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The human chin revisited: what is it and who has it?

Although the presence of a ''chin'' has long been recognized as unique to *Homo sapiens* among mammals, both the ontogeny and the morphological details of this structure have been largely overlooked. Here we point out the essential features of symphyseal morphology in *H. sapiens*, which are present and well-defined in the fetus at least as early as the fifth gestational month. Differences among adults in expression of these structures, particularly in the prominence of the mental tuberosity, are developmental epiphenomena and serve to emphasize the importance of studying this region in juveniles whenever possible. A survey of various middle to late Pleistocene fossil hominids for which juveniles are known reveals that these features are present in some late Pleistocene specimens assigned to *H. sapiens*, but not in all of the presumed anatomically modern *H. sapiens* (i.e., Qafzeh 8, 9, and 11). The adult specimens from Skhūl, as well as the adult Qafzeh 7 specimen, are similarly distinctive in symphyseal morphology. Neanderthals are quite variable in their own right, and they as well as other middle to late Pleistocene fossils lack the symphyseal features of *H. sapiens*. Some of the latter are, however, seen in the Tighenif (Ternifine) mandibles.

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Introduction

More than two centuries ago, Blumenbach (1775) identified the ''chin'' as being among the most fundamental of the features that he considered uniquely human. Of course, when Blumenbach presented his discussion of ''what distinguished humans,'' it was in the context of ''compared to other extant primates.'' But with the acceptance in the nineteenth century of hominid fossils as real entities, and the subsequent documentation of a well-represented and diverse human fossil record, features such as the chin, which had a specific kind of significance when the primary goal of the taxonomist was to distinguish between humans and other extant primates, became cast in a different light. Rather than being static entities, as would be expected of organisms that had been specially created, morphological characteristics became incorporated into scenarios of evolution. With regard to the chin, which essentially became synonymous with ''a prominence at the front of the mandible,'' the general concern among paleoanthropologists was with how an ape-like jaw could be converted to that of *Homo sapiens* (Hrdlička, 1911; Robinson, 1913; Wallis, 1917; Gregory, 1922; Howells, 1959; Enlow, 1982; Stringer *et al.*, 1984; Daegling, 1993).

Discussion of the human chin has been approached from several different perspectives. Anatomical descriptions have focused on the protrusiveness of the symphyseal region, with the mounded structure being identified in extant humans as the ''mental protuberance'' (Johnston & Willis, 1954), the ''mental eminence'' (Lieberman, 1995), the ''mental osseum'' (Bräuer, 1984; Rosas, 1995), or the ''tuber symphyseos'' (Hublin

& Tillier, 1981; Inke, 1967). Thus defined, the mental protuberance may continue laterally on each side to some extent as a thickening of the inferior margin of the corpus. In some individuals, each lateral extremity of the mental protuberance may bear a blunt ''corner,'' which has been referred to as a ''mental tubercle'' (Johnston & Willis, 1954; Rak, 1998) or ''tubercula lateralia'' (Hublin & Tillier, 1981; Inke, 1967). Above each lateral extremity and to each side of the mental protuberance, lies a depression, or ''mental fossa'' (Wolpoff, 1996), which would appear to exist as a default of the midline field of bone being elevated or protrusive. Collectively, the mental protuberance and lateral extremities, especially if they bear tubercles, have been identified as the ''mental trigon'' (Rak, 1998), the ''mental trigone'' (Smith, 1984), or, if the structure is restricted quite inferiorly along the corpus, the ''trigonum basale'' (Bräuer, 1984). Just below the alveolar margin, the bone may be curved inward, presenting a shallow depression that has been referred to as the ''incurvatio mandibularis'' (Hublin & Tillier, 1981), the ''incurvatio mandibulae'' (Rosas, 1995), or the ''impressio subincisiva externa'' (Inke, 1967). Although there is obviously much morphological detail to be recognized in the symphyseal region of *H. sapiens*, the human chin has frequently been identified solely on the basis of the general protrusiveness of the symphyseal region (Lieberman, 1995; Smith, 1984; Wolpoff, 1980; Lam *et al.*, 1996).

The development of the human chin is typically described as a postnatal phenomenon, a simple matter of bone resorption near the alveolar margin, with concomitant deposition of bone more inferiorly (Enlow, 1982; see also Aiello & Dean, 1990; Daegling, 1993; Lieberman, 1995). Individual differences or variations in chin development result essentially from differential rates of resorption *vs.* deposition (Enlow, 1982).

It is the basal protrusion which has, of course, been the primary criterion for identifying the mental protuberance; and this, in turn, has become the primary element in the identification of a chin. From this perspective, it is perfectly reasonable to conclude that ''chins are a notoriously variable character, as many modern humans lack them'' (Lieberman, 1995:174). And when the focus of attention in this region is the degree of symphyseal protrusion anteriorly—which is often judged against the vertical plane of the lips or incisors (see Enlow, 1982)—there might, indeed, appear to be ''chinless'' and ''almost chinless'' human beings.

The evolution of the human chin has been discussed in various ways. Hrdlička (1911) ventured the suggestion that this structure evolved as a result not of the specific development of a protrusion, but of the reduction of the dental arch (which essentially left the protrusion behind as the anterior margin retreated). This idea was elaborated upon by Robinson (1913), who proposed that it was the demands of the tongue and laryngeal musculature that maintained mandible length inferiorly as the region above it supposedly retreated posteriorly. Gregory (1922) added to these notions the possibility that the chin provides space at the front of the jaw that is necessary for the enlarging crowns and roots of incisors and canines. Howells (1959) reiterated Robinson's (1913) proposition and suggested further that bone thickening, which ultimately produced the chin, must have evolved in order to reinforce the front of the jaw against masticatory stresses (which, in apes, were absorbed by the internal buttress known as the ''simian shelf''). Reisenfeld (1969) thought that he had refuted this kind of functional explanation by inducing in mice what he believed to be a chin by extracting the continually growing anterior teeth and severing the muscles of mastication (which did, of course, have the effect of eliminating

masticatory stress at the symphyseal region). Wolpoff (1980) adopted a different stance on the subject by speculating that the appearance of the chin was correlated with expansion of the neurocranium and a concomitant shift of the temporal muscles to a more medial angulation. Most recently, Daegling (1993) surveyed the various functional interpretations put forth to explain the presence of the chin, and concluded that the best was "the hypothesis that the human chin represents a structural response to resist vertical bending in the coronal plane."

Regardless of the proposed mechanisms behind the appearance of the chin as a structure, the language of the literature is invested with the notion of an evolutionary trend, in which a perceived increase in swelling of the symphyseal region ultimately leads to the formation of the typical human chin. Thus, it is common to read of the supposed existence of incipient chins in various Neanderthals (themselves considered merely an archaic, primitive version of *H. sapiens*). These include adult specimens from Guattari, Šipka, and Vindija (Lam *et al.*, 1996; Lieberman, 1995; Smith, 1984; Wolpoff, 1980; Wolpoff *et al.*, 1981) and the Archi Neanderthal child (Ascenzi & Sergi, 1971*a,b*; Mallegni & Trinkaus, 1997; Stringer *et al.*, 1984). Hence, because discussions of later human evolution are often informed by anticipation of discovering such a transformation series, it is not surprising to find statements such as: "[W]hile mental eminences and trigones are markedly more developed in modern *H. sapiens* (even the EMH [=early modern human, especially from Skhūl and Qafzeh] sample), a clear trend towards the EMH condition is present in the LN [=late Neanderthal] group" (Smith, 1984:190). Even some of the larger mandibles from the middle Pleistocene Sima de los Huesos sample have been portrayed as having chinlike symphyseal regions, which have been described as displaying "a well-developed trigonum mentale and

a conspicuous incurvatio mandibulae" (Rosas, 1995:550).

The impetus for the present review came from two different and unexpected sources. First, in the course of conducting a twenty-year analysis of the skeletal remains of perinatal individuals from the Punic site of Carthage (*n*>650 individuals; Schwartz & Houghton, in preparation), one of us (JHS, unpublished data) discovered that it was possible to identify very small fragments of the symphyseally unfused mandibles of these highly immature individuals on the basis of specific features of this region: namely, a continuous everted margin that proceeds along the edge of the symphysis and laterally around along the inferior edge and that, consequently, subtends a deep fossa. Second, as a result of realizing that the configuration of the brow in some of the most familiar of the supposed early "anatomically modern" *H. sapiens* (i.e., from Skhūl and Qafzeh) was not bipartite (cf. Stringer *et al.*, 1984), as it is in late Pleistocene and extant representatives of this species (Schwartz & Tattersall, 1999*b*), we came to realize that these same fossils were also not *H. sapiens*-like in mandibular symphyseal morphology. For the record, we must admit that when we first studied the Skhūl specimens, we were not initially struck by these disparities. But it was during our second round with these specimens, after we had benefited from studying at first hand many more middle to late Pleistocene fossil hominids, that the differences in details of brow and mandibular morphology became apparent between these specimens (as well as some specimens from Qafzeh) and extant *H. sapiens*.

Here, we present the results of an extended developmental and morphological overview of the symphyseal region in *H. sapiens* that focuses on distinguishing between those features that are invariably present from fetal to adult stages and those that represent individual variation. We

suggest that only the constellation of morphological detail present from fetus to adult (in which *H. sapiens* appears to be strongly derived) should be referred to as a chin—although we wonder, given the history of broad usage of this term, whether the retention of this term as an anatomical descriptor is actually necessary or even constructive. We also review the middle to late Pleistocene hominid fossils from Europe, the Levant, and northern Africa, with an emphasis not only on morphology, but on the ontogenetic context. We conclude that one can identify a chin, complete with detailed morphology, in all late Pleistocene fossils traditionally assigned to modern *H. sapiens*, but not in all early modern humans from this time period; some of the latter possess a configuration that differs from those of both modern *H. sapiens* and *H. neanderthalensis*. In addition, the Tighenif mandibles provide further evidence that it is the specific morphology of the symphyseal region, rather than its simple protrusion or lack thereof, that is potentially phylogenetically and systematically significant.

Materials

Our developmental series of extant *H. sapiens* from second trimester through birth are in the permanent study and teaching collections of the anatomy department of the University of Pittsburgh School of Dental Medicine (UPD; $n=10$) and the American Museum of Natural History (AMNH; $n=8$). These series are comparable in detail and essentially identical to collections in medical schools (e.g., see the series at Washington University) and are consistent with the descriptions and illustrations in standard textbooks (e.g., Johnston & Willis, 1954). Since we are not presenting these data as novel discoveries, but are rather using them as the basis for our descriptons and comparison, corroboration of our descriptions is readily available. One of us (JHS) also studied a sample of five hundred recent *H. sapiens* (Department of Anthropology, AMNH) and, as an outgroup, three hundred nonhuman anthropoid primates (Department of Mammals, AMNH) (Table 1). The middle to late Pleistocene fossils hominids that we have analyzed to date and that preserve enough of the mandibular symphyseal region to be relevant to this discussion are listed in Table 2. For the sake of simplicity, and in order to facilitate reader recognition, we present a rather traditional grouping of these specimens in Table 2, identifying them conservatively either as ''Neanderthal,'' ''*Homo sapiens*,'' or ''Other,'' even though we believe there are more satisfactory alternatives.

As is usually the case with fossils, most of the available specimens are of adult individuals. Nonetheless, the later human fossil record does contain an important representation of younger individuals. The youngest fossil individual in our sample is the 10-month-old Neanderthal from Amud (Rak *et al.*, 1994). The probable age range for the Skhūl child and the typical Neanderthal children [from Gibraltar (Devil's Tower), Peche de l'Azé, and Roc de Marsal] is 3–4 years (see Dean *et al.*, 1986; Zollikofer *et al.*, 1995), although an older age of 5–6 years has also been suggested (Tillier, 1983).

We shall first discuss the morphology and development of the symphyseal region in extant *H. sapiens* and of those specimens that are thought of as closely resembling them. We then turn to Neanderthals, and, finally, to the remaining middle to late Pleistocene fossil hominids. We refer to the central and lateral incisors as I1 and I2, and the anterior and posterior premolars as P1 and P2.

Results and discussion

Extant Homo sapiens
In adults (Figure 1), the symphyseal region bears a variably long and raised vertical keel

Table 1 Human and other anthropoid specimens at the American Museum of Natural History used in this study★

Nonhuman anthropoid primates
  New and Old World Monkeys
      Ateles geoffroyi ($n=19$)
      Cebus apella ($n=20$)
      Cercopithecus cephus ($n=19$)
      C. mona ($n=1$)
      C. neglectus ($n=2$)
      C. pogonias ($n=7$)
      Colobus polykomos ($n=6$)
      Macaca fascicularis ($n=20$)
      Mandrillus sphinx ($n=12$)
      Papio anubis ($n=1$)
      P. cynocephalus ($n=7$)
      Presbytis entellus ($n=3$)

  Hominoids
      Hylobates agilis ($n=39$)
      H. hoolock ($n=14$)
      Gorilla gorilla ($n=21$)
      Pan troglodytes ($n=35$)
      Pongo pygmaeus ($n=14$)

Recent *Homo sapiens*
  Africa (sub-Saharan; $n=71$)
  East Asia ($n=80$)
  China ($n=25$)
  Korea ($n=6$)
  Japan ($n=13$)
  Ainu ($n=4$)
  Siberia (Indian Point) ($n=32$)
  Australia
      Aborigine ($n=26$)
  Europe ($n=70$)
      Hungary ($n=9$)
      Czech—Bohemia ($n=10$)
      Austria ($n=10$)
      Germany ($n=13$)
      Italy ($n=8$)
      "Yugoslavia" ($n=10$)
      Greece ($n=10$)
  India ($n=26$)
  North America (Arctic; $n=139$)
      Thule ($n=33$)
      Near Ipiutak (Point Hope, Alaska) ($n=12$)
      Ipiutak (Point Hope, Alaska) ($n=46$)
      Tigara (Point Hope, Alaska) ($n=48$)
  North America (Sub-Arctic, Southwest; $n=51$)
      Native American, Utah, New Mexico ($n=30$)
      Arizona ($n=21$)
  South America
      Bolivia, Chile, Peru ($n=41$)

★A complete list of specimens is available upon request.

that lies along the midline. This keel, which originates at or just below the alveolar margin, becomes more prominent inferiorly as it fans out laterally along the somewhat distended inferior margin of the mandible. In some individuals it terminates in variably thickened, but not discretely separate, "corners" (the lateral tubercles). When present, each blunt terminus of the distended inferior margin lies well anterior to the mental foramen, which, in turn, lies variably anterior to the second premolar (see also Aiello & Dean, 1990; Daegling, 1993; Lieberman, 1995). Together, the symphyseal keel and the distended inferior margin form an inverted, roughly "T"-shaped structure; it is at the junction of the keel and distended inferior margin that a mental protuberance is identified. A variably shallow, scallop-shaped depression (mental fossa) lies to each side of the central keel. These mental fossae emphasize the keel as well as the distended inferior mandibular margin below. As can be observed even among the handful of specimens illustrated in Figure 1, variation exists among individuals in the degree to which these various features are expressed. However, the essential aspects of shape, location, and morphological detail of the keel, protuberance, distended inferior margin, and mental fossae, are maintained throughout.

