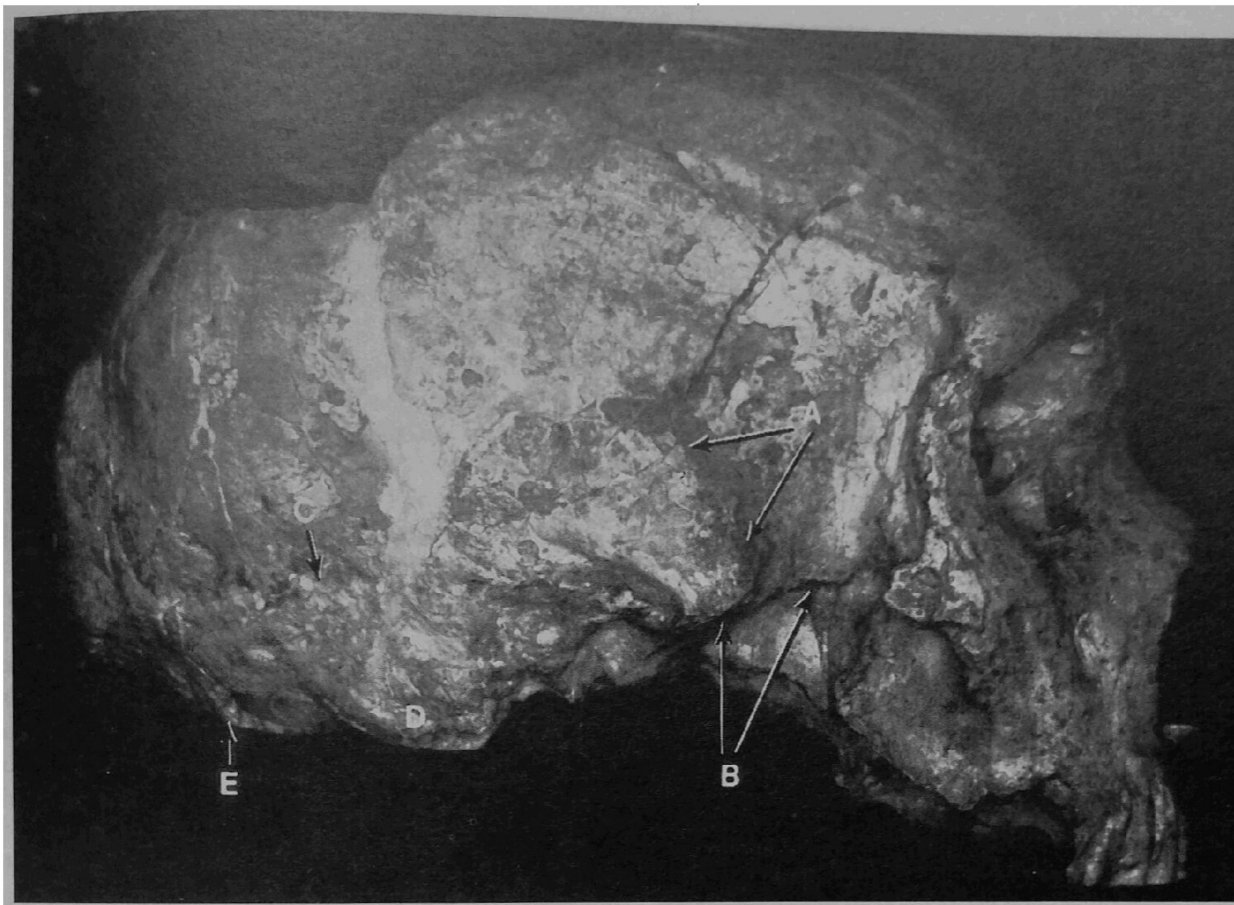


FIGURE 1. Lateral view of Gibraltar 1 (Natural History Museum, London). A = medially reflected squamosal, B = edge of squamosal and petrosal delineating temporal fossa above and infratemporal fossa below, C = long, horizontal parietomastoid suture, D = mastoid process, and E = occipitomastoid crest (see text for discussion). Not to scale. (© J. Schwartz)

tallest squamosal (Saban 1963). In all extant primates, the lateral surface of the squamosal is relatively flat or smoothly concave (Saban 1963). Although there may be severe postorbital constriction in some taxa, the anterior portion of the squamosal arcs smoothly into that depression. In neonates and older juvenile anthropoids, including *H. sapiens* (e.g. Clemente 1984, Schwartz 1995), the inferior portion of the squamosal curves in toward the cranial base. Adult *H. sapiens* retains the juvenile configuration. In most adult anthropoids, however, the transition inferomedially toward the cranial base is marked by an angular flexure, which defines a boundary between temporal and infratemporal fossae. Thus, in most anthropoids, and also Neanderthals, the juvenile configuration is altered ontogenetically.

