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On the phylogenetic position of the pre-Neandertal specimen from Reilingen, Germany

This paper describes the morphology and phylogenetic significance of a well-preserved fossil human cranium found near Reilingen, Germany in 1978. The specimen consists of two complete parietals, most of the right temporal, and 70% of the occipital. The specimen displays several features characteristic of early ''archaic'' *Homo sapiens*: maximum breadth at the supramastoid crests, roughly pentagonal occipital view, an angular torus, superoinferiorly elongate/anteroposterior shortened squamous temporal, strong mastoid, and separation of the tympanic and mastoid temporal portions. Other features align the Reilingen cranium with the ''classic'' Neandertals: developed suprainiac fossa, bilaterally protuberant occipital torus, strong juxtamastoid eminence, a highly convex occipital plane, and lambdoid flattening. This morphology and our cephalometric analysis support the assignment of this specimen to a Stage 2 ''pre-Neandertal'' group (e.g., Steinheim, Swanscombe, and Atapuerca [SH site]). Following an ''Accretion Model'' of European hominid evolution, Stage 2 succeeds Stage 1 European ''early-pre-Neandertals'' (e.g., Mauer and Petralona), and precedes both the Saale-Eem Stage 3 ''early Neandertals'' (e.g., Biache 1), which present greater platycephaly, a reduced mastoid process, an enlarged juxtamastoid eminence, and true ''en-bombe'' parieto-occipital form), and Weichsel Stage 4 ''Neandertals'' (*sensu stricto*, i.e., ''classic'' Neandertals).

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Introduction

In May 1978 the Staatliches Museum für Naturkunde in Stuttgart (SMNS) acquired an ''archaic'' hominid partial cranium found in a gravel pit in southwestern Germany near the small town of Reilingen. The geological context of the specimen is not fully

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certain because it was collected as part of a dredging operation (Ziegler & Dean, 1998). However, this skull presents characteristics similar to the Steinheim and Swanscombe crania.

The cranium was collected from the Reilingen gravel pit by SMNS staff on 17 May 1978 along with 38 mammalian bones and teeth. The exact date of discovery cannot be ascertained, but was most likely a

few weeks to months before the acquisition date. The bones and teeth recovered with the Reilingen cranium constitute a mixture of different faunas, a common occurrence at gravel pit excavations. The site shows no evidence of seriation and the hominid specimen does not seem to have undergone high energy diagenesis. Therefore, we suggest that the skull could be a member of the oldest Reilingen fauna which, as a whole, ranges from the Holstein interglacial to the Late Würm glacial (Ziegler & Dean, 1998).

This paper represents the first full description of the Reilingen specimen by SMNS staff involved with the discovery and colleagues with first-hand access. However, it should be noted that several others have published opinions on this specimen. Adam (1989, 1996) challenged Czarnetzki's (1989, 1991) description and attribution of the specimen to *Homo erectus reilingensis*. Adam emphasized the morphological affinities of this specimen with modern humans and evaluated the specimen as "archaeomorphous" *Homo sapiens*. Schott (1990) later concurred with Adam. In conference presentations, Waddle (1993) and Condemi (1995, 1996) concurred largely with the authors' initial finding that this specimen shows affinities with European Neandertals (Dean, 1993; Dean *et al.*, 1994, 1996).

The Accretion Model: a four stage schema for the evolution of Neandertal features

Recent discoveries of late Early-early Middle Pleistocene European specimens may present evidence for late *Homo erectus* (Ascenzi *et al.*, 1996), if not another taxon (Bermudez de Castro *et al.*, 1997). Well known "archaic" *H. sapiens*, e.g., Bodo (White, 1986), Elandsfontein (Klein & Cruz-Uribe, 1991), Ternifine (Dean, 1993; *incertae sedis* Hublin, 1985), or Atapuerca (Arsuaga *et al.*, 1997; Parés & Pérez-González, 1995), are poorly dated to the early-middle Middle Pleistocene (Dean, 1993). After Howells (1974), Stringer *et al.* (1979), Clarke (1990), and Bräuer (1992: but see Rightmire, 1996), we refer to all non-modern *H. sapiens*, generally, as "archaic" *H. sapiens*, saving one additional distinction for the "archaic" moderns (e.g., Djebel Irhoud, Skhūl, and Qafzeh). We see evidence for a slow accretion of Neandertal characteristics beginning in early Middle Pleistocene European "archaic" *H. sapiens*, continuing through the middle Late Pleistocene, and finally resulting in the Würm "classic" Neandertals. The "Accretion Model" of Neandertal evolution (Hublin, 1988c, 1990, 1991, 1992; Howell, 1994; Carbonell *et al.*, 1995), and its associated terminology (Table 1), is used throughout this paper.

The Accretion Model presented here refers to four Neandertal "stages" (Table 1), however we fully expect others to note aspects of specimens, known or yet to be found, which make assignment to a specific stage difficult. Rather than providing a classificatory scheme, it is our intent to document the successive origin of classic Neandertal craniofacial traits and their reduced variation as this lineage approaches the Würm. We consider it likely that this pattern was due to Neandertal populations having experienced a high degree of endemism (Hublin, 1982, 1988c, 1990, 1991).

In Table 1 we indicate Neandertal "stage" affinities for Asian specimens. However, Hublin (1982, 1984, 1988c) and Stringer (1985) have long made the case that paleodemographic evidence suggests that the Neandertal "core" population was always European.[1] Bräuer and colleagues

[1]We limit our presentation of this model to the European fossil hominid record. We have also chosen not to address the issue of Neandertal clinal variation in this paper. While we will mention mideast "archaic" *Homo sapiens*, archaic moderns, and Neandertals, we will not deal with their position in the Neandertal lineage, the relationship of middle eastern populations and modern humans, or relationship of modern humans and Neandertals. We are not sure these questions can be answered.

Table 1 The four stages of Neandertal evolution

Neandertal stages: (Stage no.) Name	Isotope stages (climate stages)	Derived European anatomical features	Example specimens
1 ''early-pre-Neandertals,'' i.e., early ''archaic'' *H. sapiens* in Europe	Pre-stage 12 (Cromerian Complex), stage 12 (Elster=''Mindel'')	Convex and receding horizontal infraorbital profile, wide occipital torus	Arago, Mauer, Petralona
2 ''pre-Neandertals,'' i.e., late European ''archaic'' *H. sapiens*	Stage 11–9 (Hoxnian, *sensu lato*, Holstein, *sensu lato*, ''Mindel/Riss'')	Bilaterally protruding occipital torus, suprainiac fossa (incipient to well defined), strong juxtamastoid eminence, styloid process not aligned with the stylomastoid foramen and the digastric groove, incipient ''en bombe'', increased occipital plane convexity, lateral post-toral sulcus deepens inferiorly, glabella moves anteroinferiorly disrupting previously horizontal supercilliary ridges, reduced maxillary buttress, anteriorly advanced and sagittally oriented face	Bilzingsleben (?1), Vértesszöllös (?1), Atapuerca SH site, Swanscombe, Steinheim, Reilingen
3 ''early Neandertals,'' i.e., show some ''classic'' Neandertal features	Stage 7–5 (part of the later Saale=''Riss'', Eem=''Riss/Würm'')	Full supra-iniac fossa, full ''en bombe,'' high occipital plane convexity, reduced mastoid, large juxtamastoid process, elongate temporal bone, anterior mastoid tubercle, external auditory meatus fully depressed, increased dolichocephaly	Ehringsdorf, Biache 1, La Chaise Suard, Lazaret, La Chaise Bourgeois-Delaunay, Saccopastore, (most of) Krapina (?u), (part of) Shanidar (?u)
4 ''classic Neandertals''	Stage 4–3 (Early Weichsel=''Würm'')	Exaggerated occipital plane convexity, and suprainiac fossa, high mid-facial prognathism, large piriform aperture, rounded circumorbital morphology, post-toral sulcus deepens	Neandertal, Spy, (rest of) Monte Circeo, Gibraltar Forbes Quarry (?u), La Chapelle-aux-saints, La Quina, La Ferrassie, La Moustier, Shanidar, Amud.