The constellation of consistent features just described for the adult is present (and its details crisply delineated) by at least the fifth fetal month (Figure 2). Although the halves of the mandible are still unfused across the midline at this gestational age, one can clearly observe that the vertical symphyseal margin of each half is raised or everted, and that this vertical ridge is confluent with a similarly everted inferior margin that diminishes in prominence posteriorly. Each everted marginal cresting system defines a deep fossa. During subsequent intrauterine growth, the two mandibular halves come together at the

Table 2   **Middle to late Pleistocene hominid mandibular specimens used in this study**

Specimen	Country	Age (ka B.P.)
Homo sapiens		
Abri Pataud	France	22·0
Brno 2, 3	Czech Republic	26·0
Chancelade	France	17·0?
Cro-Magnon 1, 2, 3	France	ca. 30?
Dolní Věstonice III, XII, XIV, XV, XVI	Czech Republic	26–29
Engis 1 (adult)	Belgium	?
Grimaldi (Grotte des Enfants, Balzi Rossi)	Italy	ca. 36
Hahnofersand	Germany	ca. 36
Isturitz (includes children)	France	18–30
Oberkassel (male, female)	Germany	15?
Ohalo 1, 2	Israel	ca. 19
Předmostí 3, 4 (casts)	Czech Republic	ca. 26
Qafzeh 1, 3, 6, 7, 8, 9, 11 (subadult)	Israel	ca. 92–95
Skhūl I (child), II, IV, V, VI, VII	Israel	80–100+
Svitavka	Czech Republic	25–30?
Vogelherd 1, 2	Germany	ca. 32
Neanderthal		
Amud (child and adult)	Israel	40–50
Archi (child)	Italy	?
Ehringsdorf 1009/69, 1010/69	Germany	ca. 320?
Engis (child)	Belgium	?
Feldhofer Grotto	Germany	ca. 40
Gibraltar 2 (child)	Gibraltar	50?
Grotta Guattari 2 and 3	Italy	50–60+
Kebara (child and 2)	Israel	ca. 60
Krapina 51, 53, 54, 55, 56, 57, 59	Croatia	ca. 130
La Chapelle-aux-Saints	France	50+
La Quina [adult (5) and child]	France	ca. 65
La Ferrassie	France	60–70?
Le Moustier (subadult)	Germany	ca. 40
Montmaurin	France	150–200?
Ochoz	Czech Republic	?
Pech de l'Azé (child)	France	45–55
Regourdou	France	?
Roc de Marsal (child)	France	50+
Saccopastore	Italy	120–130
Saint-Césaire	France	36
Šipka (juvenile, cast)	Czech Republic	?
Spy 1 and 2	Belgium	?
Subalyuk (adult)	Hungary	60–70?
Tabūn C1	Israel	34
Tabūn II	Israel	?
Vindija 75/206, 76/231, 76/226	Croatia	ca. 40+
Zafarraya	Spain	ca. 30
Other		
Arago 2	France	400?
Biache 2 (cast)	France	150–175?
Bilzingsleben	Germany	280–400
Jebel Irhoud 3 (cast, child)	Morocco	90–125++
Mauer	Germany	ca. 500
Rabat (Thomas Quarry)	Morocco	ca. 400
Tighenif (Ternifine) 1, 2, 3	Algeria	ca. 700?

symphysis, with the inverted ''V''-shaped gap between them closing in a supero-inferior direction (i.e., from the region of the presumptive alveolar crest down to the inferior margin of the jaw) (see also illustration in Johnston & Willis, 1954:296). At this stage of growth, the mental protuberance is represented merely by the juncture of the inverted ''T'' that emerges with the formation of a single midline symphyseal ridge and its intersection with the everted inferior margin. In individuals in whom the two mandibular halves have closed up but have not totally obliterated the symphyseal gap, one can sometimes observe a shallow inverted ''V'' indenting the inferior margin at its midline (Figure 2). It is also important to note that the everted margins and the mental fossae retain their integrity throughout growth in spite of the bone alteration that takes place around them in conjunction with tooth crown and crypt expansion.

Postnatally, the features that are so well delineated in the fetus become softened and less sharply defined (Figure 3). In two-year-olds, for instance, the symphyseal keel is faint below the alveolar region. The keel is even less crisply defined in five-year-olds, in whom the mental fossae are also shallower as well as less expansive. The mental protuberance of postnatal individuals is, however, more prominent than in perinatal individuals, not only as a forward projection, but also as a generally triangular eminence with its base seated along the inferior margin of the jaw (forming the so-called trigonum basale). When viewed from below, the front of a young child's mandible is quite thick anteroposteriorly (=buccolingually) in the area subtended by the variably developed lateral tubercles, although immediately lateral the bone is thinner (also see metric analysis by Zollikofer et al., 1995). In addition to an overall enlargement of the mandible, including in its superoinferior depth, it is the continued softening or blunting of some features (such as the keel and

fossa) and, at the same time, the potential enlargement of other features (such as the mental protuberance and lateral tubercles), that results in the variation we see among adults. Further, any increase in depth of the mandible with concomitant expansion of the domain of alveolar bone (Enlow, 1982) would account for the absence in some individuals of any trace of the keel near the alveolar border—precisely because alveolar bone is a cellular derivative of tooth-producing stem cells and not of presumptive mandibular osteoblasts (e.g., see Ten Cate & Mills, 1972).

If we apply the term ''chin'' to the development of a prominent mental protuberance alone, then those (e.g., Lieberman, 1995) who describe some humans as lacking a chin, as well as others (specifically, Enlow, 1982) who define chin development as the resorption of bone near the alveolar margin with concomitant deposition of bone more inferiorly, are, in general, correct. But, as we illustrate here, the size of the region of the mental protuberance, which can vary from one individual to the next, is independent of those features—the inverted ''T'' and its attendant mental fossa—that are established fetally. In this context, Enlow's observation (i.e., that differential bone resorption superiorly in the symphyseal region, along with bone deposition more inferiorly creates a protuberance that projects farther forward than the alveolar region), is exactly what one would expect in the development of those features that vary individually in adults, but not in the formation of the symphyseal details seen in the fetus.

Late Pleistocene Homo sapiens

The inverted ''T'' and associated mental fossae are found in specimens from the late Pleistocene sites of Barma Grande, Brno, Chancelade, Cro-Magnon, Dolní Věstonice, Grimaldi, Isturitz, Oberkassel, Ohalo, Předmostí, and Svitavka (see Figure 4). In many of these Upper Paleolithic individuals,
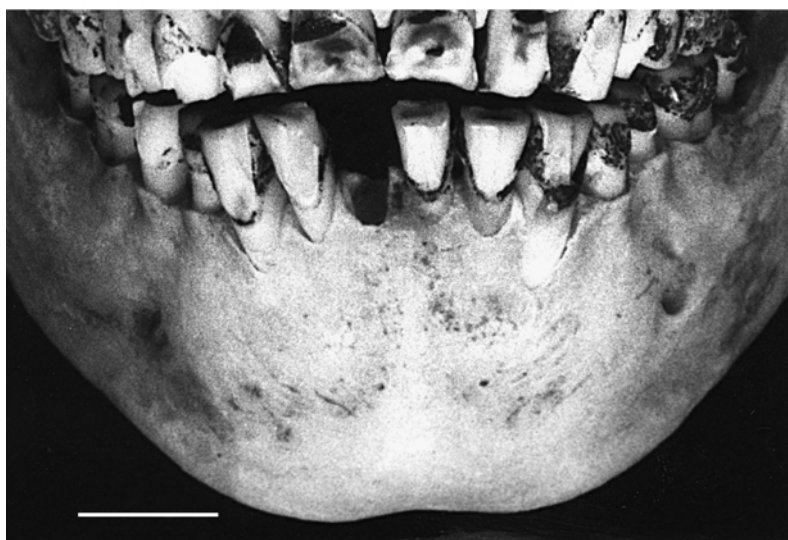
the mental trigon/protuberance is expansive, as well as protrusive, and often (e.g., Brno, Předmostí, Okerkassel) exceeds that seen in the most markedly endowed individuals in our sample of extant *H. sapiens*. The Isturitz sample, which contains a number of juveniles of varying ages, as well as old adults, is particularly interesting in terms of what is apparently a populational development variant: the ''cleft chin.'' As seen in Figure 5, individuals from this site have an inverted midline ''V''-shaped cleft that parts the inferior margin with varying degrees of openness and upward extension. As inferred from our study of extant *H. sapiens*, the simplest and developmentally most reasonable interpretation is that in these individuals from Isturitz, as well as in others from the site not illustrated here, coalescence of the mandibular halves did not proceed fully down from the alveolar crest to the inferior margin. Symphyseal clefting among individuals simply reflects the differing degrees to which the symphysis fused along its length. Aside from this developmental peculiarity, however, in every other detail of morphology, the Isturitz mandibles are typically *H. sapiens* in possessing the inverted ''T'' and mental fossae.

Middle to Late Pleistocene Homo sapiens *from the Levant*

In this sample, only the adults Qafzeh 8 and 9 and the subadult 11 present any indication of having had an inverted ''T'' and mental fossae (Figure 6). The adult Qafzeh 7 does not possess these features, nor does any individual from the broadly contemporaneous site of Skhūl, including the child, Skhūl I (Figures 7 and 8). These observations are interesting in light of the fact that of this group only Qafzeh 9 and 11 may have borne bipartite brows, whereas the supraorbital margins of the adult specimens from Skhūl, and of Qafzeh 6, are definitely smoothly continuous (Schwartz & Tattersall, 1996b).

The intact symphyseal region of the Qafzeh 11 subadult bears a long, thin central keel that begins its gentle rise a short distance below the alveolar margin (Figure 6). Toward the inferior margin of the mandible the keel fans out bilaterally into a short, broad, and somewhat protruding triangular mental protuberance, which becomes most protrusive just prior to curving into the less distended inferior margin. Shallow mental fossae are also discernible on either side of the keel, and the mental foramen lies just anterior to the root of P_2. In inferior view, although the front of the jaw is not squared off as it can be in *H. sapiens*, the symphyseal region is more thickened anteroposteriorly than the short stretch of bone on each side of it, posterior to which the corpus, in turn, becomes thicker.

The symphyseal regions of the adults Qafzeh 8 and 9 are, unfortunately, somewhat damaged (Figure 6). However, in Qafzeh 9 the bone on each side of the damaged midline appears to have been inflected outward, and the inferior margin of the symphyseal region would have been somewhat projecting. In the even more poorly preserved Qafzeh 8 mandible there is in concert definite evidence of a raised mental protuberance lying close to the slightly distended inferior margin. The latter two features together present the configuration of an inverted ''T.''

Figure 1. Mandibles of recent adult *Homo sapiens* to illustrate the basic configuration of the mental protuberance and trigon. Top, UPD #95 (provenence unknown); middle, AMNH 99/108 (Thule, Smith Sound, Alaska); bottom, UPD #66 (Indo-Pakistan?). Although the degree to which these features are pronounced, all three possess paired mental fossae and a clearly defined central keel that thickens at the mental tuberosity and fans out along the margin of the symphyseal region, terminating bilaterally in variably thickened ''corners.'' Bar=1 cm.

In contrast to Qafzeh 8, 9, and 11, Qafzeh 7 (Figure 7) presents a distinctive symphyseal configuration. Immediately below the alveolar crest lies a superoinferiorly short but moderately deep depression, which is laterally confined to the region of the incisor roots. The remainder of the symphyseal region is adorned with a low, teardrop-shaped bulge. The apex of this bulge arises within the subalveolar depression and its body broadens toward the inferior margin of the mandible. The sides of this bulge slope gently and smoothly into the contour of the surrounding bone of the corpus. The incisors overhang the subalveolar depression and the bulge presents a continuous and gently backwardly tilted profile. Consequently, when seen in profile, the subalveolar depression represents the space between the somewhat procumbent incisor region above and the longer slope of the symphyseal bulge below. In inferior view, although the latter bulge is noticeable, it is also the case that, buccolingually, the bone of the corpus is fairly uniformly thick throughout its length. The mental foramen lies under the region of P_2.