The extent to which this flexure extends anteriorly along the squamosal, much less onto the greater wing of the sphenoid, varies among anthropoid taxa, but such a flexure is usually found at least near the root of the zygomatic process. Among fossil hominids other than Neanderthals, a flexure along the squamosal that continues onto the greater wing of the sphenoid is identifiable in the Kabwe specimen, *H. ergaster* (cf. Wood 1991, e.g. KNM-ER 3883 and 3773), and possibly *H. rudolfensis* (ibid.;

KNM-ER 1470). Other fossils, such as from Steinheim and Arago, and the Sima de los Huesos specimens, although having temporal and infratemporal fossae delineated in the region of the squamosal, do not have an inferiorly flexed alisphenoid. Skhul V, Crô-Magnon 1, and Abri Pataud display neither a distinction between an infratemporal and temporal fossa (i.e. the inferiorly portions of the temporal and sphenoid are not flexed medially), nor is there a "step" between the anterior margin of the squamosal and the greater wing of the sphenoid.

Because of its rather ubiquitous representation, an inferomedially flexed squamosal appears to be primitive for anthropoids. However, the extension of this flexure onto the alisphenoid – resulting in the delineation anteriorly of temporal and infratemporal fossae, as in Neanderthals and a few other hominids – emerges as a derived character. In addition, if *H. sapiens* is apomorphic in its lack of an inferiorly flexed squamosal (delineating infratemporal from temporal fossae), then so are Skhul V, Crô-Magnon 1, and Abri Pataud. Thus, although Skhul V may lack some of the apomorphies of extant *H. sapiens* (e.g. in the vaginal process, see below), it is not totally lacking synapomorphy with the extant species.

Also apparently derived among anthropoids is the peculiar inward flexure that the anterior portion of the Neanderthal squamosal makes just behind the squamosal suture. In contrast, in the majority of anthropoids, there is a smooth transition from the squamosal into the alisphenoid, even if the sphenoid wing also happens to be depressed or concave. Among fossil hominids, KNM-ER 3733 may have had a bulging and angled anterior portion of the squamosal; however, this may be due to taphonomic accident (i.e. distortion) rather than development (see Wood 1991). Nonetheless, even if KNM-ER 3733 were to have developed an anterior flexure in its squamosal, Neanderthals still emerge as apomorphic among anthropoid primates in this aspect of squamosal morphology.

The mastoid region

a) Description: The mastoid process of Gibraltar 1 is damaged, but the preserved base is small (*Figure 1*). The mastoid processes of La Quina 5 are stout and low, whereas, in La Ferrassie 1 and 2, they are long and broad. In La Chapelle-aux-Saints, the mastoid process is moderately prominent and its base somewhat broad. The mastoid processes of Spy 1 and 2 are thick at their bases, as is the mastoid process of Reilingen, which is relatively elongate and quite pointed at its tip. In Biache, the mastoid process is distinct, but very small. The mastoid processes point downward in all of these specimens. As would be expected in a juvenile, the mastoid process is tiny in the three to four year old Gibraltar 2 and Engis 2 specimens. The mastoid process of Steinheim, however, is small and thin at its base; it is slightly broken distally, but appears to have been somewhat projecting, with a slight anterior orientation. In Skhul V, the mastoid process is almost horizontal at its base, arching slightly downward at its tip, whereas Skhul VI's mastoid process is thicker (i.e. blunt and stubby) and almost vertical.

A small hole in the posterosuperior margin of the mastoid process of Reilingen reveals a large, cavernous sinus inside; the distal portion of the process is pervaded by a number of small air cells. La Quina 5 possesses large but inferiorly emplaced anterior mastoid tubercles, whereas La Chapelle-aux-Saints and La Ferrassie 1 have a small tubercle located just posterior to the acoustic meatus, while La Ferrassie 2 has a low crest in that position. There is no separate anterior mastoid tubercle or crest in Spy 1 and 2; rather, a small crest, which runs inferior to, and in parallel with, the suprameatal crest, terminates in a small swelling that lies level with the acoustic meatus. There is a slight swelling in the supramastoid area of the Engis 2 child. Skhul VI possesses an anterior mastoid tubercle, which lies opposite the inferior margin of the large acoustic meatus.

b) Comments: Although an inferior projection of the mastoid region of large-bodied hominoids is identified as a mastoid process (e.g. Aiello, Dean 1990, Ashton,

Zuckerman 1952, Kimbel *et al.* 1984), the development of a well-delineated, if not markedly projecting, mastoid process is restricted to species or specimens referred to the genus *Homo*. In *H. ergaster*, for example, the process is low in KNM-ER 3733 and prominent in KNM-ER 3883, but it is a distinguishable feature in and of itself, not just the apex of a swollen mastoid region (cf. Wood 1991). The mastoid process is typically low and stubby in Asian *H. erectus* (e.g. Weidenreich 1943, 1945, 1951), but protrusive to some extent in the mid-Pleistocene Sima de los Huesos specimens (Arsuaga *et al.* 1993), Neanderthals, the Reilingen temporal bone, the Steinheim skull, and *H. sapiens* (e.g. Aiello, Dean 1990, Saban 1963, Schwartz 1995).