Specimens are assigned by most recent dating. Those followed by a question mark and stage number indicate morphological affinities, e.g., ?1 indicates a specimen is morphologically most similar to Stage 1 Neandertals. A ''u'' for stage number indicates, usually for largely incomplete partial specimens, that the morphology is unclear. There are no known specimens from isotope stage 8.

(Bräuer & Rimbach, 1990; Wu & Bräuer, 1993) opt not to elevate geographically restricted populations of ''archaic'' *H. sapiens* to specific status, instead classifying them as ''early'' or ''late-archaic'' *H. sapiens.* Some workers have raised the possibility of Neandertal-modern hybridization for Late Pleistocene Central European and Middle Eastern Neandertal and ''archaic'' modern fossils (Trinkaus & Smith, 1985; Santa Luca, 1978). At this time we prefer not to assign specific status to the Neandertals. Consistent with Bräuer & Rimbach (1990), the Accretion Model merely identifies Neandertals as a distinctly European lineage within ''archaic'' *H. sapiens.*

We suggest that the earliest known European ''archaic'' *H. sapiens* specimens,

e.g., Petralona and Arago, already evince Neandertal features. The first Neandertal stage can be represented by a Vértesszöllös-Bilzingsleben-Arago-Petralona group which displays incipient Neandertal facial morphology, although there is strong individual variation as demonstrated by the Arago 2 and 13 mandibles. We propose that the anteriorly shifted maxillary buttress and obliquely placed malar of Petralona and Arago most likely represent, minimally, subspecifically derived features when compared to African conspecifics such as Bodo and Kabwe I.

Much of the cranial morphology in Stage 1 Neandertals is plesiomorphic for *H. sapiens*, especially the temporal and occipital areas. The occipital torus is wide and strong with maximum development at its median part. A coronal section from the posterior portion of these skulls presents a pentagonal, or ''en tent'' form.

The second Neandertal stage (''Hoxnian'' or ''Holstein'') is represented by intermediate specimens such as Swanscombe and Steinheim. This stage displays clearer Neandertal apomorphies, especially in the occipital area. An extended suprainiac fossa develops above a weak to moderate, bilaterally protruding, occipital torus. The occipital lip of the Swanscombe juxtamastoid eminence is well developed. A posterior view of the braincase exhibits an intermediate shape between the primitive pentagonal and ''en bombe'' shapes.

The second Neandertal stage exhibits posterior skull features that cannot be considered synapomorphous with modern humans (Hublin, 1982, 1988*b*). In our view the Reilingen specimen belongs to this stage. These specimens display plesiomorphic ''archaic'' *H. sapiens*, non-Neandertal, morphology of the temporal bone, especially the supero-inferiorly elongate temporal squama. This suggests that the antero-posterior elongation observed in later Neandertals represents a reversion, a secondary platycephaly,

not a primitive retention. Facial, especially palatal and mandibular, features suggest great individual variation, perhaps mosaicism, in the Stage 2 (e.g., prognathy in Atapuerca 5) and 3 (e.g., orthognathy in Montmaurin) Neandertal mid- and lower-face.

Stage 3 Neandertal remains roughly correspond to oxygen isotope stages 7–5 (no specimens are yet known from isotope Stage 8). We agree with Vandermeersch's (1984) assessment of these specimens and thus reference this group as ''early Neandertals''. Most ''classic Neandertal'' features in the rear of the skull are present in Stage 3 Neandertals. The suprainiac fossa is well defined in, for example, La Chaise Suard. The occipital plane exhibits greater convexity (i.e., ''bunning''). The ''en bombe'' morphology is better expressed than in Stage 2, for example, in Biache 1. There is a significant reduction of the mastoid process.

The morphological division between Stage 3 and 4 Neandertals is the least clear cut. The later ''early Neandertals'' of oxygen isotope stage 5, such as Saccopastore 1 and 2 (Condemi, 1985, 1992) or the La Chaise Bourgeois-Delaunay specimens, display intermediate conditions between these two hypothetical groups. The regular accretion of Neandertal features appears to come into best focus between specimens dated to isotopic stages 6 and 4. It is possible that once more is known about the intra- and inter-population variation of these last two stages this distinction will not be warranted.

General morphology and overview measurements

The four recovered fragments of the Reilingen skull (Figure 1), SMNS 6717.1.5.78.1,[2] include two complete parietals, a nearly

[2]The catalog number of SMNS specimens are composed of: 1st the number of the topographical map 1:25,000 (6717), 2nd the number of the site, 3rd the month of acquisition, 4th the year of acquisition, and 5th the number of the specimen of this date.
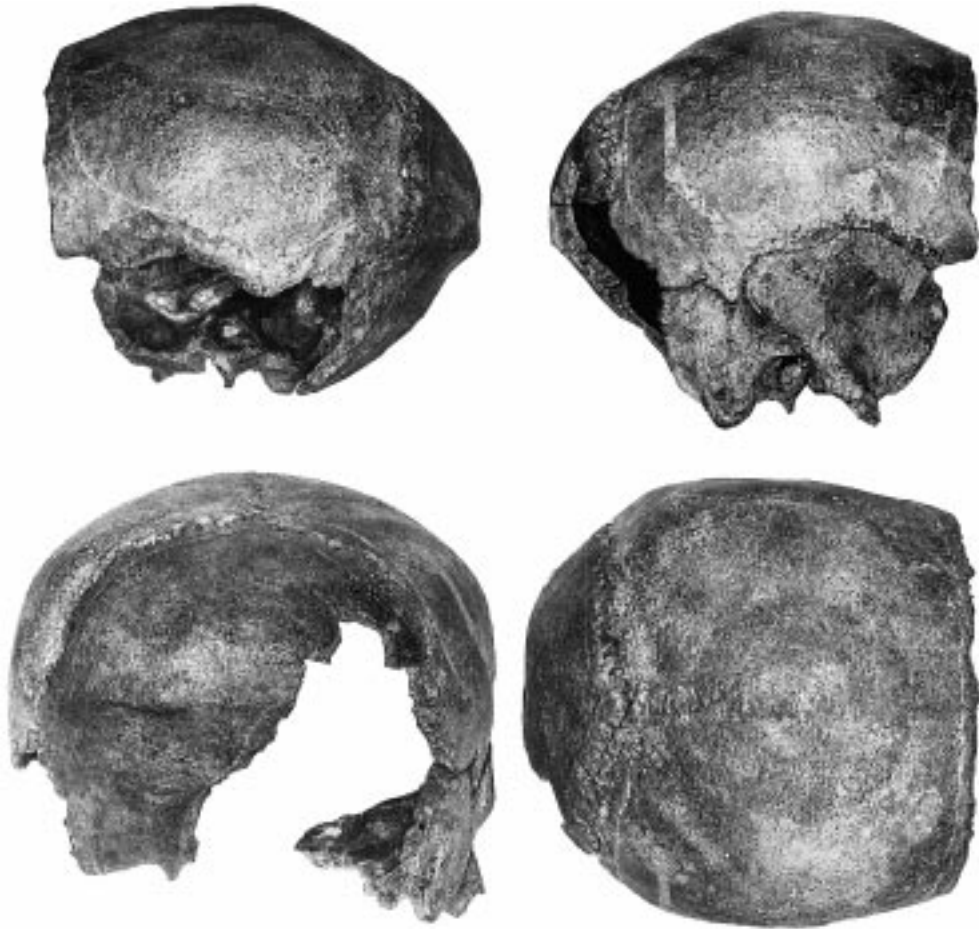
Figure 1. Four views of the Reilingen skull. Views, clockwise from upper left: left lateral, right lateral, dorsal, posterior.

complete right temporal bone, and a partial occiput. The complete and well-preserved parietals are joined along the sagittal suture. The petrous temporal is broken off medially as is the anterior part of the zygomatic process. Approximately 70% of the occipital bone is preserved including the complete upper scale. The jagged edge of the right inferior half presents a square-shaped notch that is approximately 8 cm^2 (Figure 1). Amino acid racemization of this excised piece resulted in an absolute date of 210 ka (Protsch von Zieten, 1991). A small posterolateral portion of the rim of the foramen magnum is preserved just to the left of the midline. It allows a reliable reconstruction of opisthion.