Tillier (1979) has described the mandible of the juvenile (6–8 years?) Qafzeh 4 as having ''modern'' symphyseal features, including mental fossae, a mental trigon, and lateral tubercles. The illustration she provides portrays a reconstructed symphyseal region that preserves a reasonable amount of identifiable morphology. Of note is the presence of two well-developed depressions that lie virtually at the inferior margin of the jaw, each on either side of the midline, with each reaching its maximum height well lateral to the midline. Because they are depressions, they leave between them what appears to be a small elevated region of bone low down in the midline. As seen in profile, however, this midline structure does not protrude beyond the normal surface of the bone itself. Posteriorly, as preserved especially well on the right side, the depression extends below a swollen region beneath the dm_2 that must correspond to the enlarging P_2 in its crypt. These depressions are strongly reminiscent of those seen in the Archi 1 Neanderthal child (see discussion below and Figure 12). Superiorly, the bone around the root of the not fully erupted right permanent central incisor is markedly indented or creased. By default, this creates the impression that the bone around this depression is elevated, although in reality it is actually a smooth, unembellished surface. Clearly, Qafzeh 4 does not display the salient features of the symphyseal region typical of *H. sapiens*, which are especially well defined in young children. As such, Qafzeh 4 cannot be regarded as a juvenile precursor of the more mature Qafzeh 8, 9, and 11. Perhaps it reflects the juvenile state of the adult represented by Qafzeh 7.

The adult specimens from Skhūl that preserve the anterior portion of the mandible (II, IV, and V) are not similar to extant *H. sapiens* and related fossils. Rather, they resemble Qafzeh 7 (Figure 7). Although there is individual variation in the degree to which the symphyseal region is broad and deep (it is most accentuated in Skhūl IV, less so in Skhūl V, and least in Skhūl II), each specimen possesses some amount of subalveolar depression as well as some swelling of the symphyseal region. In all three

Figure 2. Fetal specimens of *Homo sapiens* to illustrate the early stages of development of the mental trigon. Top right, 5 months (AMNH 99/7321); top left, 6 months (AMNH 99/7322); middle, 7 months (AMNH 99/7323); bottom, 8 months (AMNH 99/7324). The right and left contributions to the central keel, which are seen coalesced or coalescing across the symphysis (from top to bottom) in older specimens, are well-developed in the 5 month fetus. In all, the raised inferior margin and mental fossae are also clearly differentiated. Bar=1 cm.
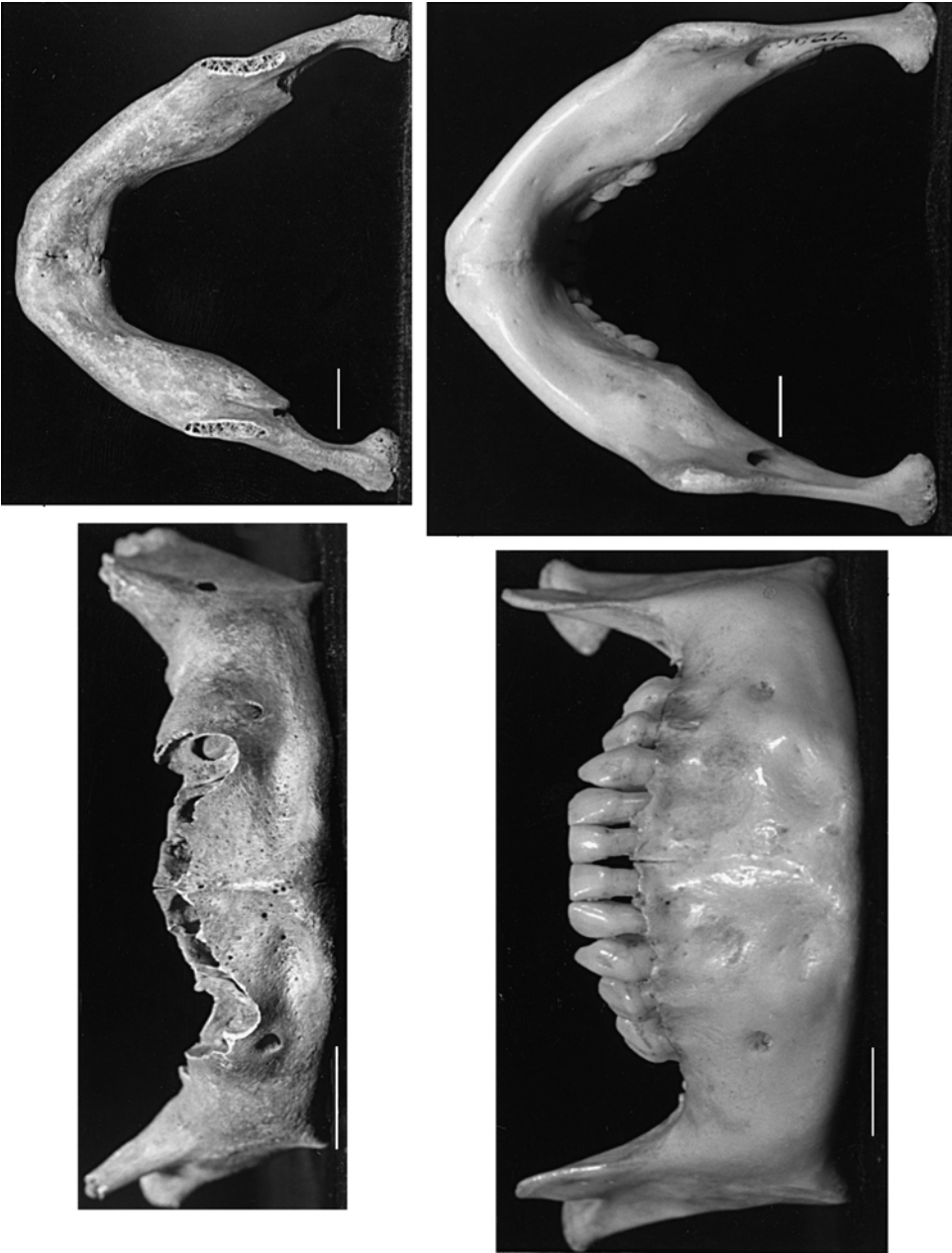
Figure 3. Mandibles of recent juvenile *Homo sapiens* to illustrate the essential features of the symphyseal region. Top, left (anterior view) and right (inferior view), 2 years old (AMNH, Education Dept, uncatalogued); bottom, left (anterior view) and right (inferior view), 5 year old (AMNH 99/7799). The central keel, which broadens at the mental tuberosity, fans out inferiorly, terminating bilaterally in blunt "corners." The inferior views demonstrate the thickness of the mandible in the symphyseal region and the impact of the marginal attributes of the mental protuberance on mandibular shape. Bar=1 cm.
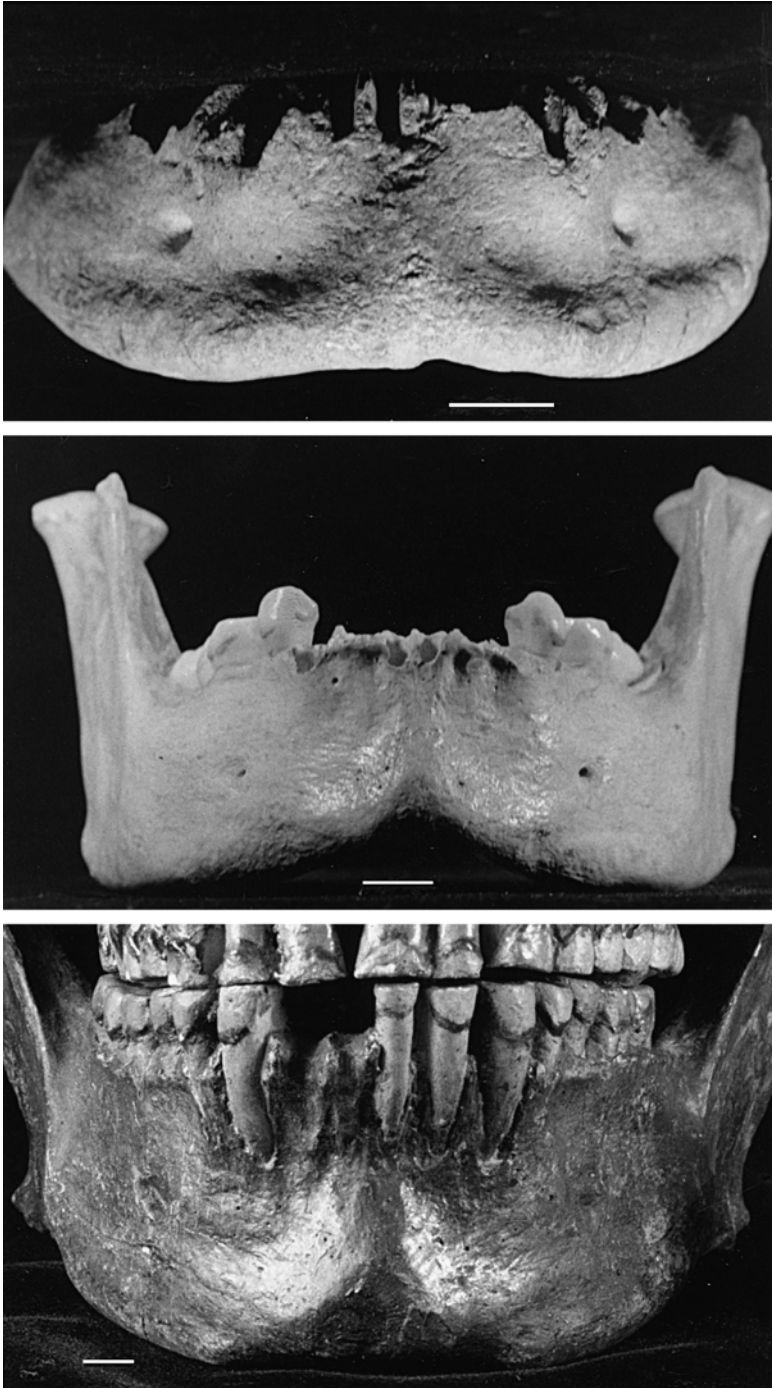
Figure 4. Mandibles of late Pleistocene *Homo sapiens*. Top: Cro-Magnon 3 [Musée de l'Homme (MH)]; middle: Abri Pataud (MH); bottom: Předmostí 3 (cast, Anthropos Institute, Brno). Although there is variation in degree of expression of the inverted "T"-shaped configuration of the symphyseal region, all specimens possess a central keel, thickened inferiorly placed mental protuberance, distended inferior margin, and mental fossae. Bar=1 cm.

Figure 5. Mandibles of late Pleistocene *H. sapiens* from Isturitz. Top: Isturitz 68 [Musée des Antiquités Nationales (MAN)]; bottom: Isturitz 70 (MAN). Each displays a low central keel, thickened inferior margin, and mental fossae. Each also possesses a cleft indenting the inferior margin at the midline that corresponds to the incompletely fused symphysis seen in fetuses (see Figure 2). Bar=1 cm.

specimens, the inferior margin of the symphyseal region is elevated somewhat relative to the plane of the inferior margin of the rest of the corpus. In the less complete Skhūl II mandible, a definite subalveolar depression lies immediately below the incisor alveoli; inferiorly, the bone of the front of the jaw is gently rounded. In the more complete Skhūl IV and V mandibles, a configuration comparable to that observed in Qafzeh 7 is more clearly discernible: there is a subalveolar depression, from which emanates a low, teardrop-shaped bulge that flows into the surrounding bone (rather than an inverted "T" delineated by mental fossae). In Skhūl V, the subalveolar depression is exaggerated by crushing, especially above and to the

right of the midline, as well as by an alveolar margin that was reconstructed to overhang the symphyseal region too severely; and to the left of the midline, the inferior margin is also damaged. The mental foramen lies under P_2 in Skhūl II and V, and under M_1 in Skhūl IV. In addition, in Skhūl V, a distinct and peaked inferior marginal tubercle lies below the level of the first molar and thus posterior to the mental foramen; a similar structure lies slightly more anteriorly in Skhūl II, beneath the mental foramen. In inferior view, and regardless of the degree of swelling of the symphyseal bulge, the bone of the corpus of each specimen is essentially uniformly thick buccolingually throughout its length.

If one were to define the possession of a chin purely on the basis of the development of a symphyseal protrusion or bulge, without taking the details of morphology into consideration, then one would certainly identify a chin in Qafzeh 7 and all adult Skhūl specimens (e.g., McCown & Keith, 1939; Smith, 1984; Stringer *et al.*, 1984; Wolpoff, 1980, 1996). Clearly, however, while in these specimens the symphyseal bulge can plausibly be assumed to have resulted from bone deposition and the subalveolar depression from bone resorption—because these are the only osteogenetic processes available for skeletal modification—neither Qafzeh 7 nor the adult Skhūl specimens possess the details of symphyseal morphology seen in *H. sapiens*. Since we know that the symphyseal morphology of adult *H. sapiens* is even more clearly delineated in young individuals, similar details in children from Qafzeh and Skhūl would be required to demonstrate that the symphyseal bulge of Qafzeh 7 and the Skhūl adults are versions of the chin in modern humans. As discussed above, however, the juvenile Qafzeh 4 specimen does not display the features of juvenile *H. sapiens*. This also appears to be the case with the Skhūl I child.

