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Barking up the Wrong Ape – Australopiths and the Quest for Chimpanzee Characters in Hominid Fossils

Jeffrey H. Schwartz

Departments of Anthropology and History and Philosophy of Science, University of Pittsburgh, Pittsburgh, USA

A B S T R A C T

With the shift during the 1980s from a human-great ape ultimately to an orangutan-(gorilla-(human-chimp)) theory of relatedness, the search for chimpanzee-like features in early hominids intensified. Reconstructions of early hominids became caricatures of chimpanzees, not only in soft tissue features (e.g. the nasal region), but in supposed bony structures (e.g. an anteriorly and especially superiorly protruding a supraorbital torus with a distinct posttoral sulcus behind). In spite of rampant »Panophilia,« actual morphologies of the majority of early hominid specimens are those cited as uniting an orangutan clade. Those specimens that are »chimpanzee-like« are probably not cladistically hominid.

Key words: Pongo*, australopith, Miocene hominoids, African apes*

A Historical and Philosophical Overview

Although now considered ancient (and perhaps irrelevant) history by most paleoanthropologists and molecular anthropologists, the events that transformed the picture of hominid evolution from that in which first *Ramapithecus* and then a group of similarly thick-enameled Miocene hominoids (referred to as ramapithecids) were thought of as ancestral in some way to geologically younger, »proper« hominids (generally the two genera *Australopithecus* and *Homo* and perhaps also *Paranthropus*) to that in which a »ramapithecid« – hominid relationship was abandoned and a »ramapithecid« – orangutan clade subsequently created

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are not only interesting, but poignantly relevant to the question of how early hominid morphology has been perceived[1–3].

As is well known, until the Sinap and Siwalik craniodental material was discovered, jaws and teeth allocated to the genus *Ramapithecus* were seen as being »hominid« primarily because the cheek teeth were relatively low crowned and the molars especially were covered in a thick layer of enamel – features that also characterized »proper« hominids, with the robust and particularly hyper-robust australopiths having the relatively thickest enamel. The discovery of facial specimens from Turkey and Indo-Pakistan (originally referred to the genus *Sivapithecus*, but more recently also assigned to *Ankarapithecus*) with features that appeared to be synapomorphic with the orangutan created a dilemma from which the field of paleoanthropology has never recovered. Namely, it was impossible to reconcile the presence of *Pongo*-like facial and also dental features in these Miocene hominoids with any of the prevailing theories of extant large-bodied hominoid relationships, whether one's preferred phylogenetic scheme was that hominids were related to a great-ape group, or to only the African apes (with the orangutan the sister taxon of them all), or to only the chimpanzee (with the gorilla the sister taxon of this dyad and the orangutan the sister taxon of this clade). The consequence of this apparent contradiction was the rejection of the hypothesis that *Ramapithecus* (which then became synonymized with *Sivapithecus*, which had priority) or any »ramapithecid« had a special relationship to hominids. Instead, the obvious facial synapomorphies of the Sinap and Siwalik specimens were deemed sufficient not only to unite *Sivapithecus* with *Pongo*, but to remove other thick-enameled Miocene hominoids from potential hominid ancestry and reassign them to an orangutan clade. Among the latter were specimens commonly referred to *Gigantopithecus*, *Ouranopithecus* (formerly *Graecopithecus*), and *Rudapithecus* (which, unfortunately, has since been subsumed in *Dryopithecus*, with the result that this genus is now a wastebasket taxon).

Further complicating this history is the fact that, during the heyday of studies that scrutinized hominoid teeth in terms of occlusal topography and especially the thickness of molar enamel, the cheek teeth of the orangutan were found to conform to the configuration otherwise taken as being »hominid«: low-cusped with thick molar enamel. From the perspective of the history and philosophy of science, it is a curious fact that this potential synapomorphy of humans and orangutans and, more broadly, of »ramapithecids«, hominids, and *Pongo* was not entertained – which is particularly perplexing since none of the competing theories of extant large-bodied hominoid relationship were actually based on any more compelling morphological synapomorphy[4]. In fact, among these competing theories of large-bodied hominoid relationships, the only one grounded in robust synapomorphy was the relatedness of the African apes (e.g. flexor tendons of hand and wrist shorter than extensors, extensive ligamentous binding of carpal region, »locking« distal radial and carpal as well as humero-ulnar joints, dorsally expansive metacarpal head articular surfaces, developmentally established friction pads on weight-bearing surfaces of manual digits II–V)[2,4,5].