Overall, the skull is in extremely good condition. It is heavily mineralized. The temporal and occipital squamous surfaces are only slightly weathered. The bony contacts at the exposed sutures (i.e., coronal, squamous, and lambdoid sutures) exhibit sharp, unbroken edges that interdigitate naturally giving further evidence that the specimen lacks distortion.

None of the sutures known for the Reilingen skull is completely closed. Only

the sagittal suture shows any signs of fusion. Internally its central third is partially fused, while there is complete fusion endosteally on the posterior third. Thus, the two parietals have effectively knitted and cannot be disjoined. The lambdoid suture is entirely patent, and the sharply serrated edges of the parietals and occipital interdigitate freely and tightly. The resulting reconstruction is assuredly undistorted. Because there are no structures anterior to the coronal suture, determination of the Frankfurt plane is only an estimation, and comparisons of cranial outlines are limited to the post-bregmatic region.

In general, we agree with Anton's (1997) suggestion that extreme cranial thickness, commonly thought to be a feature of *Homo erectus*, may in many cases be related to known pathologies. The cranial vault bones of European ''archaic'' *H. sapiens* and Neandertal specimens do not show extreme thickness (Brown, 1994; but see Lieberman, 1996). While thickness generally increases toward the base of the Reilingen specimen, none of the usual areas of thickening seen in *H. erectus* was detected to be over 10 mm, while most locations are on the order of 4–6 mm. Using Twiesselmann's (1941) method, the thicknesses of the bones are given in Table 2.

When compared to other European Middle Pleistocene hominid crania, such as Swanscombe (Le Gros Clark, 1964) and Steinheim (Weinert, 1936), the Reilingen vault bones do not appear to be very thick overall. However, the squamous temporal area and the postero-inferior angle of the parietal, where the torus angularis develops, is especially thick. The rest of the vault provides more moderate measurements. Overall, we find the Reilingen specimen to be within the range of variation for European Neandertals cranial thicknesses and above that of modern humans. It should be noted that this feature is known to display a great deal of intrapopulational variation in modern humans (Twiesselman, 1941).

The Reilingen specimen exhibits several ''archaic'' *H. erectus* apomorphies. Further, a few Neandertal apomorphies suggest an advanced morphology compared to the earliest known European ''archaic'' *H. sapiens*, e.g., Petralona and Arago. Although larger, this specimen is most similar to the middle Middle Pleistocene ''pre-Neandertal'' (Table 1) crania from Steinheim and Swanscombe.

Features such as large cranial capacity and high degrees of brachycephaly were once thought to indicate modern, or perhaps ''pre-sapiens'' (Boule & Vallois, 1957), morphology. As shown most dramatically by the finds at the Atapuerca SH site (Arsuaga *et al.*, 1993), these features occur in some early European ''archaic'' *H. sapiens* populations. Similar to the specimens from Steinheim and Swanscombe, the Reilingen vault shows additional features that tend more toward later Neandertal ''en bombe'' morphology than specimens of the earliest known European ''archaic'' *H. sapiens*.

Norma lateralis

The Reilingen skull is rather low and elongate when compared to most modern humans. The auriculobregmatic height is 104 mm. This value is clearly less than those observed in early modern humans of the Qafzeh-Skhūl group (116·0; std. dev.=3·6; *n*=5) and the European Neandertals (112·2; std. dev.=1·4 mm; *n*=6). It is just below the upper limit of the Zhoukoudian series (93·5–106·0 mm, *n*=5).

When viewed in the Frankfurt horizon, the earliest European and African ''archaic'' *H. sapiens* crania exhibit a vertically oriented upper occipital scale relative to a nearly horizontal nuchal planum (lower occipital scale). Although the Frankfurt horizon can only be estimated, it is reasonable to assume that the lower scale of the Reilingen

Table 2 Cranial thickness

Landmark measured (mm)		Reilingen	Steinheim	Swanscombe	European Neandertals (classic)	Modern French male n=100 (Twiesselmann, 1941)
TW4, parietal tuber	Right	7·0	6·5	10·0	8·0, std dev.=1·5, n=6	6·2, std dev.=1·0
	Left	6·5				6·3, std dev.=1·0
TW6, 5 mm posterior lambda		8·0		11·0	7·9, std dev.=1·7, n=6	6·5, std dev.=1·0
TW7, temporal squama	Right	4·5			3·5, std dev.=0·5, n=4	1·2, std dev.=0·4
TW8, cerebral fossa	Left	6·25		6·0	6·7, std dev.=1·5, n=8	4·1, std dev.=0·9
TW9, cerebellar fossa	Left	1·5		4·0	3·1, std dev.=2·0, n=5	1·35, std dev.=0·4
TW11, asterion	Right	8·5			6·1, std dev.=1·6, n=6	4·3, std dev.=0·9
	Left	8·0		8·0		4·4, std dev.=0·9

The Reilingen cranium and selected specimens. Key: TW$_n$ = Twiesselmann's measures. (Measurement of Steinheim from Hublin, 1988a.)
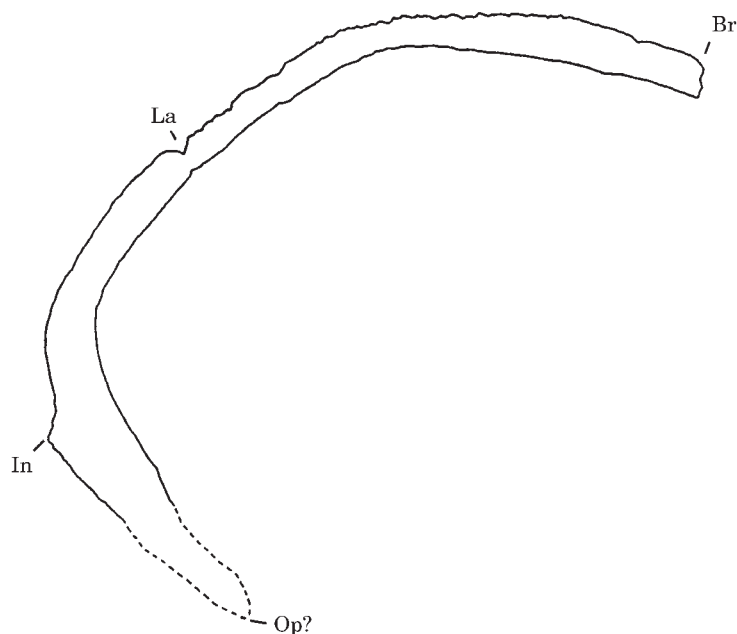
Figure 2. Mid-sagittal craniogram tracing of the Reilingen skull. Intersecting lines from anterior to posterior (right to left): bregma, obelion, lambda, and inion. Opisthocranion reconstructed.

specimen tilts supero-posteriorly from opisthocranion to inion, as seen in Figure 2. Thus, a lateral view of the Reilingen cranium finds the base of the upper occipital scale (i.e., at the level of inion) elevated relative to the position in earliest ''archaic'' *H. sapiens*. The inferior placement of inion in earliest ''archaic'' *H. sapiens* is more similar to modern humans than the condition seen in stage 2–4 Neandertals (Table 1). Thus, the ''out of Africa'' model might predict that a relatively short, and horizontal, lower occipital scale was preserved in the African ''archaic'' *H. sapiens* populations that had reached anatomically modern form by 100 ka.

As with Steinheim, Swanscombe, and later Neandertals, the portion of the Reilingen sagittal suture, from obelion to lambda, is absolutely and relatively shorter and more convex than that seen in earliest ''archaic'' *H. sapiens* specimens such as

Petralona and Kabwe. In this feature the Reilingen cranium presents an incipient occipital ''bun''. This arc segment is usually concave in *H. erectus* and earliest ''archaic'' *H. sapiens*.

The taxonomic value of this feature was questioned by Trinkaus & Le May (1982) who rejected it as a Neandertal trait because of its occurrence in other groups. In fact ''bun'' shape morphology is rather vaguely defined and difficult to measure (Ducros, 1967; Trinkaus & Le May, 1982). Indeed, what is specific to the ''classic'' Neandertal skull is the association of posterior elongation, great medial-lateral breadth, supero-inferior shallowness, and a convex upper occipital scale (Hublin, 1988*a*). In this respect the Reilingen skull is similar to Swanscombe, within the limits of ''classic'' Neandertal variation, and quite different from modern *H. sapiens* or Asian *H. erectus* (see Hublin, 1988*a*: Figure 1).