Although the specimen is heavily reconstructed in some areas, bone is preserved on the right side of the Skhūl I child's mandible at least as far as the midline of the root of the right first deciduous incisor, as well as internally across the symphysis at least as far as the region of the left di_2 (Figure 8). This makes it possible to determine accurately the morphology, thickness, and curvature of the symphyseal region. In contrast to juvenile *H. sapiens*, the Skhūl I mandible is broad and somewhat arcuate from side to side across the region of the anterior teeth, and, in profile, this region is slightly convex. In further contrast to extant *H. sapiens* of similar age, but as in Neanderthals (see discussion below and Zollikofer *et al.*, 1995), the anterior region of the Skhūl I mandible is

essentially uniformly thick in inferior view, with maximum thickness being achieved farther back along the corpus. In addition, since on the right side the bone extends externally almost as far as the symphysis as well as superiorly to a point significantly below the alveolar crest, it is evident that this specimen lacked a mental fossa, at least on that side. Since this bony surface is not concave with an increasingly everted medial contour, but is essentially flat, it is equally clear that the symphyseal region bore neither a keel nor a protrusion of any kind. The large mental foramen lies very posteriorly, under the bony septum that separates the roots of adjacent deciduous molars.

Aside from the impressions created by the roots of the teeth, the symphyseal region of the Skhūl I child's mandible is devoid of significant morphology. Like the Qafzeh 4 child, it thus lacks in comparable parts the distinctive and easily identifiable morphological details of juvenile *H. sapiens*. This observation is particularly revealing because the diagnostic features of the symphyseal region of *H. sapiens* are more pronounced in younger than in older individuals. Consequently, the absence of these features in the Skhūl I child certainly provides evidence of significant developmental differences between this individual and extant *H. sapiens* of similar age, as has also been demonstrated to be the case with regard to dental growth rates in the Skhūl I child *vs. H. sapiens* (Smith *et al.*, 1997).

If the Skhūl I child had become a typical Skhūl adult, then the developmental differences between the entire Skhūl assemblage (with which, on morphological grounds, we would include the Qafzeh 7 adult) and *H. sapiens* would have been evident from childhood. However, one cannot accept without question the biological affinity of the Skhūl I child with the adults from the same site. Indeed, in its general shape, disposition of cusps, and presence and orientation of the
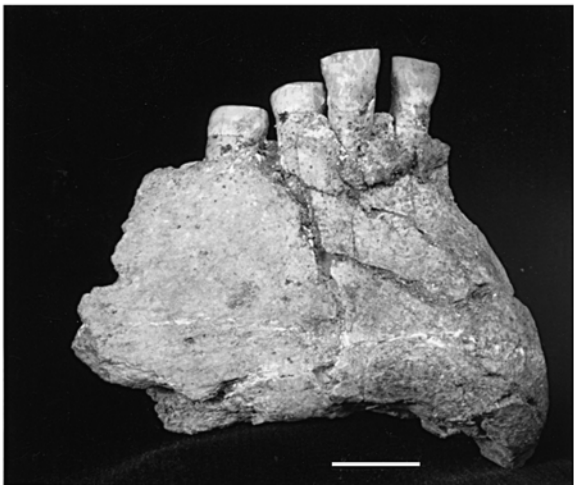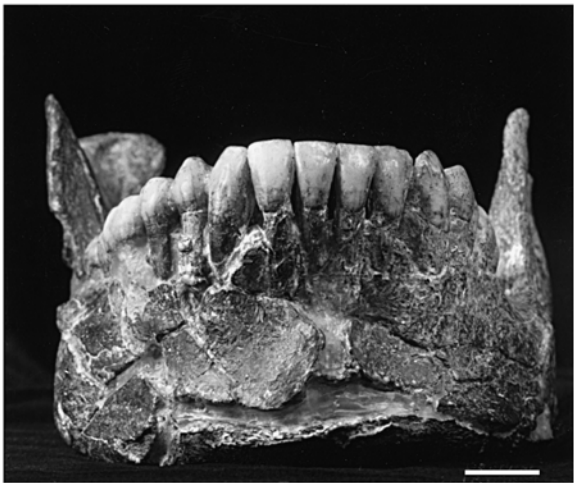
''deflecting wrinkle'' (elongate centroconid), the child's M_1 is a good match for the M_1 of Tabūn C1 while, unfortunately, such details of morphology of adult Skhūl M_1's are not preserved. Thus we cannot be certain of the juvenile state from which adult Skhūl mandibular morphology emerged. Nonetheless, given that the distinctive features of the symphyseal region in *H. sapiens*, so salient in younger individuals, diminish in clarity with growth and bone remodeling, we feel that we can at least hypothesize that, in their juvenile mandibles, the Skhūl (and Qafzeh 7) adults would not have been configured as in *H. sapiens*. Rather, we suggest that, as in various Neanderthal specimens (see below), the bulge observed in the Skhūl adult and Qafzeh 7 specimens was created through a process of bone deposition upon a morphologically featureless symphyseal region, while the subalveolar depression would have been produced by bone resorption in the region of the incisor root tips. However, even if one were to claim that the symphyseal bulge could have been derived from the configuration seen in the fetuses and juveniles of *H. sapiens* (i.e., the inverted ''T'' and attendant mental fossae), one would have to admit that the subsequent and total obliteration of this configuration was achieved by a process of development that differed significantly from the extant hominid in terms of the regions and interactions of the domains of bone resorption and deposition.

On the basis of morphological dissimilarity, then, we must conclude that Qafzeh 4 and Skhūl I are, morphologically, not specimens of *H. sapiens*, as also appears to be the case with regard to all Skhūl adults and Qafzeh 7.

Neanderthals
Although variable in its verticality, the anterior surface of the adult Neanderthal mandible is very broad and, if not flat, is often slightly arced from side to side (Figure 9; see also e.g., Wolpoff, 1980:285). In some specimens, this broad surface may be adorned inferiorly by a pair of peaked or angular distentions of the inferior margin of the mandible (identified here as ''inferior marginal tubercles''). When present, the inferior marginal tubercle lies below the mental foramen, which, in turn, lies quite posteriorly, beneath either M_1 or the bony septum separating the mesial alveolus for this tooth from the alveolus for P_2 (see Krapina 59 and Spy 1 in Figure 9; see also Wolpoff, 1980:285). In some specimens, the inferior margin of the anterior mandibular plane is elevated. There may also be a shallow subalveolar depression coursing below, if not also across, the entire region of the outwardly bowed incisor roots; the more procumbent the incisor roots, the more they overhang and emphasize the subalveolar depression. In some specimens, the region below the subalveolar depression may be slightly and broadly swollen, providing a smooth curve from side to side in frontal view and a gently convex profile (e.g., see Spy 1 in Figure 4; see also Grotta Guattari 2 in Wolpoff, 1980:285). Clearly, although there is variability within the Neanderthal sample in the presentation of the features

Figure 6. Mandibles of adult specimens from Qafzeh with the symphyseal configuration of *H. sapiens*. Top: Qafzeh 11 [Tel Aviv University (TAU)]; middle: Qafzeh 9 (TAU); bottom: Qafzeh 8 (TAU). Qafzeh 11 possesses a thin central keel that is bound on each side by a mental fossa and which arises from below the alveolar region and expands into a well developed, inferiorly placed mental protuberance that expands somewhat laterally into a thickened inferior margin. Qafzeh 9 preserves a thickened inferior margin, above which the bone becomes everted toward the midline, suggesting that a central keel had been present and bounded by mental fossae. The more fragmentary Qafzeh 8 displays a thickened inferior margin. Bar=1 cm.
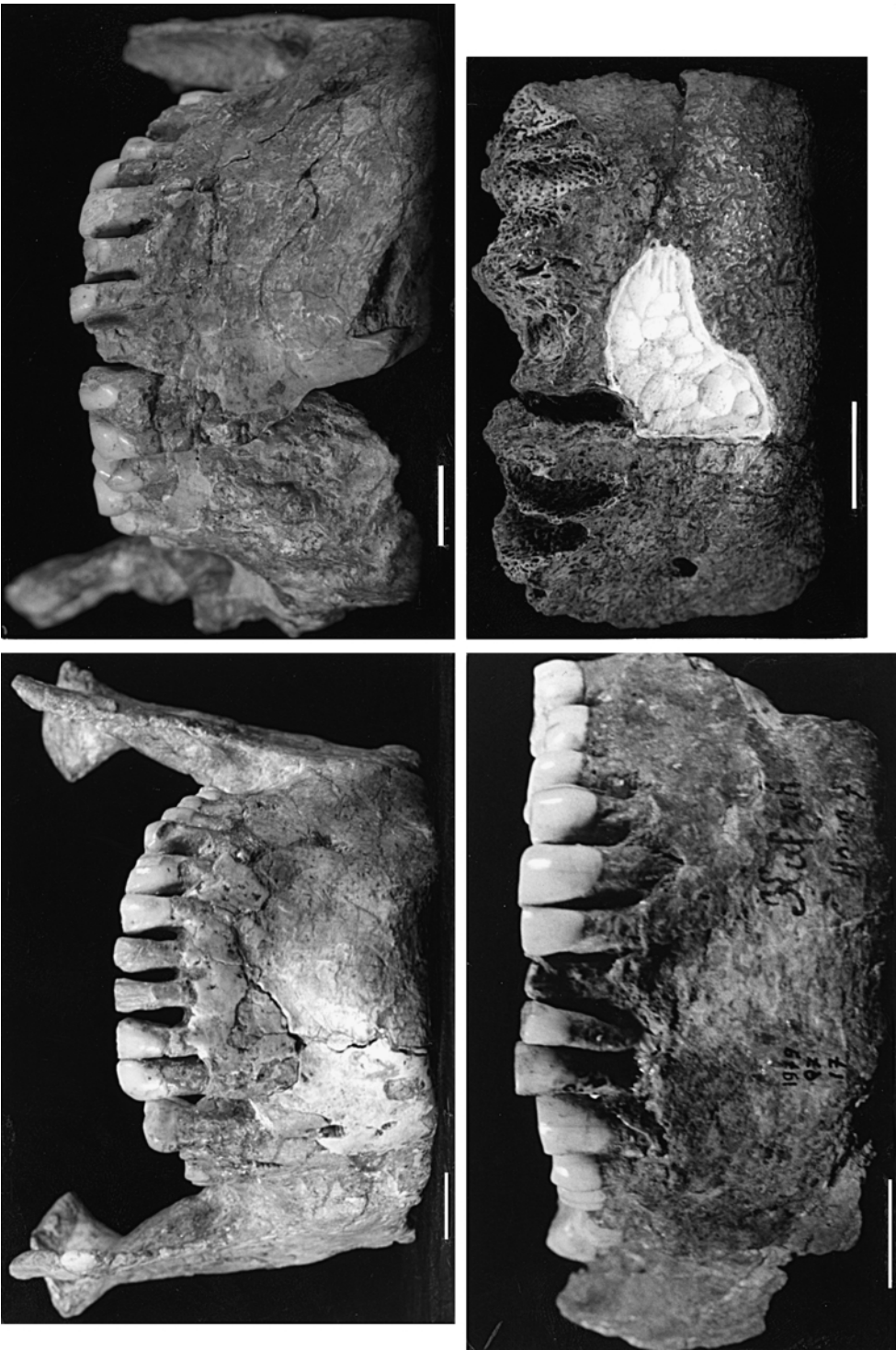
Figure 7. Mandibles of adult specimens from Skhūl and Qafzeh with similar symphyseal configurations. Top row left, Skhūl V [Harvard Peabody Museum (HPM)]; top row right, Skhūl IV (TAU); bottom row left, Skhūl II (HPM); bottom row left, Qafzeh 7 [Institut de Paleontologie Humaine (IPH)]. Although differing from one another in degrees of expressions of features, all mandibles are anteriorly broad and display a subalveolar depression below. Skhūl IV and V and Qafzeh 7 clearly possess a subalveolar bulge that is protrusive above the inferior margin and which lacks a central keel and attendant mental fossae. Skhūl II lacks mental fossae and an inferiorly thickened margin. Bar=1 cm.
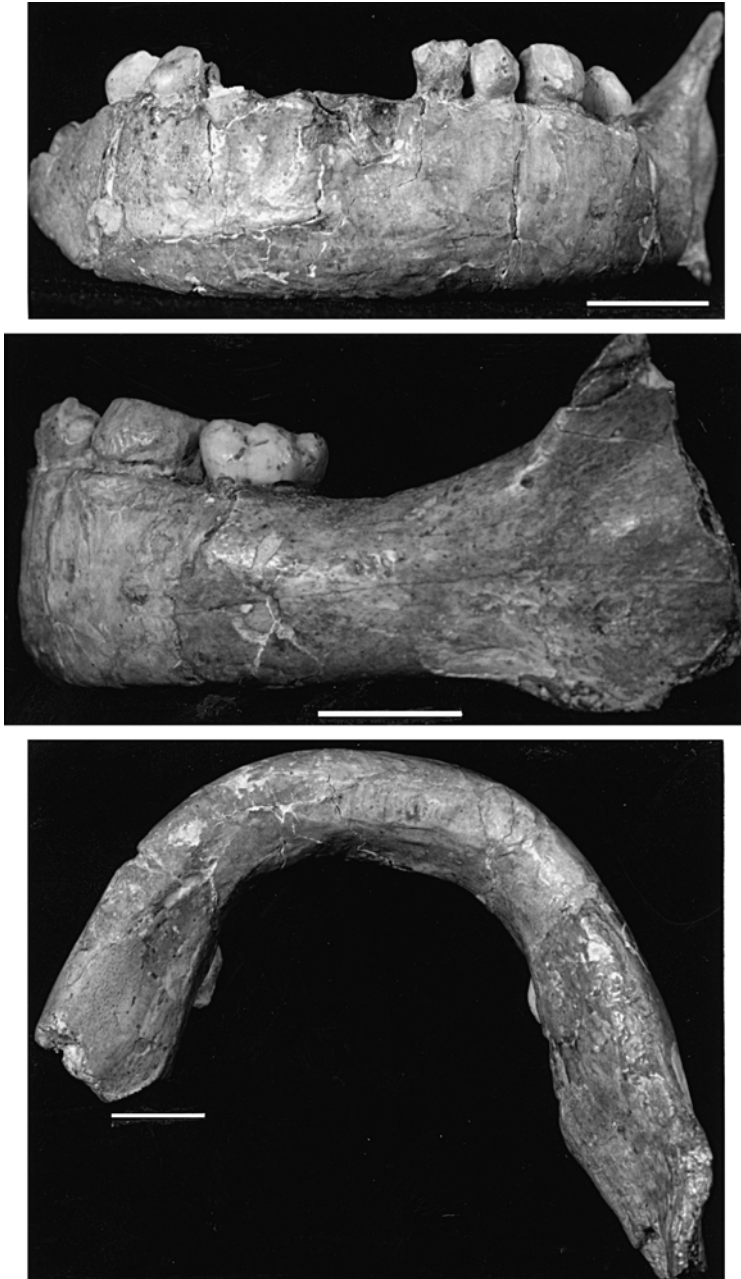
Figure 8. Mandible of Skhūl I (TAU); top (anterior view), middle (left lateral view), and bottom (inferior view). The reconstruction of the front of the jaw is based on the right side being preserved to the midline: it is very broad and somewhat arcuate from the side. In contrast to juvenile *H. sapiens*, Skhūl I lacks a central keel and mental fossae, and is thin anteroposteriorly in the symphyseal region. Bar=1 cm.