If development of a true mastoid process is an apomorphy for a clade (comprising some number of species) within the genus *Homo*, then the development of a distinctively protrusive mastoid process [as in the specimens from Sima de los Huesos, Reilingen, and Steinheim, as well as in Neanderthals, Skhul V and VI, and *H. sapiens* (including Crô-Magnon and Abri Pataud)] is further derived within this clade. *H. sapiens* appears to differ apomorphically from all of these fossils (including Skhul V and VI), with the possible exception of Steinheim (in which the region is damaged), in having a more anteriorly inclined mastoid process, in which the posterior margin of the process is angled forward, while the anterior margin remains vertical. Finally, our survey indicates that a well-defined anterior mastoid tubercle, or a crest-like variant, situated opposite the acoustic meatus is not consistently enough represented in morphology or position to justify its recognition as a potential Neanderthal apomorphy (cf. Santa Luca 1978).

The occipitomastoid crest and parietomastoid suture

a) Description: Although Neanderthals have been distinguished from *H. sapiens* on the basis of having an occipitomastoid crest that 1) straddles the occipitomastoid suture, 2) is well-delineated both on its medial and lateral sides, 3) is large relative to the mastoid process, and 4) projects farther inferiorly than the occipital condyles (e.g. Howells 1973a, b, Santa Luca 1978, Stringer *et al.* 1984), we believe that is appropriate to redescribe this region for individual specimens. Following in part the nomenclature in Aiello and Dean (1990), we identify as many as three crests lateral to the mastoid process: 1) the para- or juxtamastoid crest, which occurs along the lateral wall of the mastoid groove (digastric notch), and thus on the temporal bone alone; 2) the occipitomastoid crest, which straddles the occipitomastoid suture; and 3) Waldeyer's crest, which lies on the occipital bone and is parallel to the occipitomastoid suture.

In Tabun C1, La Quina 5, La Chapelle-aux-Saints, Spy 1 and 2 (*Figure 2*), and La Ferrassie 1 and 2, a large occipitomastoid crest lies astride the occipitomastoid suture; it probably also did so in Gibraltar 1 (*Figure 1*). In

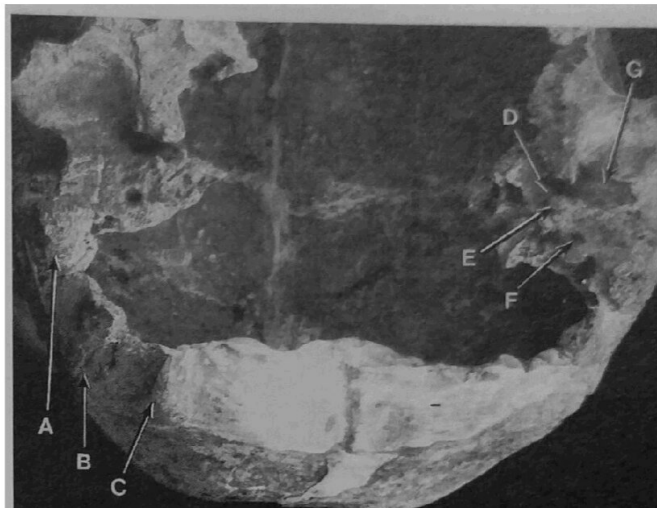
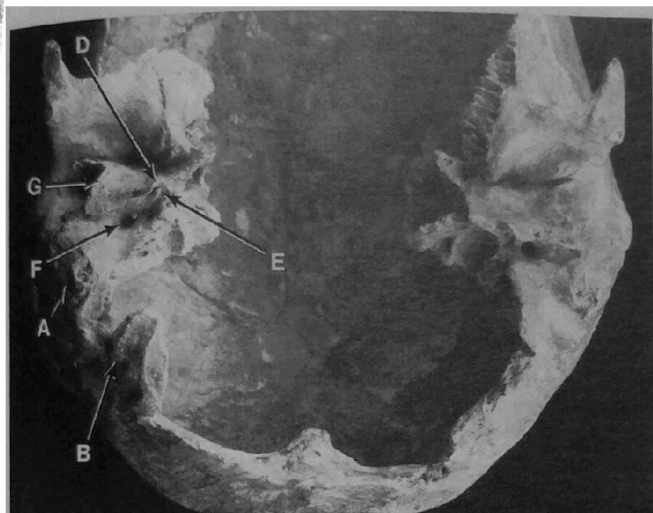
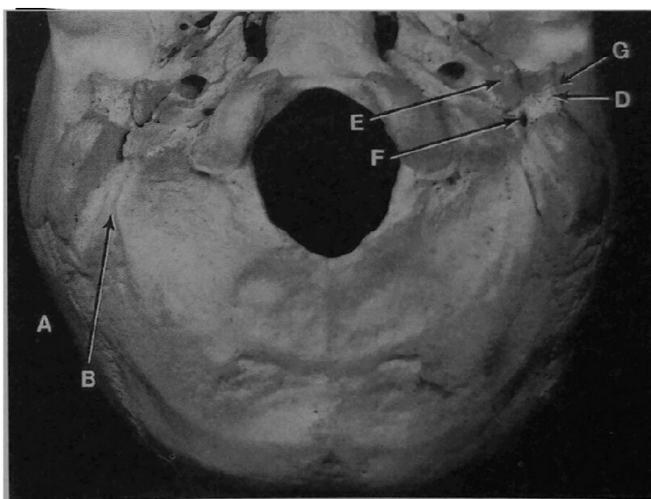