Norma occipitalis

Compared to modern humans the Reilingen skull is relatively low in posterior view. The index of the auriculo-bregmatic height on the maximum breadth (using Martin & Saller's [1957] landmarks, M20/M8 × 100) is 71·2. This is far below the values observed in the early modern humans of the Qafzeh-Skhūl group (80·6; std. dev.=4·1; n=5) and nearer to the lowest values of the European Neandertals (74·8; std. dev.=3·7; n=6) and the mean of the Ngandong series (72·2; std. dev.=2·9; n=3). It is equal to the index observed in the isotopic stage 5 ''early Neandertal'' (Table 1) Saccopastore 1.

The occipital view is intermediate between the clearly pentagonal shape observed in the primitive condition (e.g., *Homo erectus*) and the derived Neandertal ''en bombe'' shape. Laterally the temporal-parietal outline is relatively flat continuing inferiorly onto vertical, robust mastoid processes. More gracile, medially converging mastoid processes are seen in ''classic'' Neandertals. The combination of this morphology and a vault that is flattened between two weak parietal tubers is reminiscent of the Swanscombe cranium. We do not consider this morphology as being shared derived with modern humans or European ''prae-sapiens'' (*sic*), rather it appears to be a plesiomorphous feature for the Neandertal lineage (Hublin, 1982, 1988*b*).

The maximum breadth, 146 mm, is found between the supramastoid crests (reconstructed symmetrically). This low position of the maximum breadth is a primitive feature. Nevertheless, it should be noted that above this point the lateral walls of the braincase are sub-parallel and do not converge superiorly as seen in *Homo erectus*.

Parietal

It appears that these two bones were discovered virtually undamaged. However, a crack of recent origin in the right parietal is visible externally on the left side of the occipital margin (near lambda). This crack appears closed and may not extend across the bone to either the coronal or the squamosal suture. There is glue in it. The left parietal shows parallel lines, possible cut-marks, in the area of the temporal muscle insertion, they are somewhat smoothed over.

There are no parietal emissary foramina. Their frequency is variable in modern populations from 64·3% in Europeans (Le Double, 1903) to 88% in Melanesians (Billy, 1955). They seem to be absent in Neandertals (Vallois, 1958; Piveteau, 1970; Vandermeersch, 1981; Condemi, 1985, 1992).

The squamous/sagittal suture length index, 0·72, is approximately the same as seen in the Petralona and Steinheim crania. All three specimens present similar lateral contours. All are reminiscent of early ''archaic'' *H. sapiens*, exhibiting sagittal keeling on the anterior one-third of the sagittal suture. Therefore, the posterior view of the skull is more or less pentagonal, depending on the orientation of the outline. An outline passing through the left and right porion and the midpoint of the sagittal suture is rounded superiorly, not pentagonal. The parietal arch is low superiorly and wide mediolaterally. The asterionic area is obliquely flattened, giving the adjacent occipital area a rather elongated appearance. The bregma-asterion chord/biasterionic breadth ratio is 1·10. Day & Stringer (1982) offer 1·14 as both a maximum value for *Homo erectus* and a minimum value for anatomically modern humans. This value is lower than Day & Stringer's (1982) *H. erectus* value of 1·14 in both European ''archaic'' *H. sapiens* and African ''archaic'' *H. sapiens*. These values seem to indicate a widening of the vault without the concomitant rounding that occurs in anatomically modern humans; another indication of Neandertal platycephaly.

The superior-inferior shortness of the parietals is also expressed by other sagittal measurements. The sagittal chord is 104 mm and the sagittal arc is 111 mm. This latter value is within one standard deviation of Western European Neandertals (mean 115·6, std. dev.=5·9, n=8), but below that of the Near Eastern Neandertals (mean 124·7, std. dev.=7·1, n=3), and well below the modern mean (122·3 with std. dev.=8·7; French series of Olivier [1974]).

The Reilingen parietals are short and moderately convex with a parietal angle of 141·5°. This value is intermediate between the mean of Zhoukoudian *Homo erectus* (150·5°, std. dev.=4·1, n=4) and that of the ''archaic'' modern humans from Qafzeh and Skhūl (136·6°, std. dev.=1·7, n=3) and almost equal to the European Neandertal mean (141·8°, std. dev.=5·4, n=9).

While the superior surface of the two fused parietals is flattened (relative to modern humans), the slight keeling over the sagittal suture gives the midline a decided rise. From either an anterior or posterior orientation the ''intermediate'' pentagonal form of the Reilingen cranium is reminiscent of Steinheim and Swanscombe. The smoothed and rounded pentagonal vault of Stage 2 Neandertals foreshadows the ''en bombe'' form of Stage 3 and 4 Neandertals.

The pentagonal contour is most noticeable at the temporal lines due to the vault's acute transition from vertical side walls to roof. This angularity seems diminished from that of the ''early-pre-Neandertals,'' such as Petralona and Arago. ''Early Neandertal'' forms, such as Biache 1, have lost this side wall verticality entirely. The lateral protrusion of the calvaria in these forms approaches the true ''en bombe,'' platycephalic appearance of ''classic Neandertals''. The extreme platycephaly of Stage 4 Neandertals makes euryon nearly impossible to locate by eye. The Reilingen specimen does not appear to be as far along this morphological cline as the Saalian forms

(e.g., Biache 1). The parietal tubers (euryonic eminences) are easily found at the postero-superior margin of the temporal lines in approximately the same coronal plane as obelion.

The superior and inferior temporal lines of the Reilingen specimen may be somewhat abraded, but even so, they are faintly visible throughout their course. The temporal lines of ''classic'' Neandertals are less prominent. There is a distinct swelling on the right side of the Reilingen vault, emerging from the superior temporal line superior to asterion and extending posteriorly. This swelling is reminiscent of the ''angular torus'', a feature first described by Weidenreich for Asian *H. erectus*, but recently observed on the Bodo, Kabwe 1, Arago 47, and Petralona crania (Hublin, 1978*a*, 1986; Bräuer & Rimbach, 1990).

Temporal

Apart from damage to the medial portion of the petrous, the right temporal bone is virtually complete and undamaged (Figure 3). Overall this bone is more similar to early ''archaic'' *H. sapiens* than to ''classic'' Neandertals or anatomically modern humans. The outline of the temporal squama does not display the primitive angular pattern observed in *Homo erectus*, rather it is regularly arched. It also differs from the primitive condition in its proportions, short horizontal length (antero-posteriorly) and relatively high vertical height (superoinferiorly), versus long and low. Estimating the Frankfurt plane we find the maximum length of the temporal squama is 65·8 mm. If accurate, this measurement is roughly intermediate between the Zhoukoudian (69·6, std. dev.=4·9, n=5; Weidenreich, 1943) and Ngandong (73; Weidenreich, 1951) series means and the European ''classic'' Neandertal mean (62, std. dev.=5·0, n=8). It is below the modern Australian (67·1, std. dev.=6·9, n=28) and Eskimo

Figure 3. Reilingen temporal bone: inferior view. Top is anterior (photo: Fred Spoor).

(76·4, std. dev. = 4·8, *n* = 30) means cited by Elyatiquine (1995).

The height of the temporal squama above porion is 49·0 mm. This value is well above the European ''classic'' Neandertal mean (39·1, std. dev. = 3·9; Elyatqine, 1995). It is close to the value observed on Amud 1 (48; Suzuki, 1970) and within the range of variation of the Qafzeh-Skhūl ''archaic'' modern human group (44–52; McCown & Keith, 1939; Vandermeersch, 1981) and living populations (Australian 42·5, std. dev. = 4·4, *n* = 28; Eskimo 50·2, std. dev. = 4·4, *n* = 30; Elyatqine, 1995). (The height of the squama above auriculare is 45·0 mm.) The height to length ratio, 0·68, is near Qafzeh 9 (0·67; Vandermeersch, 1981) and modern values (European 0·69, *n* = 40; Schultz, 1915). This is well above the Zhoukoudian mean (0·50, std. dev. = 0·05, *n* = 7; Weidenreich, 1943) or Ngandong mean (0·47; Weidenre-

ich, 1951). It is also above the range of values observed in ''classic'' Neandertals (0·55–0·67; Heim, 1976). The Reilingen tall temporal profile is observed at Petralona, Atapuerca (SH site), and Steinheim.