Figure 9. Mandibles of adult Neanderthals to illustrate features in common and differences between individuals. Top, left (anterior view) and right (left lateral view), Tabūn C1 [Natural History Museum, London (NHML)]; middle, left (anterior view) and right (left lateral view), Krapina 59 [Hravatsku Prirodoslovni Muzej, Zagreb (GPM)]; bottom, left (anterior view) and right (left lateral view) of Spy 1 (Institute Royal des Sciences Naturelle de Belgique, Brussels). In all, the front of the mandible is very broad and somewhat arcuate from side to side; also, all clearly display a retromolar space between the last molar and the ramus. Individual variation is noted in differences in depth of the mandible, development or lack of inferior marginal tubercles (noted beneath the very posteriorly placed mental foramina of Krapina 59 and Spy 1, but lacking in Tabūn C1), development or lack of subalveolar depression along the incisor roots (tall and shallow in Krapina 59, shorter in Spy 1, absent in Tabūn C1), presence or absence of slight subalveolar swelling (only somewhat pronounced in Spy 1), and elevation of the inferior margin at the front of the jaw (noted in Krapina 59 and Spy 1, but not Tabūn C1). Bar=1 cm.

described above, no adult Neanderthal specimen possesses, even vaguely or subtly, the inverted ''T'' and attendant mental fossae that are otherwise seen in *H. sapiens*. In addition, the Neanderthal symphyseal prominence, when present, does not have

the same configuration as the symphyseal bulge seen in the adult Skhūl specimens and Qafzeh 7.

Study of the mandibles of juveniles identified as Neanderthal on the basis of various cranial features demonstrates that none in our sample displays the inverted ''T'' and mental fossae of *H. sapiens*. For instance, the symphyseal region of the mandible of the 10-month-old child from Amud (Rak *et al.*, 1994) (Figure 10) is essentially smooth from side to side across the midline; there is no trace of a long, raised central keel, distended inferior margin, or mental fossae. Surface topography is confined to the swelling of the region above the very laterally and posteriorly placed mental foramina due to the expanding crypts of developing tooth germs. The mandible is very broad and gently arced frontally from side to side, and, in profile, is slightly arced from top to bottom. When viewed from above, and in contrast to juvenile *H. sapiens*, the broad (from side to side) front of the Amud mandible is thinner anteroposteriorly than the rest of the corpus is more posteriorly. Below the large mental foramen on the right side, the inferior margin of the mandible bears a long, blunted inferior marginal tubercle which is bounded on either side by a slight upward depression.

As would be expected from a growth trajectory that is predicted upon the configuration seen in the Amud child in contrast to juvenile *H. sapiens*, 3–4-year-old Neanderthals (Roc de Marsal, Gibraltar 2, Pech de l'Azé) also lack the inverted ''T'' and mental fossae seen in extant humans (Figure 11; see also Tillier, 1983). In frontal view, the mandibles of these children are broad and somewhat arcuate from side to side. In profile, the symphysis may be smoothly vertical or slightly convex and retreating. In contrast to extant *H. sapiens* of similar age, the Neanderthal symphyseal region, when viewed from below, is also

noticeably relatively thin from front to back, with the corpus being thickest in the region of the first deciduous molar (see also Zollikofer *et al.*, 1995). As noted in the Amud child and in the occasional Neanderthal adult, there may be a discrete, peaked inferior marginal tubercle lying below the posteriorly placed mental foramen (see Gibraltar 2 in Figure 11).

Among the Neanderthal children, the Gibraltar 2 (Devil's Tower) mandible is of further interest in that a shallow midline cleft indents the inferior border (Figure 11). This indentation lies at the mandibular symphysis, which is where fusion of the right and left mandibular halves occurs. In all other details, this specimen is recognizably similar to the other Neanderthal children. If we accept that early symphyseal fusion, which is synapomorphic of Anthropoidea (e.g., see review by Schwartz, 1986), occurred in Neanderthals as it does in *H. sapiens*—from the top down—then the indentation in the midline of the inferior margin of the Gibraltar 2 mandible is simply a vestige of incomplete symphyseal fusion, as is obviously the case in the Isturitz specimens (Figure 5). This, of course, is the most parsimonious explanation of this feature in the Gibraltar 2 child. But even if this is not a completely accurate interpretation, it would be incorrect to identify this specimen's inferior marginal indentation as constituting a ''hint'' of a ''chin.''

The morphology of the Archi child's mandible, which is generally assumed to represent a juvenile Neanderthal (Ascenzi & Sergi, 1971*a*,*b*; Stringer *et al.*, 1984; Mallegni & Trinkaus, 1997) (see Figure 12), can be better understood in light of the Gibraltar 2 specimen. In terms of relative chronological age, the Archi individual, in which only the deciduous teeth had erupted, would have been younger than the Gibraltar 2 child but comparable to the Roc de Marsal and Peche de l'Azé children. In overall mandibular shape, the uniform anteroposterior

Figure 10. Amud Neanderthal child. The mandible is broad and relatively featureless across the anteroposteriorly thin symphyseal region, which is adorned below the posteriorly placed mental foramina by distinct inferior marginal tubercles. This specimen (TAU) lacks a central keel, mental fossae, and thickened inferior margin. Bar=1 cm.
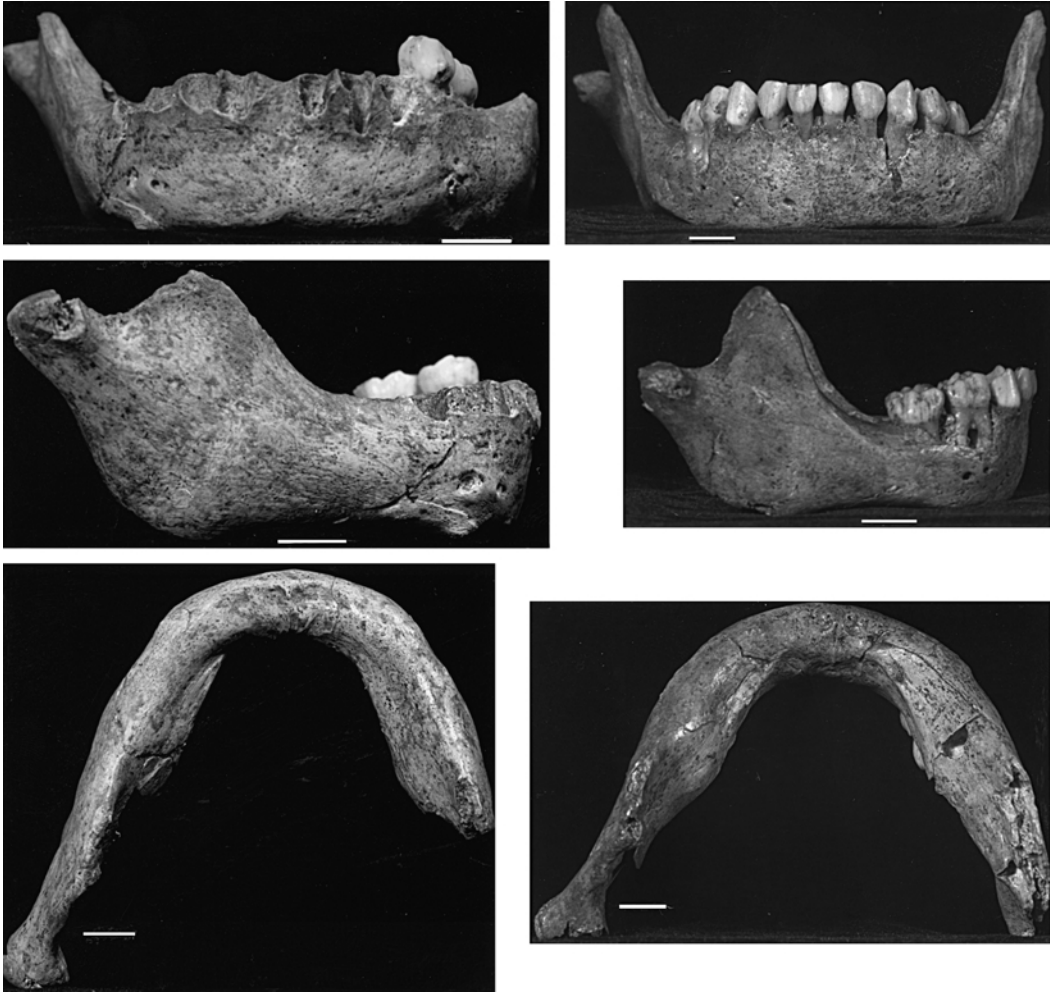
Figure 11. Mandibles of 3–4-year-old Neanderthals. Left column, Gibraltar 2 (Devil's Tower) (NHML); top (anterior view), middle (right lateral view), bottom (inferior view). Right column, Roc de Marsal (Musée National de Prehistoire, Les Eyzies); top (anterior view), middle (right lateral view), bottom (inferior view). As in adults, the front of the mandible is broad and somewhat arcuate from side to side. With the exception of a slight upward indentation at the midline in the Gibraltar 2 child (which probably represents incomplete symphyseal fusion), both mandibles are essentially featureless across the antero-posteriorly relatively thin symphyseal region. The Gibraltar 2 specimen bears well developed inferior marginal tubercles below the extremely posteriorly placed mental foramina. Bar = 1 cm.

thickness of bone across the broad symphyseal region, and the thickening antero-posteriorly of the corpus posteriorly, the Archi child is quite similar to the Gibraltar 2 child, and thus to other Neanderthal children as well (Ascenzi & Sergi, 1971a). A large inferior marginal tubercle lies beneath each large mental foramen, hence beneath the dm_2. Anterior tooth crowns in the process of growing within their crypts swell out the mandible externally, creating a depression just superior to the inferior margin of the bone. In profile, the relatively straight midline of the jaw is tilted somewhat forward. The central incisor roots noticeably overhang the symphyseal region. The

Figure 12. Archi 1 Neanderthal child. As in the mandibles of other juvenile Neanderthals, this specimen (Istituto Italiano di Paleontologia Umana) is broad across the symphyseal region, which lacks a central keel, mental fossae, and thickened inferior margin (for view of the anteroposteriorly thin symphyseal region see Mallengi & Trinkaus, 1997). The slight indentation of the inferior margin at the midline probably reflects incomplete fusion of the symphysis. Anterior to each mental foramen and extending to the thinned inferior margin is a longitudinal depression, whose posteroinferior extent is bounded by a distinct inferior marginal tubercle. Bar=1 cm.

inferior margin is slightly elevated anterior to the inferior marginal tubercles.

Although clearly lacking the general mandibular and specific symphyseal configurations of juvenile *H. sapiens*, the Archi specimen has been described as having ''some chin development'' (Ascenzi & Sergi, 1971*a*,*b*; Stringer *et al*., 1984:79; Mallegni & Trinkaus, 1997). In particular, Ascenzi &

Sergi (1971*b*) thought that ''the slightly inward curve of the outline which corresponds to the alveolar part suggests an initial incurvatio mandibulae anterior'' and that ''[i]n the basal margin a low triangular elevation in the median line, the trigonum mentale, is visible.'' And Mallegni & Trinkaus (1997:657) even ventured to state that while ''the discrete traits that contribute

to the development of a mental trigone, the tuber symphyseos, the fossa mentales, the tubercula lateralia and the incurvatio mandibulae, are clearly present on most immature Neandertal mandibles . . . Archi 1 exhibits generally weak development of them.'' As is evident from the foregoing description of immature human and Neanderthal mandibles, however, modern humans and Neanderthals are not at all similar in symphyseal morphology or general mandibular proportions. And the same holds true for modern children and the contrasting Archi child, although the latter nonetheless does display an interesting developmental feature in this region.

Compared to the same region in the Gibraltar 2 child (Figure 11), the ''chin'' of the Archi child becomes recognizable as what it is: a slight indentation at the midline of the inferior margin of the mandible. In contrast to the Gibraltar 2 child, the Archi child's incompletely formed right and left permanent tooth crowns, still in their crypts, markedly swell out the bone on either side of the midline beyond the plane of the surrounding external surface of bone. This creates a noticeable depression beneath, as well as another, but more shallowly depressed, area medial to, each swollen region of bone. The latter depressions delineate between them a narrow midline field of bone, at the base of which lies the inferior marginal cleft. The hint of a chin in the Archi mandible, therefore, results not from any of the morphologically consistent features in *H. sapiens* that form the inverted ''T'' and attendant mental fossae, but from the combined effects of incomplete coalescence of the inferiormost extremity of the mandibular symphysis and the intrusiveness of tooth crown formation.