Thus, the great-ape group, which had originally been argued by Huxley[6], and subsequently defended for decades by Schultz[7,8], rested primarily on the development in these hominoids of markedly elongate cervical vertebral spines, but little else[4]. A human-African ape scheme of relationship was sought in these hominoids' development of ethmoidally derived frontal sinuses[9], in spite of the fact

that the bonobo typically lacks frontal sinuses[7]. As far as Schultz (ibid.) was concerned, Weinert's[10] human-chimpanzee relationship lay primarily in misinformation and inaccurate anatomical comparisons. Consequently, in the early 1980s, when the faces of *Sivapithecus* were discovered, with the exception of a chimpanzee-gorilla group, there was little morphological basis for any of the prevailing and competing theories of relationship among the extant large-bodied hominoids. In fact, even though Groves[11] subsequently claimed from his scrutiny of a huge body of literature, from which he extracted hundreds of comparative features, the existence of substantial morphological support for a close human-chimpanzee relationship within a human-African ape clade, it turned out that this interpretation was largely phenetic and not based on character polarity established by outgroup comparison[2,5].

When considered in the context of outgroup comparison, however, a human-chimpanzee sister grouping was found to be the least supported by potential synapomorphy of any of the popular theories of extant large-bodied hominoid relatedness[2,5]. An unexpected demonstration, however, was that, in addition to the development of low-cusped cheek teeth and thick molar enamel, humans shared a significant number of derived features uniquely with the orangutan [e.g. in reproductive physiology (gestation length, estriol levels, absence of estrus), degree of cerebral asymmetries, fetal adrenal zone size, lack of keratinized ischial callosities, mammary gland separation, hair length, incisive foramen number][1,2]. Although Groves[12] objected to some of these suggested synapomorphies, he accepted (or could not refute) upward of a dozen of those features he discussed, which was not inclusive of all features shared exclusively by humans and orangutans. Not too many years later, as a result of a comparative study among mammals in which they discovered a unique pattern of the superficial veins of the forelimb in humans and orangutans, Thiranagama et al[13] were also forced to admit that this complemented an already substantial number of synapomorphies between these two hominoids.

In this light, it is of interest to inquire: What, then, formed the basis of paleoanthropological »thinking« shifting its »preferred« theory of human-ape relationship to that in which the orangutan was the sister taxon of a human-African ape group, within which first the African apes were seen as sister taxa and subsequently the gorilla was taken as the sister taxon of a human-chimpanzee grouping? It was, of course, the increasing emphasis and then reliance on interpretations of molecular data in which, according to the »molecular assumption« first articulated by Zuckerkandl and Pauling[14], and subsequently identified as such by Caccone and Powell[15], molecules were assumed to change in a regular (»clock-like«) fashion. This, in turn, led to the assumption that overall similarity was a reflection of closeness of relatedness because the degree of similarity (distance) between taxa represented the recency or antiquity of divergence of continually changing molecules. As Caccone and Powell (ibid.) argued, if you accept the molecular assumption, everything else follows from it. And, indeed, it is internally consistent – so much so, that it cannot be falsified. Thus, when, as was inevitable, conflict eventually arose between molecularly and morphologically based phylogenies, or between molecularly versus paleontologically determined dates of cladogenic events and/or common ancestors (the human-chimpanzee theory satisfies both examples), it was (at least in retrospect) not surprising that molecular anthropologists were emboldened to deny a role to morphology in deciphering

phylogenetic relationships[16]. This, unfortunately, has become a virtual truism.

In light of what has been conceded as a »true« phylogeny provided by many molecular anthropologists, morphologists, put on the defensive, now find themselves in the position either of trying to find explanations for why morphology is not phylogenetically revealing[17,18] or of denying validity to what in other areas of evolutionary biology are systematically rigorous approaches to comparative morphology in favor of phenetic morphometric computer analyses that, contradictorily, begin by accepting the molecularly »true« phylogeny to the extent that the tree is rooted in the orangutan. By default, then, the orangutan is defined as the primitive sister of humans and the African apes (and, in turn, its morphologies representative of the primitive character states relative to those of other large-bodied hominoids)[19] – which, one would think, should be among the hypotheses in need of testing.