Another way to estimate the relative height of the temporal squama is to compare it to the height of the vault (basion-bregma or auriculo-bregma). Elyatqine (1995) demonstrated that this ratio is above the modern mean in ''early-pre-Neandertals'' (e.g., Petralona) and ''pre-Neandertals'' (e.g., Steinheim) whereas this ratio declines in ''early Neandertals'' (e.g., Saccopastore I) and ''classic Neandertals'' (e.g., La Quina H5, La Ferrassie 1, La Chapelle-aux-Saints, or modern humans). In other words, the temporal squama is more involved in the elevation of the cranial vault in ''early-pre-Neandertals'' and ''pre-Neandertals'' than

in later ''early Neandertals'' and ''classic Neandertals''. With its low vault and relatively high squamosal, the Reilingen cranium clearly displays a typical ''pre-Neandertal'' condition.

The morphology of the Reilingen tympanic bone is primitive. The vaginal crest separates the anterior and posterior slope of the tympanic. This feature is observed throughout Neandertal evolution and in *Homo erectus*. The tympanic directly adjoins the mastoid process in modern humans.

The supramastoid crest is continuous with the inferior temporal line. The somewhat robust postglenoid and zygomatic processes are similar to the Steinheim cranium. Anterior to the glenoid fossa there is a strong articular tubercle and zygomatic process root. Posteriorly and medially, the postglenoid and entoglenoid processes show a robusticity common to ''archaic'' *H. sapiens.* The glenoid fossa and tympanic tube are not oriented obliquely forward as in African ''archaic'' *H. sapiens* (Bräuer & Leakey, 1986). The tympanic plate is robust, but not as robust or as long mediolaterally as in Kabwe 1 or Salé. The supramastoid crest extends less laterally over the auditory meatus than in African forms, such as Kabwe, but more than in ''early'' or ''classic'' Neandertals or anatomically modern *H. sapiens.* The shape of the auditory meatus is more elliptical (with the long axis vertically oriented) and less compressed than is the case for most *H. erectus* (but see Picq, 1990). Beginning around climatic isotope Stage 5, the transition to ''classic'' Neandertals is marked by the shift from an elliptical to a round external auditory meatus (Elyatqine, 1995).

Posteriorly, the supramastoid crest exhibits a strong tubercle of Waldeyer. Unlike modern humans, the root of the zygomatic process is not separated from the squama by a deep groove, i.e., the ''sulcus processus zygomatici'' of Weidenreich (1943). Rather, this process projects laterally in a sub-horizontal plane and its superior surface is wide and slightly concave as it extends transversely.

The overall primitive aspect of the Reilingen temporal zygomatic process is related to the development of the masticatory muscles. It is similar to that observed in ''classic'' Neandertals, but this morphology is also present in the most robust individuals of the Qafzeh-Skhūl group (e.g., Skhūl 4 and 9, and Qafzeh 1).

In comparison with the supramastoid crest, the mastoid crest is weak. It is regularly arched and does not present the highly angular pattern of the anterior mastoid tubercle described by Hublin (1978*b*) as characteristic of ''classic'' Neandertals. Nevertheless, the Reilingen circum-mastoid morphology is typical among European ''pre-Neandertal'' specimens.

The root of the mastoid process, from the posterior end of the external acoustic meatus to the most posterior point on the temporal bone proper, is 42 mm long, horizontally. The ratio of this length to that of the temporal squama is 0·64. This value is just below the ''classic'' Neandertal range (0·67–0·74; Vallois, 1969; Condemi, 1985). When compared to modern humans, the ''classic'' Neandertals are characterized by strong development of the mastoid root relative to the temporal squama. Vallois (1969) recorded 0·62 as the mean for this ratio in modern Europeans.

The Reilingen mastoid shows strong development relative to the squama. The mastoid process is not as obliquely oriented and reduced as in most ''classic'' Neandertals. It does not project strongly from the digastric groove. However, in spite of the strikingly different morphology, linear measurements of the mastoid process from the Frankfurt plane do not distinguish Neandertals as a lineage from modern humans (Vandermeersch, 1981; Trinkaus, 1983). Alternatively, Zoja (1864) measured the projection of the mastoid process from

the nearest point of the digastric groove. According to this technique, European Neandertals display an average projection of 7·1 mm (std. dev. = 1·3, and $n = 7$; Vallois, 1969), while the modern human average is 12·6 mm (Zoja, 1864). The tip, mastoidale, is broken off. The Reilingen mastoid length is estimated to be 8 mm. This places the Reilingen skull nearer Neandertals (within 1 std. dev.), as a group, than modern humans.

The Reilingen digastric groove is separated inferiorly from the stylomastoid foramen by a well marked ''step''. This is the primitive condition for *Homo*. In modern humans the digastric groove ends anteriorly at the level of the stylomastoid foramen. The strongly developed juxtamastoid eminence is reminiscent of, but less robust than, Stage 3 or 4 Neandertals.

The mastoid process is supero-inferiorly long but extremely narrow mediolaterally, more so than on most early ''archaic'' *H. sapiens* or anatomically modern *H. sapiens*. There is a relatively deep digastric groove, and the juxtamastoid eminence is prominent, but not extremely large. Its likely occipital contribution can be determined because this region is preserved on the left side of the occipital bone. This groove is clearly defined but is not as marked as, for example, Kabwe 1 or most modern humans. It is similar to Steinheim, both of which show more development than most Stage 3 and 4 Neandertals.

Parts of the mastoid surface appear to be thin bone. They have broken away from the postero-inferior surface leaving wormian tracks. These pits may have exposed the internal surface of mastoid foramina.

The base of the styloid process is present. It is important to note that the root of the styloid process is medial to the alignment of the digastric groove axis and stylomastoid foramen. This configuration is not observed in *H. erectus* and is rare among ''archaic'' *H. sapiens*. It seems to be a Neandertal apomorphy first seen among ''pre-Neandertals''.

For example, it is seen on Atapuerca AT 84a, AT 86, Steinheim, Biache 1, and is well marked on Stage 4 Neandertal specimens (Elyatqine, 1995).

More anteriorly it can be seen that the medial 2/5 of the carotid canal is exposed because its floor is broken away. The openings of the jugular foramen and the stylomastoid foramen are similarly degraded.

Occipital

Middle and Late Pleistocene hominid populations exhibit highly diagnostic occipital morphology (Hublin, 1988*a*). The Reilingen occipital bone demonstrates several clear affinities with Neandertals, for example: the unique combination of a broad and strongly convex occipital plane, a well defined suprainiac fossa, and a bilaterally, well-developed occipital torus (Hublin, 1978*a*, 1988*a*; Santa Luca, 1978).

Compared to modern humans, the biasterionic diameter is wide. This primitive feature does not discriminate any of the Neandertal stages from other contemporary ''archaic'' *Homo sapiens* populations or even from the ''archaic'' modern *Homo sapiens* Qafzeh-Skhūl group. The occipital plane is low and wide with a high metasterical angle on the lambdoid suture. The depressed and flattened lambdoid suture can be represented by the lambda-inion chord/biasterionic diameter ratio: 0·54. The convexity of the upper occipital scale is expressed in the Reilingen skull's subtense/chord ratio of the lambda-inion arc of 19·2. This value is intermediate between Stage 1 early-pre-Neandertals, such as Vértesszöllös, and the bulk of Stage 3 and 4 Neandertals (see Hublin, 1988*c*: Figure 1).

The relative shortness of the upper occipital scale in stage 3 and 4 Neandertals is probably not primitive, but is more likely an apomorphy related to an increase of the convexity of this part of the occipital

squama. Lambdoid flattening, as compared to earlier ''archaic'' *H. sapiens* in Europe, might also be due to increasing dolichocephaly (*norma lateralis*) and platycephaly (*normal occipitalis*) in Neandertals (Trinkaus & LeMay, 1982; Lieberman, 1995).