Neanderthals obviously differ from extant *H. sapiens* in the development and specific morphology of the symphyseal region of the mandible. In no Neanderthal specimen seen by us are there any signs of an inverted ''T''

and its attendant mental fossae. The only features that could possibly be invoked as demonstrating similarity between these two hominids—the occasional subalveolar swelling and the equally occasional inferior marginal tubercle—are just as clearly not comparable either in detail or overall morphological context. But, exactly as adult *H. sapiens* retain the fetally established morphology of the symphyseal region, so, too, do adult Neanderthals retain features seen in their juveniles. In particular, adult Neanderthals retain the broad, somewhat arcuate shape of the symphyseal region, which remains anteroposteriorly uniformly thick. Furthermore, just as the differences among adult *H. sapiens*, in, say, the development of the inverted ''T'' and mental fossae reflect individual differences within the species, so, too, do differences between adult Neanderthals reflect variations between individuals of this particular hominid. Such differences occur in the *degrees* of depth from top to bottom, flatness *vs.* arcuateness from side to side, and/or verticality *vs.* inclination of the symphyseal region. Individual differences between Neanderthals are also found in the presence or absence of inferior marginal tubercles, subalveolar depressions, low, broad swellings below these depressions, and/or in the elevation of the inferior margin of the front of the jaw. In fact, a qualitative assessment of symphyseal morphology indicates that Neanderthals are probably more frequently and noticeably variable in morphological embellishment of this region than extant *H. sapiens*.

As evolutionary kin, Neanderthals and *H. sapiens*—even if not very closely related— would be expected to share many, if not most, aspects of their skeletal morphology. These would, of course, have been retained from a common ancestry that they shared to the exclusion of other hominids. The additional insight provided by the juveniles in the Neanderthal sample contributes

significantly to our ability to determine whether apparent similarities shared by adults of these hominids and *H. sapiens* are, indeed, present by virtue of common ancestry. When juveniles, especially of close related taxa, are distinctly different, as juvenile Neanderthals and *H. sapiens* are in details of symphyseal morphology, it becomes even more evident that what might in some adult specimens appear superficially as homologous features (such as a sub-alveolar depression or bony build-up in the symphyseal region) are actually homo-plasies, having arisen through independent courses of development.

This realization is true even if the cellular processes—resorption *vs.* deposition—that created the features of a particular speci-men are similarly operative among all indi-viduals of all taxa. For, after all, as the only active phases of osteogenesis, how else if not through an interactive process of bone deposition and resorption can skeletal features achieve their adult size and shape? Thus, although it is commonplace when considering the evolution of later hominids to arrange adult specimens along the lines of a *scale naturae* as a reflection of changes that might have occurred in a transfor-mation sequence leading to the morphol-ogy of *H. sapiens* (Gregory, 1922; McCown & Keith, 1939; Wolpoff, 1980, 1996; Bräuer, 1984; Smith, 1984; Lieberman, 1995), we suggest that this is not a produc-tive way in which to address the situation. Actually, it is rather Haeckelian. Instead, following a von Baerian approach, we advocate that, especially when they are available for study, juveniles should be compared in order to elucidate develop-mental commonalities. For it is only at this level of comparison that the differences and similarities among the adults can be fully understood. In light of this, it is patently obvious from comparisons between juvenile *H. sapiens* and Neanderthals that only one of these species of hominid possesses a

chin in a meaningful morphological and phylogenetic sense.

The Case of Tabūn II

The preserved symphyseal region of the Tabūn II mandible has been said to display some chin development (McCown & Keith, 1939; Quam & Smith, 1996; Rak, 1998). It thus requires separate discussion.

The Tabūn II mandible (Figure 13) is anteriorly broad and deep. In even more exaggerated form than in the mandibles of some Neanderthal adults (e.g., Spy 1 and Regourdou), this specimen displays a tall, broad, and shallow subalveolar depression that is overhung considerably by the out-wardly curved roots of the permanent inci-sors. Although there has been some damage to the region around the left central incisor root (which is filled in with plaster), bone is preserved to the midline on the right side, where it clearly lacks any sign of a vertical keel. The only elevation of bone in the symphyseal area is a small smooth fragment (delineated by its edges) that has become displaced from the plane of the bone's sur-face. In addition, there are no signs of any structures that might be identified as mental fossae anywhere within the expected areas of the otherwise well preserved symphyseal region. The inferior border of the most central portion of the symphyseal region is missing and has been reconstructed with plaster. However, more posteriorly, the inferior border of the jaw is present on each side, extending to some extent medially from a blunt inferior marginal tubercle. In these regions, the inferior border is not everted. The inferior marginal tubercles lie beneath the large mental foramina, which are situated below the bony junctions between P_2 and M_1.

Clearly, had this specimen possessed the inverted ''T'' and mental fossae that charac-terize *H. sapiens*, there is sufficient bone preserved to demonstrate their presence. In their absence, therefore, we cannot ascribe

Figure 13. Mandible of Tabūn II (TAU). As is typical of Neanderthals, the front of the jaw is very broad and somewhat arcuate from side to side. As in some Neanderthals, the symphyseal region is very deep, bears a subalveolar depression with a slight bulge below, and is elevated slightly along its inferior margin; there are also inferior marginal tubercles beneath the very posteriorly placed mental foramina. Bar=1 cm.

this specimen to this species. Further-more, since the Tabūn II mandible lacks the "tear-drop" shaped symphyseal bulge seen in the adults from Skhūl, we cannot include this specimen with that sample, either. In its bulk, depth, and in various morphological features (e.g., subalveolar depression, inferior marginal tubercles), however, this specimen is more strongly reminiscent of the mandibles of some western European Neanderthals—particularly those from Spy and Regourdou—than it is of the Tabūn C1 mandible (cf. McCown & Keith, 1939; Quam & Smith, 1996; Rak, 1998) (see Figure 9). Rak (1998), however, has argued that Tabūn II should be regarded as *H. sapiens* because, like the latter, it differs from Neanderthals in the depth of the mandibular notch crest, the position of greatest depth of this notch, and the point of termination of this crest on the mandibular condyle. While this is true of the left side, the Tabūn II mandible displays the Neanderthal con-figurations on the opposite ramus. Rak (1998) also suggests that the Tabūn II mandible would not display a marked retro-molar space, as in Neanderthals, if it did not have a pre-angular notch. But since such a notch becomes defined when the coronoid process of the ramus is expanded anteriorly, it is not clear that one can therefore "fill in" the notch and eliminate the retromolar space. In our experience, one can find mandibles of *H. sapiens* that also display a pre-angular notch, but they do not also have a retromolar space.

While it is clear to us that the Tabūn II mandible is not *H. sapiens*, it is less easily demonstrable that it is a Neanderthal. Nevertheless, this seems highly probable on the basis of the specimen's broad sym-physeal surface, inferior marginal tubercles, posteriorly placed large mandibular foramina, slightly procumbent anterior tooth roots, and large medial ptyerygoid tubercle (Schwartz & Tattersall, in prep-aration).

Other Middle to Late Pleistocene Western Old World Fossils

Mauer. As is well known, the Mauer jaw lacks any morphology that could be described as "chinlike" (e.g., Condemi & von Koenigswald, 1997). The symphyseal region is broad and arcs strongly from side to side (Figure 14). In profile, it curves gently inferoposteriorly. Anterior to the thickest parts of the mandible, which lie below the bilaterally doubled mental foramina (which, in turn, are beneath the P_2–M_1 alveolar septum), the inferior margin is elevated well above the plane of the inferior border of the posterior corpus. The margin of this elevation can be described as shallowly bow-shaped: prior to reaching the midline, the bone on each side curves down to form a low inverted peak. From the subforaminal points of greatest thickening, the inferior border thins anteromedially such that the broad central portion of the sym-physeal region is devoid of embellishment, while posteriorly it has thinned maximally by the level of M_3. When viewed from below, the broad symphyseal region is more or less uniformly thick anteroposteriorly, though thickening at its lateral most extremities.

This specimen is obviously distinctly dif-ferent in its symphyseal region from *H. sapiens* and the adults from Skhūl (plus Qafzeh 7). One might claim similarity between extant humans and the Mauer jaw in the development of inferior marginal thickening, but, in detail, the configurations differ strongly. In *H. sapiens* (see above), inferior marginal eversion and thickening occurs anterior to the mental foramina and are thus restricted to an area that is well within the symphyseal region. In contrast, inferior marginal thickening is most promi-nent in the Mauer jaw at and posterior to the mental foramina, while it is lacking anterior to these foramina. Although similar to some adult Neanderthal specimens in display-ing elevation of the inferior border of the

Figure 14. Mauer Mandible. Although damaged obiquely along the symphysis, it is still obvious that this specimen (Geologish-Paläontologisches Institut, Ruprecht-Karls-Universität Heidelberg) lacked any morphological embellishment in this region. Inferior marginal thickening, which is highlighted by a horizontal sulcus above, is noted well posteriorly, beginning in the vicinity of the large inferior marginal tubercle that lies beneath the mental foramina.

symphyseal region, the Mauer jaw is clearly distinguished from Neanderthals in general not only in the contour of the inferior margin, but also in the development of inferior marginal thickening, not to mention other details of mandibular morphology not described here (e.g., Condemi & von Koenigswald, 1997). Given the lack of external embellishment in the Mauer adult, we would predict that the symphyseal region of Mauer juveniles would have been similarly unadorned.

Arago. Arago 2 preserves a laterally broad and broadly arced symphyseal region (Figure 15). In profile, the anterior alveoli

Figure 15. Mandibles of Arago 2 (left column) and Arago 13 (right column) (Université de la Méditerranée). In Arago 2 the mandible is broad and essentially featureless surficially across the front of the inferior margin, which is elevated; the incisor roots had been angled forward, creating a subalveolar depression; an inferior marginal tubercle lies below the posteriorly placed mental foramen. Enough of the symphyseal region of Arago 13 is preserved to demonstrate that it, too, lacked a central keel, mental protuberance, thickened inferior margin, and mental fossa. Bar=1 cm.

are inclined forward and thus overhang the bone below, which curves smoothly down and back into the inferior margin. The inferior margin rises anteriorly, beginning its ascent in front of the first molar on the left side and the second on the right. Thus the symphysis is short superoinferiorly. On both sides the large mental foramen lies level with the M_1. Although bone missing from the midline deprives us of information concerning the existence of a keel, the lack of both an everted inferior margin and mental fossae bilaterally demonstrates the absence of two of the major aspects of the symphyseal region in *H. sapiens*. In addition, the bone of the symphyseal region and well along the corpus is more or less uniformly thick buccolingually.

Only a small portion of the symphyseal region to the left of the midline is preserved in Arago 13. Neither a keel nor a mental fossa is present. In profile, the alveolar region is smoothly confluent with the fairly vertical symphyseal region, which curves gently back below into the inferior border. On the preserved right side, below and posterior to the fully exposed canine alveolus (which may have been opened as a result of abscessing), the inferior margin is thickened into a torus that extends posteriorly to reach the level of the front of the second molar. The large mental foramen lies below the anterior root of M_1. The inferior border of the corpus is not elevated anteriorly. When viewed from below, what there is of the external symphyseal surface is relatively flat across and the bone of the region is uniformly thick anteroposteriorly. The corpus does not begin to thin until much more posteriorly.

Clearly, the Arago mandibles present a morphology different from those so far discussed.

Weimar-Ehringsdorf. We discuss the two Ehringsdorf mandibles (1009/69 and 1010/69; Figure 16) in the ''other'' category because, while Smith (1984) is inclined to see the Ehringsdorf material as Neanderthal-like and Vlček (1993) views it as *H. sapiens*-like, our preliminary assessment of the material suggests a different interpretation (Schwartz & Tattersall, in preparation). The adult mandible Eh 1009/69 is relatively narrow across the symphyseal region, which is slightly curved from side to side as well as from top to bottom. Between a pair of low but distinct inferior marginal tubercles that lie just posterior to the large mental foramina (which, in turn, are situated beneath M_1), the inferior border of the front of the jaw is elevated relative to the posterior corpus. The roots of the anterior teeth are inclined forward (those of the central incisors being especially procumbent), so that the alveolar margin markedly overhangs the symphyseal region. Bone remodeling due to subperiosteal as well as to periapical lesions has created deep craters on either side of the retained left central incisor. These greatly accentuate the inclination of the anterior teeth, to which this pathology may also have contributed. By default, alveolar bone eversion in conjunction with these massive concavities (particularly the larger of the two on the right side) gives the false impression of a faintly mounded symphyseal surface near the inferior margin.