FIGURE 2. Basicranial views of Spy 1 (top left), Spy 2 (top right; both specimens, Institut Royal des Sciences Naturelles de Belgique, Bruxelles), and *Homo sapiens* (right; American Museum of Natural History, New York). A = mastoid process, B = occipitomastoid crest, C = Waldeyer's crest, D = vaginal process, E = styloid process, F = stylomastoid foramen, and G = tubular ectotympanic (see text for discussion). Not to scale. (© J. Schwartz)



La Quina 5, Spy 1 and 2, and La Ferrassie 1, the occipitomastoid crest probably projected inferiorly at least as far as the mastoid process; it definitely did so in La Ferrassie 2. The occipitomastoid suture is preserved on the temporal bone of Steinheim and it is devoid of a crest. La Quina 5 (right side) bears a Waldeyer's crest, which is more elevated than the occipitomastoid crest. Waldeyer's crest is weakly developed in Spy 1 and La Ferrassie 1, but quite substantial in Spy 2 (Figure 2). In La Chapelle-aux-Saints, Waldeyer's crest, but not the occipitomastoid crest, protrudes inferiorly as far as the mastoid process. Biache, however, possesses a thick paramastoid crest (which forms the posterolateral margin of a broad and shallow mastoid groove), a thick, ridgelike occipitomastoid crest along the occipitomastoid suture that is at least as tall as the mastoid process, and a low, but rugose, Waldeyer's crest. Although the mastoid processes of the Gibraltar 2 and Engis 2 children are tiny (see above), the occipitomastoid crests are already huge; in the Engis child, it is evident that the occipitomastoid crest straddles the occipitomastoid suture.

The occipitomastoid crest of Reilingen is noted as a very slightly raised area along the suture; a sharp and markedly prominent paramastoid crest (which is not as

elevated as the mastoid process), greatly constricts the width of the mastoid notch, and a long, low Waldeyer's crest is found well lateral to the occipitomastoid suture. Skhul V apparently lacks an occipitomastoid crest, but has a paramastoid crest and a faint Waldeyer's crest. In Skhul VI, a large occipitomastoid crest (which apparently straddled the suture) comes to join the broad and deep mastoid groove. In Crô-Magnon 1 and Abri Pataud, the occipitomastoid crest (visibly astride the occipitomastoid suture) is puny, and Waldeyer's crest is even weaker.

The parietomastoid suture is long and horizontal in Steinheim, Gibraltar 1 (Figure 1), La Quina 5, La Chapelle-aux-Saints, Spy 1 and 2, La Ferrassie 1 and 2, Skhul V, and the Engis 2 and Gibraltar 2 children; it is at least long in the Roc de Marsal child, and quite long, but not very straight, in Reilingen and Biache. The parietomastoid suture probably would have been horizontal in Fontchevade.

b) Comments: Howells (1973a, b) and Santa Luca (1978), among others, have described Neanderthals as differing apomorphically from *H. sapiens* in having an occipitomastoid crest that is at least as elevated as the

mastoid process. Howells (ibid.) also contrasted the Neanderthal occipitomastoid crest straddling the occipitomastoid suture with that crest in *H. sapiens* and other hominids being confined to the temporal bone.