One of the ironies of morphologists' attempts to gain acceptance in what has become a molecularly dominated field is that paleoanthropology, as with paleontology in general, can only be pursued through comparative morphological analyses – which produces the schizophrenic situation of paleoanthropologists, on the one hand, accepting without question a human-chimpanzee sister group and, on the other, continuing to speculate about the affinities of fossil taxa. Another dilemma derives from a lack of a philosophical perspective of science, which should make it obvious that, while intuitively attractive, the »molecular assumption« is actually only an assumption that was conceived by Zuckerkandl and Pauling on the basis not only of a minuscule sampling of vertebrate taxa (human, gorilla, horse, and fish), but also because of the apparent compatibility of the pattern of hemoglobin/anti-hemoglobin similarity among these taxa (fish-(horse-(human-gorilla))) with a theory of relationship based on morphology. Although one could argue that it was inappropriate for Zuckerkandl and Pauling to include a fish in their sample – because of differences in hemoglobin biochemistry between water-dwelling fish and terrestrial mammals – the philosophical point is that, because the molecular assumption was based on an apparent consistency between immunological distance (but between only four taxa) and a morphological phylogeny, the latter should be able to falsify an inconsistent theory of relationship derived from the former. From a systematist's point of view, one could equally argue that Zuckerkandl and Pauling's demonstration of similarity was actually a demonstration of the lack of change (that is, of primitive retention) in humans and gorillas, with dissimilarity in the horse and even more so the fish reflecting their respectively derived molecular states.

This is not a trivial point and should cause reflection in light of the reason Collard and Wood[17] rejected hard tissue morphology as having any phylogenetic valence. In their PAUP analyses of the craniodental features in Shoshani et al[20] [which were derived largely from an unpublished manuscript by Groves as well as Groves,[11] the two most parsimonious sister groups that emerged were human-orangutan and chimpanzee-gorilla. Since these two theories of relationship were inconsistent with the phylogenetic arrangement of the large-bodied hominoids that Collard and Wood accepted from the very beginning as being the »true« one – (gibbon-(orangutan-(gorilla-(human-chimpanzee)))) – they had no choice but to conclude that, since both of these sister groupings were supposedly incorrect, craniodental morphology was an unreliable reflection of evolutionary relationship, as well.

The Chimpanzee and Interpretations of Fossil Hominids

While clearly affecting the course paleoanthropology has taken in recent years with regard to approaching the study of extant hominoids, the focus on the chimpanzee as our closest living relative has also had an enormous impact on the way in which fossil hominids and fossils considered potentially ancestral to hominids have been interpreted.

Although he has been cited as having demonstrated a morphologically close relationship between humans and chimpanzees[19], Begun[21] actually approached the issue of chimpanzee-hominid relationships by attempting to link the extant ape with an unspecified assemblage of specimens referred to *Australopithecus*. As shown by Conroy[22], Begun's analysis was predicated on the assumption that *Pan* and *Australopithecus* were closely related (and the list of their presumably uniquely »shared« features generated from this assumption). A no less important point, however, is that *Australopithecus* has become a wastebasket taxon that now includes such a jumble of specimens that the only comparisons one can and should make at this time are between individual specimens[4,23]. It is, therefore, impossible to generalize about »*Australopithecus*« because there is often no rhyme or reason for specimens being allocated to this genus other than that they are presumed to be more primitive than those accepted as belonging to the genus *Homo* (which is still a systematically undefined taxon).

Of further note is Begun's argument linking Rudabanyan *Dryopithecus* (= *Rudapithecus*) and the chimpanzee with hominids via *Australopithecus* on the basis of one specimen, RUD 44, which was described as having a wide glabellar region and an »incipient« supraorbital torus that anticipated the supposedly bar-like torus of *Australopithecus* which, in turn, was stated as being similar to the supposedly bar-like supraorbital torus of African apes.

As discussed and illustrated elsewhere[24], the supraorbital region of neonatal anthropoid primates is devoid of later-emerging morphological detail and it is only for a few extant cercopithecids – particularly *Papio* and *Mandrillus* – that one can describe a truly »bar-like« supraorbital torus. In chimpanzees and gorillas, the supraorbital torus grows not only somewhat anteriorly, but also and markedly upward; as a result of the latter, there is a well-defined posttoral sulcus. The superior margin of the African ape supraorbital torus is not straight across, but, rather, often follows the contour of the orbit, and then dips down as its crosses the glabellar region. True, the glabellar region of African apes, RUD 44, and australopiths in general is somewhat broad, but it is also broad in humans and specimens attributed to *Homo*, hylobatids, colobines, many platyrrhines, and various Miocene non-orangutan-related hominoids. A broad glabellar region would, therefore, seem to be the primitive condition.