In contrast to Eh 1009/69, the anterior teeth in the juvenile mandible (Eh 1010/69) are relatively orthal, but the entire alveolar region is shifted slightly anterior to the plane of the symphysis below. Although broken and glued inferiorly, and reconstructed below and posterior to the region of the left canine, the symphysis is relatively broad and somewhat arced from side to side. In profile, it is fairly vertical below the anteriorly displaced alveolar region as far as its inferiormost extremity, where it curves gently posteriorly into the somewhat elevated anterior margin. The expanse of symphyseal region that is perfectly preserved

Figure 16. Mandibles of Ehringsdorf (Eh) 1009/69 (left column) and Eh 1010/69 (Museum für Vor- und Frühgeschichte Thüingsisches, Weimar). Neither specimen displays a central keel, mental fossa, mental protuberance, or thickened inferior margin, and the symphyseal region in each is broad across. In Eh 1009/69 the central incisors greatly overhang the bone below and the inferior marginal tubercle lies level with the posteriorly placed mental foramen. Bar=1 cm.
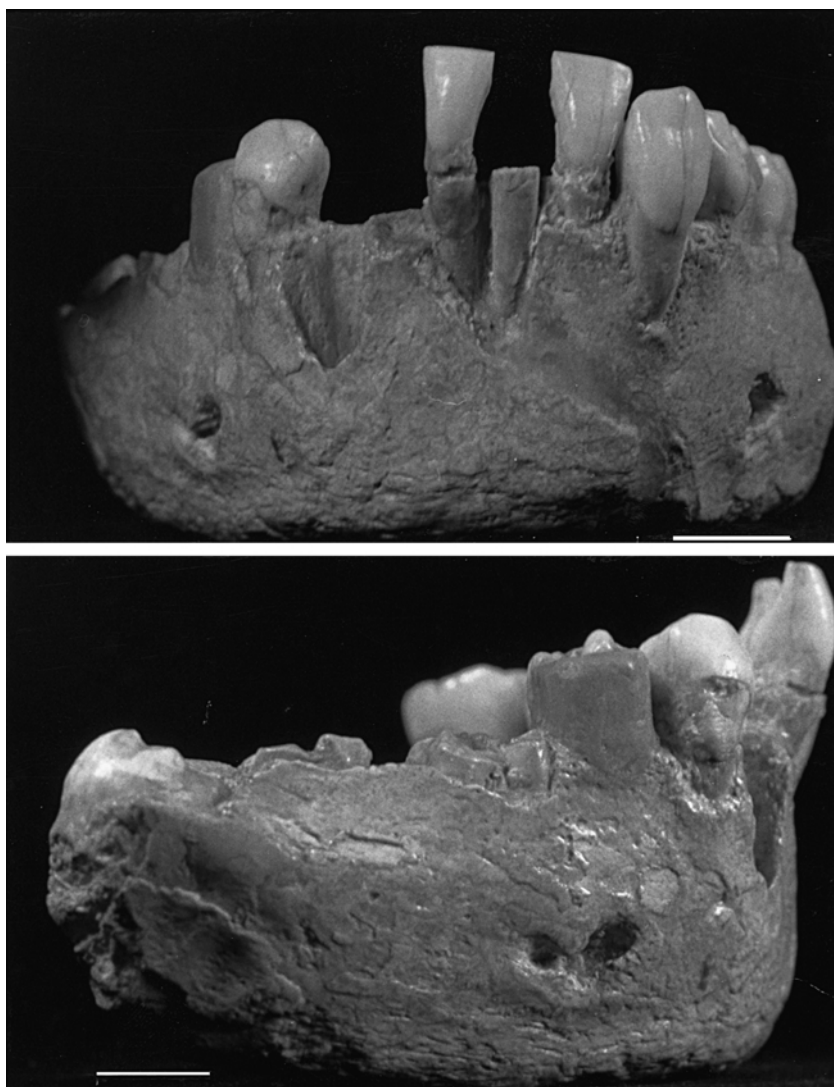
Figure 17. Rabat (Thomas Quarry) mandible (IPH). The incisors overhang somewhat the essentially featureless symphyseal region.

between the canine roots/alveoli and on down to the inferior border is devoid of surface morphology.

Rabat. The Rabat partial mandible preserves the entire symphyseal region, which was broken postmortem below the roots of the left anterior teeth, and has been repaired (Figure 17). Despite these attentions, it is obvious that the symphyseal region is well curved but not broad from side to side. On the intact right side is a shallow subalveolar depression, inferior to which the bone is featureless, bearing neither a central keel nor a mental fossa more laterally. In profile, the superoinferiorly not very tall symphysis curves slightly down and back into the unembellished inferior border. More clearly seen on the right side, a short longitudinal groove separates the mental foramen (which

is level with the P_2) from the inferior border, which, in consequence, appears to be thickened in that region. When viewed from below, the bone is relatively uniformly thick anteroposteriorly throughout the symphyseal region as well as more posteriorly along the corpora.

Although taxonomic allocation of this specimen is uncertain, it clearly is not *H. sapiens* or a variation on the European or Levantine hominids discussed above.

Tighenif (Ternifine). Even the least complete of the three Tighenif mandibles, Tighenif 2, preserves a good portion of the front of the jaw (Figure 18). The symphyseal region of Tighenif 2 is narrow and transversely arced. This specimen is particularly interesting in that it bears a distinct—broad and low—midline keel that emerges just below the alveolar region and fans out as it courses toward the inferior margin, thereby creating a well-defined, triangular protuberance. On each side of this keel lies a small, shallow depression, which accentuates the lateral extremities of this protuberance. As preserved on the left side, there is a distinct inferior marginal tubercle, which lies under the large mental foramen (which, in turn, is level with the mesial side of P_2). This tubercle is separate from, hence not a terminus or ''corner'' of, the triangular protuberance. In profile, the symphysis is straight and slopes back quite markedly.

The symphyseal region of Tighenif 1, which retains both corpora, is moderately broad and strongly arced from side to side. In profile, it forms a smooth arc, from the slightly inwardly inclined anterior tooth roots to the posteriorly curved and modestly elevated inferior border. There is a low but rather broad central keel coursing from the alveolar region to the inferior margin. The presence of this central keel creates shallow fossae on either side of the midline. When viewed from below, the bone of the symphyseal region and the portion of the corpora behind is uniformly thick anteroposteriorly, becoming thickest in the region of M_2.

The symphyseal region of the most completely preserved mandible, Tighenif 3, is also moderately broad and strongly arced from side to side. In profile, the alveolar region of the anterior teeth is tilted forward and then up and lingually very slightly, and the minimally arced symphysis courses back and down to the elevated inferior margin, which begins its ascent from the region below the first molar. There is the faintest hint of a broad, low, midline keel, which widens as it courses down from the alveolar region to become confluent with the slightly thickened inferior border. As is well preserved on the left side, there is a distinct horizontal sulcus that courses beneath the region of the cheek teeth to the region of the midline keel that serves to emphasize further the thickening of the inferior border.

Bräuer (1984) described a trigonum basale only in Tighenif 2 and 3, but clearly Tighenif 1 is similar to the other two specimens in displaying a midline keel that courses to the inferior border of the mandible. Indeed, the keel is actually more pronounced in Tighenif 1 than in the other two specimens. It is of potential phylogenetic and systematic importance that all three Tighenif specimens are unique among the middle Pleistocene fossils we studied in displaying some of the features distinctive of the symphyseal morphology of extant *H. sapiens*. It is of further interest that one of these features—the central keel—is observed in fossil jaws that do not also have the supposed hallmark of the human chin, a clear-cut mental protuberance. This should not be surprising when one considers that the mental protuberance of *H. sapiens*, which is itself a variable character, emerges postnatally, as does the occasional symphyseal bulge in Neanderthals and presumably other fossil hominids in which evidence of a central keel is lacking.
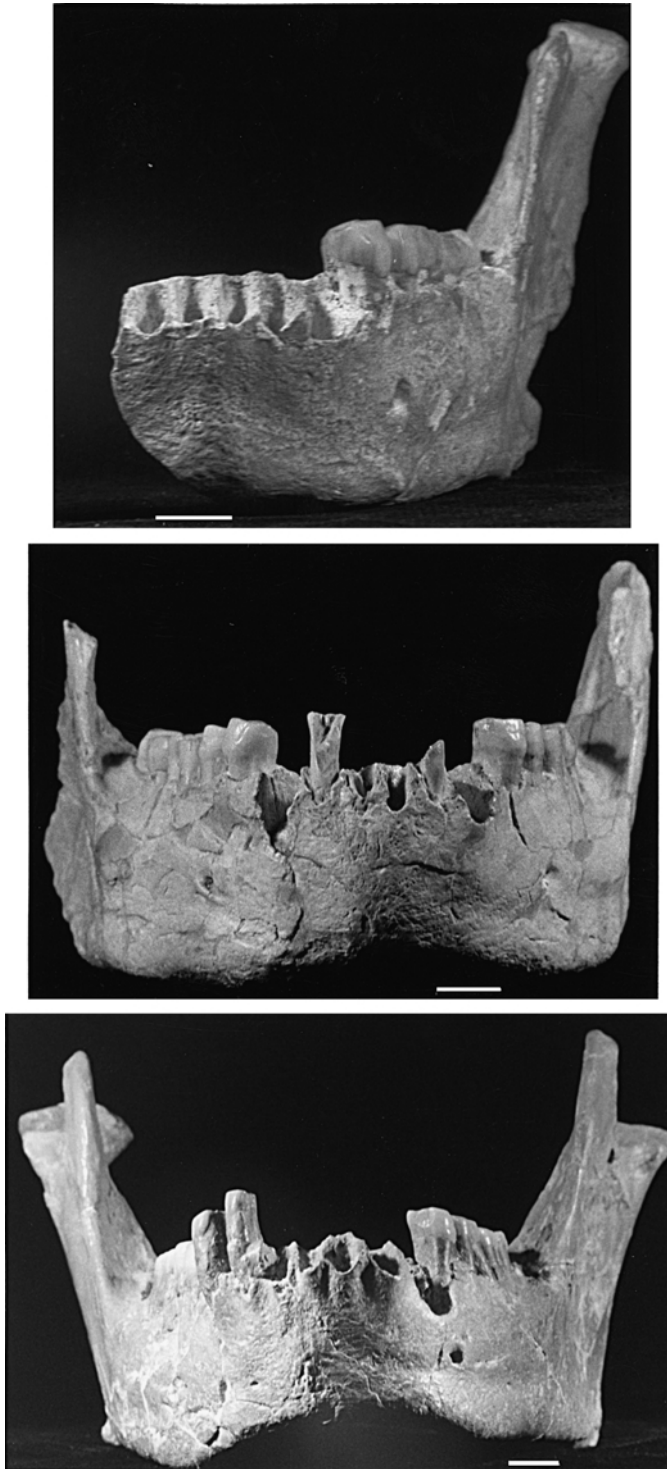
Figure 18. Mandibles from Tighenif (Ternifine) (Muséum National d'Histoire Naturelle, Paris). Top: Tighenif 2; middle: Tighenif 1; bottom: Tighenif 3. Although with some variation in degree of expression, all display a central keel, with slightly depressed mental fossae on either side, that broadens into an inferiorly placed mental protuberance; the inferior margin of the symphyseal region is somewhat elevated.

Implications

From a phylogenetic perspective, if we accept on developmental grounds that *H. sapiens* is unique among primates (indeed, among mammals) in the details of its symphyseal morphology, then it is possible to entertain the following hypothesis: The Tighenif specimens' possession of a central keel and a variably small, low-set triangular protuberance (a mental trigon or trigonum basale) could reflect potential synapomorphy with *H. sapiens*. Obviously, these apomorphies would have characterized the last common ancestor of a clade that included extent *H. sapiens* as well as those late Pleistocene fossils possessing all of the symphyseal details seen in the extant species: i.e., at least the Qafzeh 11 and the Tighenif mandibles.

In this regard, we look forward to future study of the Jebel Irhoud juvenile mandible (Hublin & Tillier, 1981) and the Klasies River Mouth mandibles (Rightmire & Deacon, 1991), all of which have been described as having some version of chin formation. As illustrated by Hublin & Tillier (1981), the former specimen may possess a central keel that expands inferiorly into a thickened inferior margin. Casts of this specimen appear to show such morphology. In contrast, the Klasies River Mouth specimens, particularly KRM 13400 and 14695, do not appear to have either a central keel or a thickened inferior margin, although the central portion of the symphyseal region is surmounted by an external swelling (Rightmire & Deacon, 1991). A cast of KRM 13400 appears to be generally consistent with this description, although it should be noted that, well lateral to the midline, the margin thickens to its greatest extent below the doubled right mental foramina, and the symphyseal profile is essentially vertical. The AMNH cast of KRM 41815, which is broken in the original just below the incisor alveoli, does, as described, appear to preserve a triangular mental protuberance, which both tapers superiorly into what might have been a central keel and expands inferiorly into bilateral mental tuberosities. When viewed from below, the symphyseal region of this specimen is relatively straight across and somewhat thickened from front to back. It will be interesting to see if the Klasies River Mouth specimens present a picture of diversity as seen in the Qafzeh hominids.

Morphologically, the primary implication of our observations is that a bulging symphyseal region is not equivalent to a chin. When humans and elephants can both be described as having chins (e.g., Enlow, 1982), it is probably time to reconsider the applicability of the term. Consequently, we recommend that the term ''chin'' no longer be used in discussions of mandibular morphology and its phylogenetic and systematic significance. If, however, one feels the need to retain this term, it should be restricted in usage only to extant *H. sapiens* and those fossils displaying the constellation of symphyseal features of this species. Since it is obvious that bulges and swellings as well as subalveolar depressions of differing degrees of expression and different morphologies have come to adorn the symphyseal regions of a diversity of hominids, we further recommend that the terms (and the synonyms of) ''mentum osseum,'' ''incurvatio mandibularis,'' ''tuberculum laterale,'' and even ''trigonum mentale'' also be limited, or even dropped from usage. As anatomical terms, they are used to refer both to sometimes superficially similar and to sometimes markedly different structures in a diversity of adult specimens that may have arisen from totally different juvenile configurations. As for children, the sometime presence of a gomphotic scar especially low down along the midline of the mandible is a naturally occurring result of symphyseal fusion. Unless it is distinctly raised and part of an everted, inverted ''T''-shaped

structure that is associated with mental fossae, it is not a "hint" or a "trace" of a mental trigon as seen in *H. sapiens*. Thus, these terms have become charged with a scenario of "chin" evolution which should itself be discarded.