As noted above, more than one of these crests, but not always the same ones, can be found in any given Neanderthal specimen; when present, Waldeyer's crest is often continuous with the inferior border of a Neanderthal's horizontal occipital torus. A Neanderthal specimen may have one crest in the vicinity of the mastoid process that rivals it in prominence, but it may not be the same crest as in another specimen. Thus, although the occipitomastoid crests of the Gibraltar 2 and Engis 2 children may be more protrusive inferiorly than their mastoid processes, it is impossible to predict how many crests, and in what order of prominence, each would have had as an adult.

With regard to the parietomastoid suture, in anthropoids, including extant large-bodied apes, *Australopithecus*, *Paranthropus*, and early *Homo* (Kimbél, Rak 1985, Wood 1991), this suture is typically quite abbreviated, and, thus, essentially coincident with the landmark, asterion. Thus, the character states "long and horizontal", as seen in Neanderthals and Skhul V, would be apomorphic within Anthropoidea.

The vaginal and styloid processes

a) Description: In Gibraltar 1, Spy 1 (Figure 2), and Tabun C1, the extremely steep posterior wall of the glenoid fossa merges strongly with the sharp vaginal process of the tympanic plate; the confluence of these structures is less marked in Spy 2 (Figure 2). The vaginal process of these specimens, as well as of Steinheim, Reilingen, La Chapelle-aux-Saints, and La Ferrassie 2, courses along the midline of the tympanic plate and peaks at the midline of the carotid foramen; in La Ferrassie 1, it extends the full length of the petrosal. Similar to these adults, the peak of the already developing vaginal process of the three to four year old from Pech de l'Azé lies near the carotid foramen. In Steinheim, the vaginal process is low and poorly developed. In all of these specimens, as well as in Biache, the vaginal process is separate from the mastoid process and its "peak" wraps anteriorly around a thin styloid process. Some specimens preserve the styloid process in its pit, while others have only the vaginal pit. In Skhul V, the small vaginal process lies right below the auditory tube and is separated from the stylomastoid foramen and mastoid process.

In Gibraltar 1, the carotid foramen lies at the midpoint of the petrosal. In Steinheim, Reilingen, Biache, La Quina 5, La Chapelle-aux-Saints, Spy 1 and 2 (Figure 2), and La Ferrassie 2, the styloid process is situated near the carotid foramen and almost directly in front of the mastoid groove. In these specimens, the large stylomastoid foramen lies medial to the acoustic meatus and away from the more medial styloid process. In Reilingen, the stylomastoid foramen is situated near the base of the styloid process,

the latter of which is in line with the mastoid groove. In Crô-Magnon 1 and Abri Pataud, the styloid process is situated close to the mastoid process and the carotid foramen more medially than in the other fossils cited. The mastoid groove of Steinheim and Reilingen is not as broad nor as gutter-like as in Gibraltar 1, La Ferrassie 1, La Quina 5, and Spy 1 and 2, nor as fissure-like as in Crô-Magnon 1 and Abri Pataud.

b) Comments: As described by Vandermeersch (1981), the vaginal and mastoid processes of Neanderthals lie apart from one another, as they also do in Steinheim and Reilingen, at least *H. ergaster* (e.g. KNM-ER 3883 and 3773; Wood 1991) among other species of the genus, and at least *Paranthropus boisei* (e.g. KNM-ER 407, 1805, and possibly 406; Wood 1991) among Plio-Pleistocene hominids. In all of these hominids, the vaginal process is a relatively low structure confined to the territory of the body of the petrosal; it peaks as it wraps around the styloid process, which is typically located rather medially, midway along the length of the petrosal.

In *H. sapiens*, the vaginal process is a tall, sheet-like structure that is contained primarily within the territory of the tubular ectotympanic (Figure 2). The lateral margin of the vaginal process in *H. sapiens* (including Engis 1), which lies close to, and may even be aligned with, the margin of the acoustic meatus, is distended downward at least as far as the base of the mastoid process, which, in some individuals, it may overlap quite extensively. In *H. sapiens*, the tall vaginal process wraps around the anterior surface of the styloid process where it may also be pointed (also see Zuckerman *et al.* 1962). In *H. sapiens*, the stylomastoid foramen lies at or near the anterior lip of the mastoid groove and at the base (laterally) of the styloid process (ibid.; Dean 1984) (Figure 2).

According to Zuckerman *et al.* (1962), a true vaginal process, which is situated medially along the tympanic plate, occurs with some frequency in *Pongo* and *Pan* (but not *Gorilla*), whereas a styloid pit (evidence of an unossified styloid process) situated medial to, and well separated from, the stylomastoid foramen is found in all non-*Homo* extant hominoids (including gibbons). Rhesus monkeys and baboons develop neither a vaginal process nor a styloid process (ibid.). Study of a diverse representation of extant anthropoid primates reveals that lack of these structures is the common condition (Schwartz, unpublished data). Thus, development of a styloid process would be derived within Anthropoidea, and, thus, apparently synapomorphic for Hominoidea.