Returning to the matter of supraorbital »tori,« the misconception of australopiths having an African ape-like, and especially chimpanzee-like torus is, unfortunately, widespread. The chimpanzee-like image of early hominids is, however, widely reflected in reconstructions (such as of »Lucy«) in which the hominid is depicted with similar supraorbital structure when, in reality, no australopith cranium shows any supraorbital development of note in either an anterior or superior dimension[3,24,26]. The only way in which an australopith could have a chimpanzee-like brow is by adorning the supraorbital region with soft tissue – which would certainly not reflect the true bony anatomy of the former. Another way of

appreciating the »artistic license« taken in reconstructing australopith faces is by recognizing that no australopith cranium has a posttoral sulcus, which exists as a result of the development of a upwardly exaggerated supraorbital torus.

Australopith supraorbital margins may be thin (e.g. Swartkrans SK 48 and West Turkana KNM-WT 17000), moderately tall superoinferiorly (e.g. Sterkfontein Sts 5 and StW 505), or quite tall superoinferiorly (e.g. Olduvai OH 5 and Koobi Fora KNM-ER 23000), but they are not tori, especially in the context of this term being applied to the supraorbital regions of African apes and various monkeys. What is interesting about australopith supraorbital regions is that they are essentially mounded, which is also how this region is configured in the orangutan, *Sivapithecus*, *Ankarapithecus*, *Lufengpithecus*, and *Ouranopithecus*. In the case of the orangutan and Miocene fossils, »mounded superior orbital margins« is one of the configurations that has been argued as being synapomorphic of them and, thus, of an orangutan clade[2,27].

Among Begun's other »evidence« for RUD 44's possessing a supraorbital torus of any kind is that it had low and well-defined temporal lines that coursed up from behind the lateral orbital margins and converged slightly toward the midline. Clearly, this does not describe a torus or even justify believing that an »incipient« torus was present in this specimen. With expected differences in degrees of midline convergence of temporal lines, this description can also be applied accurately, for example, to the orangutan, *Sivapithecus*, *Ankarapithecus*, *Lufengpithecus*, and *Ouranopithecus*, as well as to all australopiths.

In further support of his theory of a close evolutionary relationship between *Pan* and *Australopithecus* Begun[28] invoked Ward and Kimbel's[29] (also ref. 30) depiction of African and Asian patterns of the subnasal region in fossil and extant large-bodied hominoids. As described, the African pattern is characterized by a descent or »stepping down« from the nasoalveolar clivus to the floor of the nasal

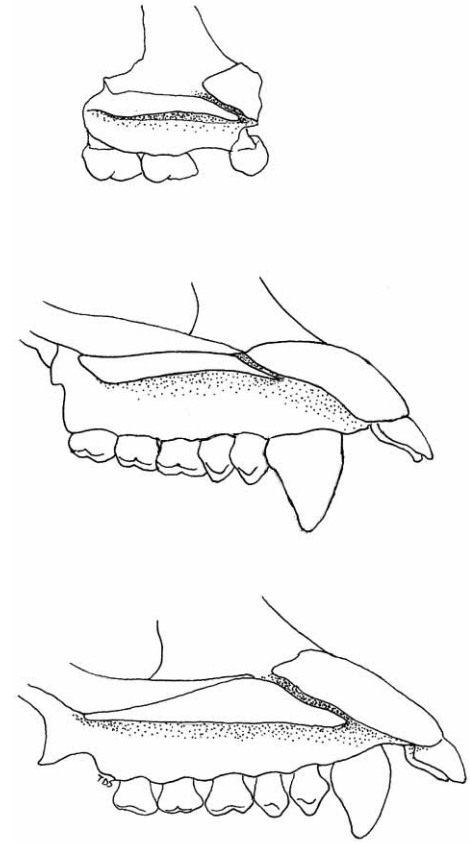

Fig. 1. Cross-sections of palates of StW 183a (top), Pongo *(middle), and* Pan *(bottom). In all the premaxilla (nasoalveolar clivus) is to the right, and is separated from the palate behind by an incisive canal. In* Pan*, the posterior pole of the nasoalveolar clivus rises above the floor of the nasal (creating the stepping down pattern), and the palate thins posteriorly. In* Pongo*, there is a smoother transition from the nasoalveolar clivus to the floor of the nasal cavity, and the palate thickens posteriorly. In the australopith, there is stepping down, but the palate thickens posteriorly. (*Pongo *and* Pan *redrawn from ref. 8). Not to scale.*