Our estimate of the Frankfurt plane places opisthocranion well above inion. This position would highlight strong curvature of the upper portion of the occipital, combined with superior rotation of the upper occipital scale. It seems to us that opisthocranion was very likely to have been situated above the suprainiac fossa, where the occipital angle is strongly flexed. Assuming a correct reconstruction of the opisthion, the occipital angle (lambda-inion-opisthion) is 113°. This value is below the European ''classic'' Neandertal range (115°–126°) and below the value for Swanscombe (119°). Nevertheless it is well above the values of stage 1 early pre-Neandertals, such as Petralona (92°) and Vértesszöllös (103°).

The upper part of the nuchal plane is strongly concave, especially the area of the semispinalis capitis muscle insertion. There is no genuine external occipital protuberance near inion, but there is a wide, triangular, and irregular *tuberculum linearum* (i.e., the meeting point of the superior nuchal lines), as is usually found on Stage 2, 3, and 4 Neandertals. If inion is set at the center of the *tuberculum linearum* (Hublin, 1978c), it is 11 mm superior to the internal projection of endinion. This condition is primitive relative to modern humans where the two points are usually coincident (Portela-Gomes, 1968). However, this feature is highly variable in modern populations. As already described in ''pre-Neandertals'' and ''Neandertals'' (Hublin, 1980), the semispinalis capitis insertion forms a localized pit on the left side of the *crista occipitalis externa* The missing right side does not allow verification of its symmetry. All of the muscular insertions in this area are well-marked.

The main branch of the inferior nuchal line is clearly defined above the insertions of rectus capitis posterior minor and major muscles, as is its anterior branch, between the rectus capitis posterior major and the obliquus capitis superior insertions. Medially there is a strongly projecting ridge which is the occipital lip of the juxtamastoid eminence. This eminence, medial to the digastric groove, is extremely well-developed in ''classic'' European Neandertals, sometimes projecting more inferiorly than the mastoid process.

The superior nuchal line is roughly straight between the two points of maximum projection of the occipital torus. These two points are situated above the center (i.e., mid-belly, of each semispinalis capitis muscle insertion scar). Laterally, the amount of projection decreases rapidly along the superior nuchal line. This torus is rather narrow and similar in shape to that of the Salzgitter-Lebenstedt Neandertal (Hublin, 1984). As often seen in ''classic'' Neandertals, the torus is not strong or projecting given the overall occipital robusticity. However it appears more significant when viewed as part of the occipital plane profile, especially the strong concavity of the upper part of the nuchal plane.

The lower part of the occipital plane displays a well-defined suprainiac fossa. This fossa extends horizontally between the two lateral points of maximum development on the occipital torus. It is an oval depression 38 mm long and 14 mm high. Its surface is irregular, with numerous pits. Its lower limit is marked by an irregular bony lip homologous to the supreme nuchal line in modern humans. The pattern of the suprainiac area appears more similar to ''classic'' Neandertals than in pre-Neandertal specimens, such as Swanscombe or Steinheim. The robusticity and derived appearance of the Reilingen suprainiac fossa may be due to the large size of this individual.

Cranial capacity

A silicone rubber brain endocast was produced from the available cranial fragments. It required total reconstruction of the frontal lobe and base, including portions of both cerebellar lobes, the brain stem, and anteromedial portions of the temporal lobe. These reconstructions were done with plasticene, and the missing portions were modeled on the basis of the complete Spy I, Spy II, and Kabwe I endocasts. (The Kabwe endocast is remarkably complete.)

Admittedly, this was a subjective process, which consisted of sculpting a frontal lobe, and other parts, that were congruent with RLH's experience in reconstructing fossil hominid endocasts. It was also a process which, compared to other manual methods, we believe led to a more accurate cranial capacity than by any other metric method, such as linear measurements or partial endocasts (e.g., Tobias, 1971). Only one reconstruction was attempted.

After the reconstruction was finished, the brain endocast was weighed in air on a balance accurate to 0·5 g. Then, the endocast was weighed again, submerged in water and attached to the balance by a cord; the second value was subtracted from the first. By Archimedes' principle, the resulting value is the volume of water displaced by the brain endocast. Eight such weighings were done, averaging 1428·75 ml, with a range of 1422–1434 ml. Rounding the mean value provides an estimate of 1429 ml. Given minor variations of shape of the brain stem, frontal lobe, the mean volume suggested is 1430 ml, plus or minus 10 ml. While we believe this to be an accurate reconstruction, it would be valuable to have an undistorted frontal lobe endocast from this time period and geographic location.

Gross endocranial morphology

Although most of the right occipital portion is missing, there is enough available curvature on the medial portion to ascertain that the right occipital pole does not protrude as far posteriorly as the left, thus the Reilingen hominid had a large left occipital petalia. Unfortunately, without knowledge of a possible frontal lobe petalia one cannot be certain whether this specimen follows the general pattern for fossil hominids, described by Holloway & de LaCoste-Lareymondie (1982), of a large lateral frontal petalia associated with a left occipital petalia. The available evidence for a petalia in the Reilingen specimen is concordant with an hypothesis of right handedness.

Cortical brain convolutions

As is the case for all fossil *Homo* brain endocasts, there are frustratingly few sulcal impressions that one can describe without equivocation. Comparing both sides, the left shows more detail. The lower limb of the postcentral gyrus on the left side suggests a strong postcentralis transversus and a postcentralis inferior some 30–40 mm posterior to the coronal suture, and about 15–20 mm posterior to the anterior branch of the middle meningeal vessel. Two faint and shallow grooves appear to be the marginal and angular gyri of the parietal lobe, but we do not believe these can be defined with any certainty. There are no clear indications of the angular or supramarginal gyri on either side.

There is a somewhat crescentic sulcus roughly 15 mm rostral to the occipital pole. Although there is a slightly concave interruption posteriorly, it would appear to be a typically modern lunate sulcus (*cf.* Connolly, 1950: 247, Figure 273–4). At roughly 16 mm rostral to the occipital pole, the medial end of this purported lunate sulcus shifts in a rostral direction and continues another 20 mm. This is probably the occipitalis transversalis sulcus leading into a

rostrad directed paraoccipitalis sulcus; however, the latter is poorly defined.

Caudally, and running through the occipital pole, there is a Y-shaped set of sulci, each roughly 1 cm in length. These grooves suggest parts of the lateral calcarine sulcus. This sulcus is sometimes seen to be broken. Medially, at roughly the same level as the proposed lateral calcarine sulcus, there is a distinct impression most similar to the retrocalcarine sulcus in modern humans. There is also a tiny sulcus about 1 cm inferior to the purported lateral calcarine sulcus which could be a remnant of the inferior occipital sulcus. Approximately 66 mm rostral and superior to the proposed lunate sulcus are some indistinct shallow grooves which suggest that a tortuous intraparietal sulcus may have been present. Rostrally, towards the anterior origin of the parietal lobe, approximately 66 mm rostral to the occipital pole, a case can be made for an intraparietal sulcus, accepting, however, that in *Homo* this sulcus is frequently tortuous.

From these observations, it appears that there are no indications of any retention of a primitive great ape pattern. If the lunate sulcus suggested here is indeed correctly identified, it is in a wholly modern human position, i.e., posterior and fragmented. The parieto-occipital fissure, separating the occipital and parietal lobes, is not visible on this endocast.

The longitudinal sulcus appears to flow mostly to the left into the transverse sinus. The estimated maximum length from the reconstructed frontal pole to the existing occipital pole on the left side is 171 mm. Maximal breadth is 138 mm, as occurs on the posterior part of the temporal lobe. The distance from bregma to the posterior rim of the foramen magnum is 133 mm. The vertical height measured from vertex to a plane of the most inferior aspect of the temporal lobe is 120 mm. The arc from lambda to bregma is 110 mm.

Meningeal pattern

The inferiomedial aspect of the temporal lobe on the right side has the middle meningeal vessel coming through the foramen spinosum as a single vessel, and then splitting into a middle and posterior branch approximately at the level of the sylvian fissure. The posterior branch appears very large relative to the medial branch, a characteristic of most fossil hominids, as seen in Figure 4. The vessels are relatively simple, not numerous, and without anastomoses. The arterial pattern is comparable with *Sinanthropus* #1, Locus L (Saban, 1984: 158, Figure A), Omo II (Saban, 1984: 178), and La Ferrassie (Saban, 1984: 198, Figure 150A), and most similar to Ehringsdorf (Saban, 1991).