Although a vaginal process can sometimes be found in specimens of *Pongo* and *Pan*, it would seem that the consistent development of a vaginal process might be synapomorphic of hominids as a clade, within which *H. sapiens* is unique in having a vaginal process that is tall and platelike, laterally situated, and in contact with the mastoid process. It is thus *H. sapiens* – not Neanderthals (e.g. Vandermeersch 1981) nor any other hominid – that is

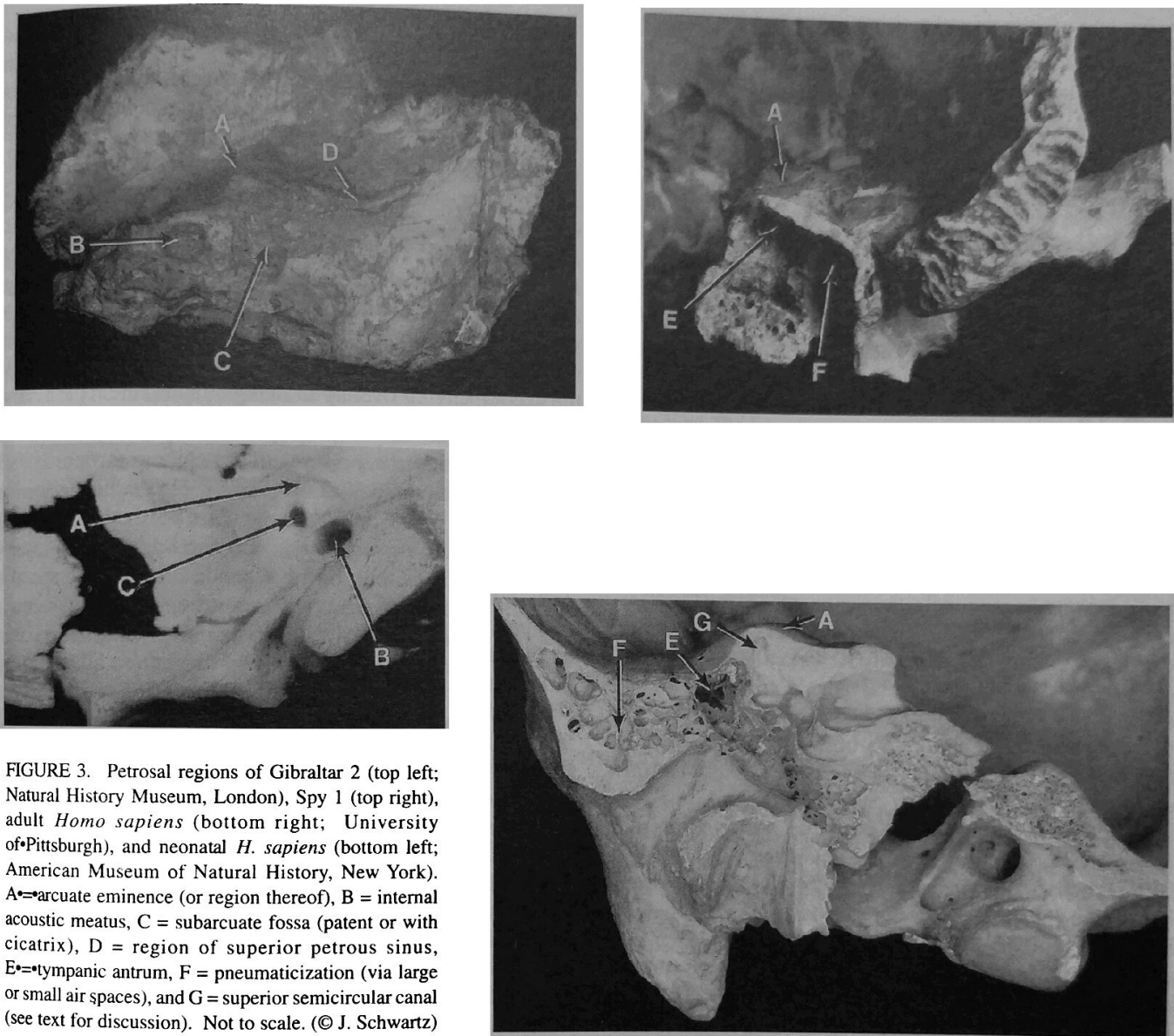


FIGURE 3. Petrosal regions of Gibraltar 2 (top left; Natural History Museum, London), Spy 1 (top right), adult *Homo sapiens* (bottom right; University of Pittsburgh), and neonatal *H. sapiens* (bottom left; American Museum of Natural History, New York). A = arcuate eminence (or region thereof), B = internal acoustic meatus, C = subarcuate fossa (patent or with cicatrix), D = region of superior petrous sinus, E = tympanic antrum, F = pneumatization (via large or small air spaces), and G = superior semicircular canal (see text for discussion). Not to scale. (© J. Schwartz)

apomorphic in this region of the basicranium. Since *H. sapiens* appears to be the only hominoid in which the styloid process lies laterally, with the stylomastoid foramen at its base, it would seem that this is yet another autapomorphy of this species. It is thus of no little taxonomic significance that Skhul V is primitive both in having a short, medially situated vaginal process and in having a medially emplaced styloid process that is dissociated from the stylomastoid foramen.