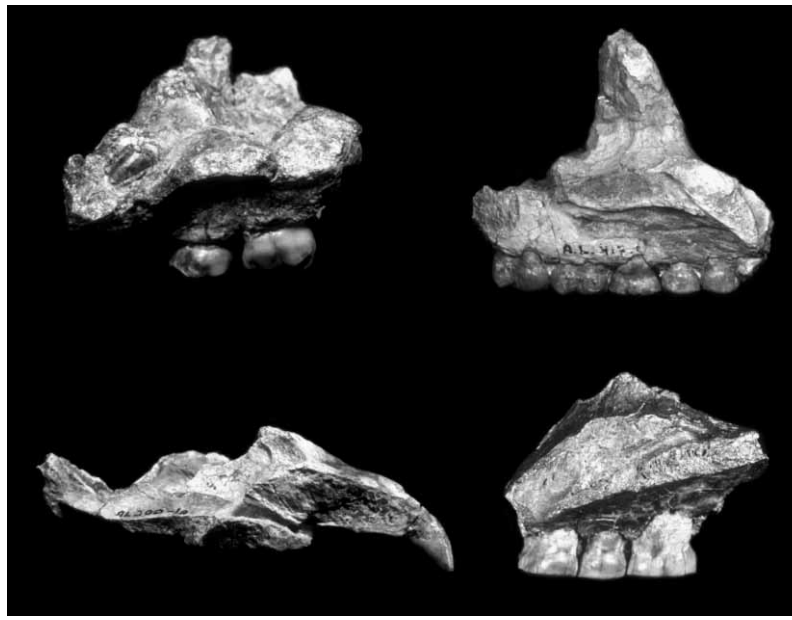

Fig. 2. Medial sections of australopith palates. Top: Hadar Al 333-86, left (left); Al 417-1d, right (right). Bottom: Hadar Al 200-1a, left (left); Omo uncatalogued, right (right). In all there is stepping down from the posterior pole of the nasoalveolar clivus to the floor of the nasal cavity. In Al 200-1a, the posterior part of the palate is broken, making assessment of palatal thickness difficult. In the others, the palate is clearly thickening posteriorly. Not to scale.

cavity and a posterior thinning of the palate. This configuration is seen in the African apes, with the degree of stepping down more markedly expressed in the gorilla. Although Ward and Kimbel discussed and illustrated only the AL 200-1a specimen from Hadar, Ethiopia, the African pattern was generally applied to australopiths (based on the notion then that *Australopithecus afarensis* was »ancestral« to all other hominids, including all other australopiths). In contrast, an Asian was distinguished from an African pattern by the criteria of there being more extensive overlap of the palate by the posterior pole of the nasoalveolar clivus, greater disparity between the posterior position of the »incisive fossa« in the floor of the nasal cavity and the position of the incisive foramen anteriorly in the palate, a relatively smooth transition from the nasoalveolar clivus onto the floor of the nasal cavity, and some thickening of the palate posteriorly (Figure 1). This configuration is seen in the orangutan and *Sivapithecus*, and has been cited as a feature uniting the two[29,30]. In his presentation, Begun (ibid.) used Ward and Kimbel's drawing of the cross- section of the palate of AL 200-1a.

Upon studying the AL 200-1a palatal specimens (right and left) I concluded that it was difficult to state definitively just how much posterior thinning there actually had been (Figure 2). The palatal pieces toward the posterior end are broken lateral to the midline, and it is typically the case that the bone of the palate thins lateral to the midline. But even if we assume that this one specimen does indeed display palatal thinning posteri-