The left side is somewhat more profuse than the right. The pattern is of the Type IIb of Giuffrida-Ruggieri (1912), whereas the Swanscombe endocast corresponds to Type IV (Le Gros Clark, 1964). These patterns are not particularly valuable as taxonomic guides given the wide degree of variability and overlapping of types within and between hominid taxa. The most that can be said is that the pattern seen on the Reilingen endocast is compatible with Neandertals and other populations of ''archaic'' *Homo sapiens*.

Cephalometrics

Two morphometric analyses found the Reilingen cranium to sort more closely with *H. sapiens* than *H. erectus*, especially ''archaic'' *H. sapiens*. First, a Principal Components ordination of 5 linear measurements (Figure 5) taken from the Reilingen cranium, 26 fossil *Homo* crania, and 2 modern samples (Tables 3 and 4) determined that the Reilingen cranium most closely resembles the Petralona cranium and other early ''archaic'' *H. sapiens*.
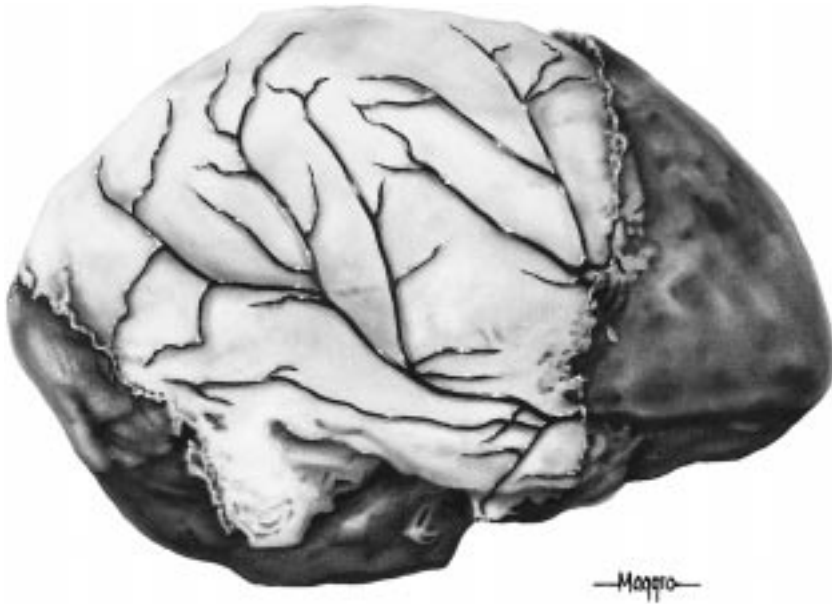
Figure 4. Reconstructed endocast. The Reilingen endocast exhibits features typical of ''archaic'' *Homo sapiens*. As with most pre-modern human fossil endocasts, the posterior limb is the dominant middle meningeal branch.

Finally, in a statistical comparison of three dimensional line tracings of the nuchal torus of the Reilingen specimen to average *H. erectus* (*sensu lato*) and average (Caucasian adult) *H. sapiens* tracings, along with the nuchal tori of Petralona, Steinheim, and Salé, the Reilingen specimen showed significantly stronger affinities with the modern human average than with an *H. erectus* average. The comparison of these space curves involved sizing, best-fit matching, and collecting point-to-point residuals between the tracings (Dean, 1993; Dean *et al.*, 1996).

Conclusion: the Reilingen specimen is a Stage 2 Neandertal

Given the uncertainties surrounding its stratigraphic origin (see Ziegler & Dean, 1998), the Reilingen specimen could conceivably have been recovered from a stratum dating to the Middle or Late Pleistocene. On this basis alone, i.e., irrespective of morphology, the Reilingen specimen might possibly be assigned to ''early-pre-'', ''pre-'', ''early'', or ''classic'' Neandertal status, or even modern human. We suggest that the last possibility can be excluded both on the basis of its lack of derived modern morphological features, primarily those related to vault shape, and the occurrence of clear Neandertal apomorphies. Thus, based on the morphological evidence alone, the remaining question is to which Neandertal stage is the Reilingen specimen best allocated.

The Reilingen cranium presents several features that are plesiomorphous for Stage 3 and 4 Neandertals and/or for modern humans. The skull is low, absolutely and relatively, compared to its width. Its maximum breadth is at the supramastoid crests. The parietal coronal arc is short and wide with a short sagittal chord. There is no genuine external occipital protuberance. Inion is well separated from endinion. Basally, the morphology of the anterior part of the digastric groove is primitive. The
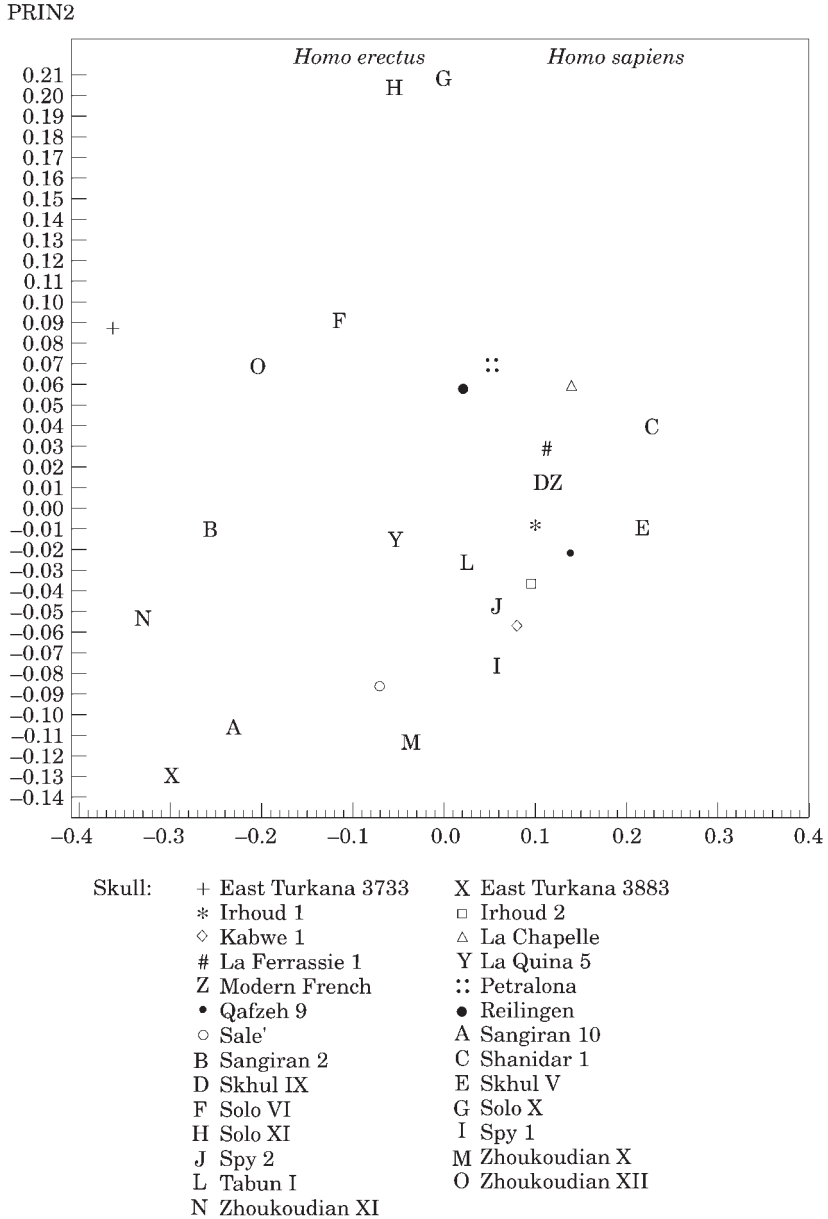
PRIN2

Figure 5. Principal components analysis. The Reilingen cranium clusters nearest ''archaic'' *H. sapiens* specimens with Stage 3 and 4 Neandertals as next nearest neighbors. See text for explanation.

tympanic plate is also primitive in its posterior slope and separation of the vaginal crest from the mastoid process. The Reilingen cranium shares the presence of an angular torus with European robust ''early-pre-Neandertals,'' such as the Middle Pleistocene specimens Arago 47 and Petralona. Its pentagonal shape in occipital view is intermediate between Stage 1 and Stage 3 Neandertals.