The petrosal (endocranially)

a) Description: In Gibraltar 1, Biache, Steinheim, La Quina 5, Spy 1 (Figure 3) and 2, La Ferrassie 1 and 2, and Reilingen, the petrosal is broad from side, especially across the region of the arcuate eminence. However, only Gibraltar 1 bears a dome-like arcuate eminence, as typically seen in *H. sapiens* (Figure 3); in the other fossils, this region is either minimally convex, following

the curvature of the superior surface of the petrosal, or flat. As can be observed particularly well in Spy 1 (Figure 3), Biache, Reilingen, and Steinheim because of breakage, the petromastoid region is rife with large, vacuous sinuses that swell out, for example, the expanse lateral to the arcuate eminence, the portion extending from the mastoid process inferiorly along the body of the petrosal, and the area around the carotid canal. Biache, Gibraltar 1, La Ferrassie 2, Steinheim, and La Quina 5 lack a definitive groove for the superior petrous sinus. The former two specimens also lack a definitive subarcuate fossa, whereas Gibraltar 1 and La Ferrassie 1 possess a well-defined, but not deeply concave, subarcuate fossa; in all specimens, however, the fossa is completely closed over by a cicatrix. The petrosal of Reilingen bears tiny traces both of a superior petrous sinus and of a subarcuate fossa. In Crô-Magnon 2 and Engis 1, the petrosal, which is narrow and inwardly tapering, bears a subarcuate fossa and a discernible superior petrous sinus; in Engis 1, the domed

arcuate eminence is prominent. The petrosals of Skhul V, which can only be observed externally, are slender, tiny, and medially tapering. In Skhul VII, the petrosal is neither highly pneumaticized nor broad mediolaterally.

The Gibraltar 2 (Figure 3) and Pech de l'Azé children possess huge, dome-shaped arcuate eminences; in the former, the subarcuate fossa is also completely closed over. In the preserved right petrosal of the La Ferrassie 5 neonate, the subarcuate fossa is closed over and the raised and well-defined arcuate eminence thinly covers the superior semicircular canal, which is expansive laterally. The slightly damaged left petrosal bone of the La Ferrassie 6 neonate is similar in all features to La Ferrassie 5; damage permits observation of the marked degree of pneumatization pervading the expansive region lateral to the arcuate eminence. As in various adults (e.g. Gibraltar 1), there is no sign of a superior petrous sinus in the Gibraltar 2 (Figure 3) or Pech de l'Azé children.

b) Comments: In mammals, the region which, in *H. sapiens*, can be accurately identified as an arcuate eminence, overlies the superior semicircular canal (Saban 1963) (Figure 3). As in other mammals, the region of the arcuate eminence of extant, non-human, anthropoid primates may be gently convex or arcuate, but it is a part of the overall contour of the superior surface of the petrosal rather than an independent eminence (as in *H. sapiens*) (e.g. see illustrations in Saban 1963, personal observations). In *Paranthropus* (*Australopithecus*) *robustus* (e.g. TM 1517; Broom, Schepers 1946), *P. boisei* (e.g. KNM-ER 407 and 732; Wood 1991), *A. africanus* (e.g. Sts 5; Broom, Robinson 1950), *H. habilis* (e.g. OH 24; Tobias 1991: 93), and *H. erectus* (e.g. Sangiran, Trinil, Ngandong, Zhoukoudian; Black 1931, Weidenreich 1943, 1945, 1951), the region of the arcuate eminence is either low and arcuate (conforming to the curvature of the superior surface of the petrosal) or flat. In KNM-ER 1813 (cast), OH 5 (bilaterally) (cast and Tobias 1991: 93), KNM-ER 17000 (left side only) (cast), and the Baringo/Chemeron 1540 right temporal fragment (cast), there is a thin, low, bandlike elevation in the otherwise flat or gently arcuate superior surface of the petrosal; this slight elevation corresponds to the uppermost curve of the superior semicircular canal. Since all of these fossil hominids are most similar to extant, non-human anthropoid primates, it would seem that they are primitive in the configuration of the superior portion of the petrosal. As such, a simple comparison between adult Neanderthals and adult anthropoids would lead to the conclusion that Neanderthals, in their possession of an often flat-surfaced petrosal, are also primitive. *H. sapiens* would appear to be autapomorphic among anthropoids in that adults often possess a prominent and elevated arcuate eminence, which broadly encapsulates and obscures the superior semicircular canal (e.g. Clemente 1984, Saban 1963) (Figure 3).