Additional discussion

Throughout this paper, we have attempted to keep our description of morphology apart from a phylogenetic and, especially, functional interpretation of it. We have, however, stressed the importance of understanding the morphology of the adult by starting first with an appreciation of the details of juveniles precisely because this is the most fundamental way in which to appreciate the similarities or differences that exist among individuals and between the average morphologies of taxa. Comparing Neanderthals with extant *H. sapiens* and those specimens that have come to be regarded as fossil *H. sapiens*, we are fortunate that there are, indeed, juveniles available for study. In other cases, such as with the Mauer or Klasies River Mouth mandibles, we have tried to inform our comparisons with insights drawn from cases based on ontogenetic series.

Although we could leave the discussion where we did in the preceding sections, comments we received from various anonymous reviewers on an earlier version of this paper have provoked us to pull together the loose ends and to detail more fully our theoretical, philosophical, and methodological position. This might be unconventional, but it may prove useful in clarifying points we raised earlier and in focusing attention on issues that those of different philosophical and methodological persuasions might also take into consideration. We have organized our comments in the context of the kinds of topic that often characterize debates on modern human origins.

Intermediate, transitional morphological states
We presented our descriptions and comparisons of the specimens as we did in order to keep them separate from our discussion of the systematic implications of the data. Often, however, there is a tendency to infuse description and comparison of specimens with interpretation of the potential significance of the described morphologies given a particular, but not overtly stated, phylogenetic scenario. Such scenarios tend to be based on assumptions not only of relatedness, but also of transformation series (in which terms such as "intermediate" are a part) and implied functional and/or developmental explanations (in which discussing how morphologies might have come to be in one form or another plays a large role).

Basically, however, the facts are that *H. sapiens* has a distinctive symphyseal configuration from its ontogenetic outset and that many other hominids, especially Neanderthals, do not share any version of these apomorphies. From this it would seem reasonable to conclude that Neanderthals and those specimens that are morphologically similar to them in symphyseal morphology are not members of the species *H. sapiens*. But if one was committed to the interpretation that there was only a single species, which encompassed a diversity of morphologically distinctive specimens—such as all or most of those we discuss here—then one would be obliged to explain *how* members of the same species could have come to be morphologically different from one another. We, however, are trying to understand as best we can what the details of difference and similarity are from the beginning. Only afterward can we bring this information to bear on our phylogenetic and systematic hypotheses, and, if we so choose, to offer explanations for how and even perhaps why certain features came to be the way they are.

Our appreciation of development also differs significantly from the more prevalent

one in the literature: essentially, if development is taken into consideration at all, it is done secondarily, after specimens of adult individuals have been sorted into a Haeckelian *scale naturae* that is regarded as reflecting a transformation sequence. This license is prevalent in paleoanthropology, as is indicated in the oft-published diagrams of fossil adult crania arranged in a presumed phylogenetic sequence. In such a scenario, for example, the symphyseal morphology of adult Skhūl and Qafzeh specimens are seen as being intermediate between Neanderthals and modern *H. sapiens*, with this intermediate morphology being attained developmentally from the nondescript symphyseal region seen in the Skhūl I child. In contrast to this type of approach, we, like von Baer (1828) and Huxley (1863), emphasize the commonalities between juveniles, since those form the substrate upon which adult morphology is predicated (see also Schartz & Tattersall, 1996*b*). In this light, especially if the Skhūl I child represents the juvenile state of the Skhūl adults, it becomes strikingly clear that the symphyseal bulge of the latter is not just a variant of the chin of *H. sapiens*. Even if this were not the case, it is difficult to sustain a compelling comparison between adult morphologies if their juvenile states, as in Neanderthals and *H. sapiens*, are so clearly different.

One might also argue, on the basis of arranging specimens in a morphological *scala naturae* of presumed evolutionary change, that a more anterior position of the alveolar process, as seen in the facially prognathic Neanderthals and some early *Homo*, merely masks the development of *H. sapiens*' symphyseal morphologies in specimens of these representatives of the genus. Consequently, the symphyseal morphologies of *H. sapiens* are not truly absent after all. Although this kind of argumentation is commonplace in paleoanthropology (e.g., ''it looks this way because of such and such, otherwise it would be identical to something else''), we must strongly reiterate that such arguments merely constitute a defense of a particular hypothesis of relatedness that one has already embraced. They do not contribute to the generation of theories of relatedness. More specifically, in terms of the above example, facial prognathism, or its lack, has no bearing on the matter at hand. Juvenile Neanderthals are not overtly facially prognathic relative to the adult state. The profile of a juvenile Neanderthal's mandibular symphysis can be vertical or anteriorly inclined. Yet, especially in cases of the former configuration, the juvenile Neanderthal's symphyseal region is devoid of any specifically *H. sapiens*-like morphology.

In *H. sapiens*, juvenile mandibles are essentially vertical in profile and yet possess the characters already described above. If a mental trigon later develops to become noticeably protrusive, it does so as a result of deposition of bone in that region (Enlow, 1982). Further accentuation of such a protrusive mental trigon can be provided by the development of a depression or an incurvatio mandibularis above it, which derives from the process of bone resorption (Enlow, 1982). Thus, the inward curve above and the protruding mental trigon below that we see in the mandibular profile of *H. sapiens* results from the modification of an essentially vertical symphyseal face, not, as the typical Neanderthal-to-*H. sapiens scala naturae* based on adult specimens would prompt one to speculate, from the retreat of the face during the emergence of the latter hominid. Furthermore, since the degree of facial prognathism characteristic of adult Neanderthals develops from the more orthognathic condition of the juvenile, if there was any basis for the ''anterior alveolar position masking *H. sapiens*' features'' hypothesis, we would expect to observe these features in the juvenile Neanderthals. But we do not.

It might also be appropriate here to explain why we must discuss features as

discrete entities, rather than as stages in a transformational continuum: The genetics and properties of development make it increasingly clear that novel characters will appear instantaneously and, therefore, define new species from the start (see reviews by Schwartz, 1999a,b). As Grüneberg (1943) demonstrated decades ago, a structure (such as a tooth) must reach a certain minimal threshold of development or it will be aborted. The evolution of the horse presents an unambiguous example (Schwartz, 1999c). In three-toed taxa, the lateral digits always consist of three phalangeal elements, even if they are small relative to the size of the central digit. With the appearance of the first single-toed horses, the lateral digits are entirely absent. From the perspective of regulatory genes, and, therefore, of the developmental advent of structures, the picture is also of the abrupt appearance or disappearance of features (Schwartz, 1999a,b). For example, in the case of the vertebrate eye, studies on the *Rx* gene in the mouse demonstrated that individuals that were either homozygous or heterozygous for the active gene had both an eyeball and bony socket, whereas homozygotes for the experimentally-mutated inactive or recessive *Rx* gene lacked both structures. There was no in-between state. Since, as has been known since Bateson's (1909) time, nonlethal mutations typically arise in the recessive state, it would only be through a process of heterozygosis leading to the production of homozygotes for the mutation that a new feature would emerge in a population (see discussion in Schwartz, 1999a,b). But when it did, it would appear as if out of nowhere and in its full-blown state in a number of individuals (Schwartz, 1999a,b). This process has most recently been documented in a report on the spontaneous appearance of a mutation affecting the *Hodx-13* gene in a laboratory colony of mice (Johnson *et al.*, 1998). At some point, and by a mechanism that remains unknown,

the mutant recessive would be converted to the dominant state (Johnson *et al.*, 1998).

With this in mind, the novel configuration of the symphyseal region of *H. sapiens* can be appreciated: whatever regulatory changes occurred that affected bone deposition and hence shape in this region, these apparently apomorphic morphologies would have emerged without a trail of transitional stages preceding them. A similar phenomenon would explain the development of the autapomorphic medial projection in the nasal region of Neanderthals (Schwartz & Tattersall, 1996a).[1] In 3–4-year-old juveniles, this structure is already present as a vertically oriented bony projection that emerges directly from the wall of the nasal cavity and that becomes larger in adults. No equivalent structure exists in the nasal region of juvenile extant primates, *H. sapiens* included, which retain the primitive mammalian condition of a low, variably horizontally oriented conchal crest, along which a separate concha articulates. In adults of these taxa, the concha may fuse to the wall of the nasal cavity.

Variation

As noted in Table 1, the specimens of extant *H. sapiens* we studied represent a global sampling. But, this fact aside, we must point out that we are not engaged in a study of human variation. We are endeavoring to undertake a systematic analysis of hominids. The latter concern entails a totally different emphasis than documenting variation within

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[1]Subsequent to our publication on the structures of the nasal cavity in Neanderthals, we restudied the Spy material and discovered that we had erred in our initial evaluation of the Spy 1 specimen. Although we were unable to publish a note of correction prior to Franciscus' (1999) article, we were able to eliminate this error from two other publications that were still in press (Schwartz & Tattersall, 1999a; Schwartz *et al.*, 1999). At present, a medial projection is documented in the following Neanderthal specimens: Engis, Gibraltar 1, La Chapelle-aux-Saints, La Ferrassie 1, Monte Circeo 1, Roc de Marsal, St Césaire, Shanidar 1, and Subalyuk.

a population or species. It involves the delineation of potential apomorphies, which, if autopomorphic, contribute to the delineation of species, or, if synapomorphic, to the delineation of sister taxa and clades. In this particular study, we have delineated what we believe to be various apomorphies of the symphyseal region of *H. sapiens*. As such, and for systematic purposes, it is therefore irrelevant whether one specimen has a more robust symphyseal keel than another. What is relevant is how many specimens possess the apomorphic features.

It is only after one accepts systematic hypotheses—how many species there are, and which specimens represent which species—that one can then embark, if one wishes, on studies of variation. But such studies do not shed light on the origins and relationships of the taxa involved, only on the ways in which individuals within the same taxon differ slightly from one another. In this light, it hardly matters if the inverted "T" with its mental tubercles is more pronounced in an Aleut than in a West African, or if the symphyseal profile of one Neanderthal is more forwardly sloping than another. But it is surely significant that no Neanderthal specimen, no Skhūl specimen, and not all Qafzeh specimens display the everted and inverted "T"-shaped configuration of the symphyseal region.

Terminology

During our now multiyear comparative study of hominids, we have become increasingly impressed by how inadequate and restrictive anatomical terminology based on the morphology of *H. sapiens* often is when describing other hominids. For instance, while *H. sapiens* does indeed have an "arcuate eminence" that is large prenatally and persists into the adult state, this condition is rarely found in specimens of any other hominid, much less any other mammal (see Schwartz & Tattersall, 1996*b*). So far, we have been able to describe an arcuate eminence only in juvenile Neanderthals and one adult Neanderthal specimen, Gibraltar 1. Clearly, if one chose to retain the term "arcuate eminence" one would be better off referring to the area in question as the "region of the arcuate eminence" (which technically would be defined as the area capping the superior semicircular canal), and then describing its configuration. With regard to the terminology applied to the chin of *H. sapiens*, a mentum osseum may refer to a bulge that straddles the midline of the jaw, but it is obvious that a bulge can emerge upon totally different substrates: compare, for instance, the bulge of Spy 1, that of Skhūl V, and that of Cro-Magnon 3. Clearly, while a bulge may be produced by the same process of bone deposition (which is the only process for increasing the size or thickness of a bony structure), this does not *de facto* mean that all symphyseal bulges are the same structure. Similarly, while an incurvatio mandibularis may be enhanced by bone resorption in that region, as well as the development of a bulge below and alveolar prognathism above, this does not mean that the details of the symphyseal regions of this array of hominids are identical.

In short, the application of terminology that had been devised for very specific features to a field of differently configured details that may be present in the same general region not only hinders productive comparisons but, in terms of human evolution, continues to obscure the differences that exist between *H. sapiens* and other hominids.

Conclusions and summary

The uniquely configured symphyseal region of *H. sapiens* forms early in fetal development and the basic shape and architecture then established are retained into adulthood. The salient features of the symphyseal region of this extant hominid species are a

raised central keel that flows into a distended inferior margin, a low-lying triangular mental tuberosity at the confluence of the keel and the inferior margin, and mental fossae that lie on either side of the keel and above the distended inferior margin. No Neanderthal included in this study, whether juvenile or adult, possesses these distinctive features. Instead, the mandibles of both juvenile and adult Neanderthals are broad and somewhat arcuate across the midline. Those features that occur variably in Neanderthal adults (e.g., a subalveolar depression, a swelling below this depression, inferior marginal tubercles that lie below the very posteriorly placed mental foramina) represent aspects of individual variation appended during postnatal growth.

Among fossils usually considered to represent *H. sapiens*, those from the latest Pleistocene and the earlier Qafzeh 11 (and possibly Qafzeh 8 and 9) display the symphyseal features seen in living humans. In contrast, all of the Skhūl adults and the other adult Qafzeh individuals differ both from *H. sapiens* and from Neanderthals in having symphyseal regions adorned with a variably developed teardrop-shaped bulge. The Skhūl I child has a featureless symphyseal region. With the exception of fossil moderns, in the entire sample under consideration here it is only in the Tighenif mandibles that one finds a central keel.

The latter observation suggests that the development of a central symphyseal keel is a synapomorphy of a clade that includes extant *H. sapiens* and those fossils similarly configured in details of the symphyseal region, plus the Tighenif specimens. Within this clade, *H. sapiens* and similarly configured fossil specimens are distinguished by the consistent possession of a thickened inferior margin that forms an inverted ''T'' with the central keel, plus a variably protrusive triangular mental protuberance at the junction of these structures and well defined mental fossae bilaterally. Clearly symphyseal

morphology, especially as considered within a developmental framework, lends support to previous suggestions of notable taxic diversity within the genus *Homo* (e.g., Howell, 1994; Santa Luca, 1978; Schwartz & Tattersall, 1996b; Tattersall, 1986; Zollikofer *et al.*, 1995): a diversity that is at present substantially underestimated.

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Note added in proof: Since this manuscript went to press, we did study the Klasies River Mouth specimens. Our preliminary suggestions were borne out.