Table 3 Reilingen interlandmark linear measurements and arcs

Measurement	Martin no.	Howells' abbrev.	Reilingen (mm)
Biasterionic diameter	(12)	(ASB)	120
Bistephanic diameter	(10b)	(STB)	113
Bregma-lambda subtense	(—)	(PAS)	18·5
Bregma-lambda arc	(27)	(PA)	111
Bregma-lambda chord	(30)	(PAC)	104
Bregma-left asterion arc	(—)	(—)	169·5
Bregma-left asterion chord	(—)	(—)	132·5
Bregma-obelion arc	(—)	(—)	74·0
Bregma-obelion chord	(—)	(—)	72·1
Bregma-right asterion arc	(—)	(—)	167·5
Bregma-right asterion chord	(—)	(—)	132·5
Bregma-subtense fraction	(—)	(PAF)	56·5
Lambda-subtense fraction	(—)	(OCF)	53·5
Lambda-inion arc	(28(1))	(—)	73·5?
Lambda-inion chord	(31(1))	(—)	65·5?
Maximum cranial breadth*	(—)	(—)	146
Obelion-lambda chord	(—)	(—)	37·2
Occipital chord	(31)	(—)	93
Occipital arc	(28)	(—)	120
Parietal angle	(—)	(—)	142
Parietal subtense	(—)	(—)	18·5
Right Porion-bregma chord	(—)	(—)	120·8
Sagittal suture	(—)	(—)	110
Squamous suture	(—)	(—)	80

*At superior margin of squamous suture. ?=estimated.

The Reilingen specimen displays a series of derived features that it shares with ''classic'' Neandertals. Specifically, these features are related to vault shape, especially the external occipital morphology. In posterior view the outline of the skull is incipiently ''en bombe,'' showing an intermediate shape between the primitive pentagonal shape observed in *Homo erectus* and the rounded shape of Stage 4 Neandertals. This feature is reminiscent of the Swanscombe Middle Pleistocene specimen.

Other more detailed features highlight the Reilingen cranium's affinities to Stage 2 Neandertals. On the temporal, the combination of primitive features (its proportions and the mastoid process) and derived features (configuration of the styloid process, digastric groove, and stylomastoid foramen) is reminiscent of Stage 2 Neandertals. The Reilingen occiput exhibits several derived

Stage 2 Neandertal conditions including: a wide and markedly convex occipital plane, a bilaterally developed occipital torus, an extensive suprainiac fossa, and lambdoid flattening.

The lack of key apomorphies suggests that this specimen should not be attributed to the Stage 3 or 4 Neandertal groups. Moreover, the ''en bombe'' morphology, as seen in posterior view, is not as fully expressed as in Stage 3 ''early-Neandertals''. Nor does the mastoid process project greatly from the bottom of the digastric groove or display the degree of reduction observed in Stage 4 Neandertals. The occipital and temporal lips of the juxtamastoid eminence do not strongly project downward. The juxtamastoid eminence often projects more inferiorly than the mastoid process on Stage 3 and 4 Neandertals. The gracile juxtamastoid area, combined with the lack of an anterior

Table 4 Comparative sample of linear measurements and arcs

No.	Fossil Crania (measurements in mm)	Maximum skull breadth	Bi-asterionic breadth	Parietal arc	Parietal chord	Lambda-inion chord
1	Reilingen	144·5	120·4	112·5	103·5	64·7
2	East Turkana 3733	142·0	119·0	85·0	82·0	57·0
3	East Turkana 3883	140·0	115·0	95·0	90·0	48·0
4	Sangiran 2	141·0	124·0	94·0	91·0	54·0
5	Sangiran 10	140·0	120·0	98·0	93·0	50·0
6	Zhoukoudian X	150·0	111·0	113·0	106·0	54·0
7	Zhoukoudian XI	145·0	113·0	92·0	86·0	51·0
8	Zhoukoudian XII	147·0	115·0	95·0	91·0	60·0
9	Solo VI	147·0	123·0	101·0	96·0	62·5
10	Solo X	158·0	127·0	105·0	102·0	72·0
11	Solo XI	151·0	126·0	102·0	97·0	71·0
12	Kabwe 1	145·0	133·0	121·0	113·0	58·0
13	Salé	139·0	118·0	109·0	103·0	55·0
14	Petralona	161·0	124·0	114·5	105·0	63·5
15	Tabun I	141·0	120·0	117·0	105·0	60·0
16	Shanidar 1	154·0	118·2	131·0	118·0	68·4
17	La Chapelle	153·0	116·4	119·0	113·5	67·0
18	La Quina 5	138·0	112·0	108·0	101·0	60·0
19	La Ferrassie 1	158·0	127·0	120·0	112·0	63·0
20	Spy 1	144·3	120·0	120·0	110·0	57·5
21	Spy 2	153·2	124·0	119·0	110·0	58·0
22	Irhoud 1	149·5	121·0	122·0	117·0	63·0
23	Irhoud 2	161·0	124·0	121·0	115·0	59·0
24	Skhūl V	143·0	122·0	131·0	120·0	66·0
25	Skhūl IX	145·0	120·0	120·0	112·0	64·0
26	Qafzeh 9	140·0	111·0	145·0	129·0	62·0
27	Modern French	143·3	111·9	122·3	110·3	65·4

mastoid tubercle, leads us to conclude that the Reilingen specimen exhibits primitive morphology and is not as derived as Stage 3 or 4 Neandertals. In addition, when compared to Stage 3 or 4 Neandertal fossils, the Reilingen vault is absolutely and relatively lower, a feature associated with its relatively short parietal chord. Additionally, the occipital angle is smaller and the convexity of the occipital plane is moderate.

Other vault features suggest that the Reilingen cranium is most similar to Stage 2 ''pre-Neandertal'' specimens. Stage 2 specimens show the earliest ''classic'' Neandertal vault features, especially on the parietal and occipital bones. As with acknowledged Stage 2 Neandertal specimens, the Reilingen cranium does not present some of the temporal features seen in ''early'' and ''classic''

Neandertals. This suggests that the final increase in platycephaly of the Eemian Neandertals, in association with the extreme prognathism of Weichselian Neandertals, did not occur together in Stage 2 Neandertals. Most convincing is that the Reilingen cranium shares the Stage 2 Neandertal apomorphic position of the styloid process relative to the stylomastoid foramen and digastric groove. We assert that the Reilingen skull is best inserted in the series of European fossil hominids of the middle Middle to late Middle Pleistocene, antecedent to ''early'' Neandertals of oxygen isotope Stage 7.

The existence of the Reilingen hominid, and other Stage 2 Neandertals, supports the ''Accretion Model'' of Neandertal Middle Pleistocene evolution. The Neandertal

lineage appears to have diverged morphologically from its African contemporaries no later than the middle Middle Pleistocene, ca 400 ka. Environmental changes may have caused genetic isolation of the Neandertal lineage at this time (Hublin, 1990, 1991).

The accretion process of Neandertal apomorphies does not constrain taxonomic interpretations of the Neandertal lineage. The proponents of the ''regional continuity'' model may view the accretion of Neandertal features as supportive evidence. However, we see only sporadic and atomistic examples where any Neandertal features may possibly show penetrance in the earliest anatomically modern Europeans. Thus, we do not agree that there is considerable evidence that ''continuity exists in the gene pool across [the Neandertal-Modern] transition in Europe'' (Smith, 1984: 198; Frayer, 1992; Frayer et al., 1993; Wolpoff & Caspari, 1997). We currently see no definitive evidence bearing on the occurrence or nature of a putative Neandertal-Modern ''transition'' in Europe.

Similarly, this model provides no direct support, nor does it refute, the major replacement (Stringer, 1994; Stringer et al., 1997), or species status (Carbonell et al., 1995; Howell, 1994; Rightmire, 1988, 1990), of some or all Neandertal populations. Instead, the primary conclusion one draws from the Accretion Model is that gene flow into Europe was restricted from the middle Middle Pleistocene well into the Late Pleistocene.

Acknowledgements

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