Although there is a disappointing lack of data on juvenile fossil hominids, it is clear from study of known Neanderthal neonates and children, which have a superiorly pronounced and dome-shaped arcuate eminence, that the flattened region in the adult results from ontogenetic remodelling. Even more prominent superiorly than in many adult *H. sapiens*, is the well-defined and domed arcuate eminence of neonates and juveniles (e.g. Clemente 1984, Fassekas, Kósa 1979, Schwartz 1995) (Figure 3). Although Black (1931: 37) described the petrosals of the juvenile *H. erectus* from Locus E of Zhoukoudian as having a prominent arcuate eminence, a dome-like structure is identifiable neither in the photographic illustrations nor in the accompanying overlay drawings; rather, the region in question is essentially flat. Our preliminary survey of extant taxa reveals that the petrosal of juvenile anthropoids is essentially flat and lacks a distinct arcuate eminence, as it is in adults. Thus, from an ontogenetic perspective, a flat arcuate eminence – present in the juvenile and retained into the adult – is the primitive condition for anthropoid primates. In contrast, a raised arcuate eminence, as seen in juvenile Neanderthals and *H. sapiens* (Figure 3) is derived and seemingly synapomorphic for these hominids. Since the prominence of this eminence is often completely obscured ontogenetically in Neanderthals, we suggest that this hominid is further derived in this region of the petrosal. It is possible that the neotenic retention of the juvenile condition seen in many adults is autapomorphic for *H. sapiens*. Given that Reilingen and Steinheim are apparently members of a Neanderthal clade (Schwartz, Tattersall, in print, Stringer *et al.* 1984) it is not unreasonable to predict that their relatively flat superior petrosal surfaces also resulted from ontogenetic remodelling of what, in youth, would have been a superiorly prominent arcuate eminence.

Ontogenetic obscuring of a prominent arcuate eminence in Neanderthals appears to be the result of excessive pneumaticization via large sinuses (Figure 3). Although pneumaticized, the petromastoid region of extant anthropoids, including *H. sapiens*, houses a myriad of small air cells (e.g. Clemente 1984, Kimbel *et al.* 1984, Saban 1963) (Figure 3). Descriptions and/or illustrations of specimens attributed to species of *Paranthropus* and *Australopithecus*, as well as to *Homo habilis*, *H. rudolfensis*, *H. ergaster*, and *H. erectus* (e.g. see Black 1931, Broom, Robinson 1950, Kimbel *et al.* 1984, Tobias 1967, 1991, Leakey, Walker 1988, Weidenreich 1943, 1945, 1951, Wood 1991), demonstrate that the petromastoid regions of these hominids, even though varying considerably morphologically, are similarly pneumaticized via the proliferation of small air cells. Given its broad distribution among anthropoids, we would interpret this latter condition as being primitive for the group. In contrast, pneumaticization via large air cells emerges as a potentially derived configuration within Anthropoidea. Thus, Neanderthals and the Reilingen and Steinheim specimens are apomorphic, and, if separate taxa, synapomorphic for

this feature. Restricted synapomorphically to Neanderthals and Steinheim is the lack of a definitive groove for the superior petrous sinus, which is otherwise present in extant primates, including *H. sapiens* (Saban 1963).

CONCLUSION

Although there already exists a considerable literature on morphological differences and similarities between Neanderthals and *H. sapiens*, much still remains to be done, particularly at the level of interpreting these comparisons phylogenetically. As is revealed in the case of the crests lateral to the mastoid process, however, one may have to reanalyze features prior to engaging in the determination of character state polarity. But even when features have been accurately described and understood developmentally, their phylogenetic significance – as primitive retentions, synapomorphies, or autapomorphies – can only begin to be appreciated in the context of comparisons that go taxonomically well beyond the specimens or handful of species of immediate interest. Only when these levels, particularly of apomorphy, are sorted out with some confidence can we then turn to identifying species and hypothesizing their relationships to one another.

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Jeffrey H. Schwartz
Department of Anthropology
University of Pittsburgh
Pittsburgh, PA 15260
USA
Fax: +1 412 648-7535
E-mail: jhs+@pitt.edu

Ian Tattersall
Department of Anthropology
American Museum of Natural History
Central Park West at 79th Street
New York, NY 10024
USA
E-mail: iant@amnh.org