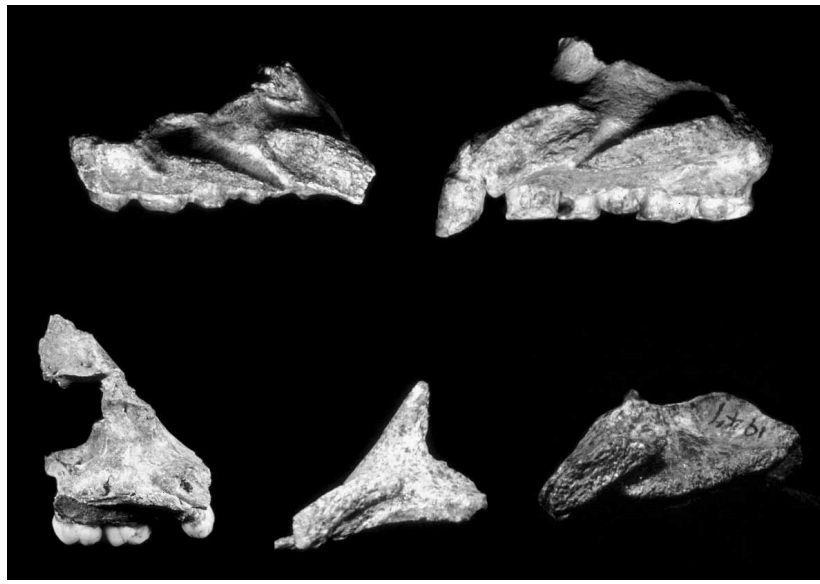

Fig. 3. Medial sections of australopith palates. Top: Kanapoi KNM-KP 29283, left and right. Bottom: Sterkfontein StW 183a (left); Makapansgat MLD 45 (center); MLD 9 (right). In all there is stepping down from the nasoalveolar clivus to the floor of the nasal cavity, and the palate thickens posteriorly. Not to scale.

orly, it is the outlier among potential australopiths (including other specimens from Hadar) inasmuch as the common configuration is palatal thickening to some degree[4] (also see descriptions in ref. 23): e.g. from Hadar, AL 333-86, AL 417-1a, AL 486-1, and probably AL 333-105; from Omo, an uncatalogued maxilla; from Kanapoi, KNM-KP 29283 (right and left maxillae, which may not actually be associated); from Makapansgat, MLD 9 and MLD 45; and from Sterkfontein, StW 183a (Figures 1–3). Although the premaxillary/nasoalveolar region of *Homo sapiens* is clearly autapomorphic in comparison with that of extant hominoids and australopiths, the palate does not thin posteriorly, as also is the case in fossil specimens referred to this genus[31–33]. Clearly, this configuration is »Asian,« not »African.«

The fact that australopiths display »stepping down« from the nasoalveolar clivus to the floor of the nasal cavity is not in contradiction with this latter observation. A survey of non-large-bodied hominoid primates, and mammals in general, demonstrates that the common and, thus, primitive, condition is a »stepping down« from the premaxillary/nasoalveolar region onto the floor of the nasal cavity. This is true even though the nasoalveolar region is not as tall as, and the palate much thinner than in, large-bodied hominoids. It is still the case that the thickened nasoalveolar region rises above the level of the floor of the nasal cavity behind. Large-bodied hominoids may be derived in having a taller nasoalveolar clivus and a thicker palate[34], but the general relationship of the nasoalveolar region rising above the level of the floor of the nasal cavity is retained in the extant African apes as well as in australopiths, *Lufengpithecus*, *Dryopithecus* from Rudabanya and Can Llobatares, and *Oura-*

nopithecus. In contrast, the derived condition would be reflected in a smoother transition from the nasoalveolar clivus to the floor of the nasal cavity, as seen, for example, in orangutans and *Sivapithecus*.

A Broader Look at Australopith Morphology

In addition to the features by which Ward and Kimbel[29] (also ref. 30) defined the »Asian pattern« and because of which they suggested that *Sivapithecus* was related to the orangutan, other apparently derived craniofacial and dental features support of this theory of relationship. These features include: tall ovoid orbits with mounded superior orbital rims; tall, narrow nasal bones; nar- row interorbital distance; small, piriform nasal aperture; forwardly facing anterior zygomatic arch roots; broad, tall, flat, and vertical infraorbital planes; marked disparity in size and shape between a large spatulate upper I1 and a small conical upper I2; facial pillars that extends from the upper canines up along the sides of the nasal aperture; and a long, slit-like single incisive foramen emergent through the palate[2,24,27,30,35] (see Figures 4 and 5 for craniofacial features).

The non-bar-/torus-like and more mounded morphology of the superior orbital rims of australopiths has already been discussed. Interestingly, although

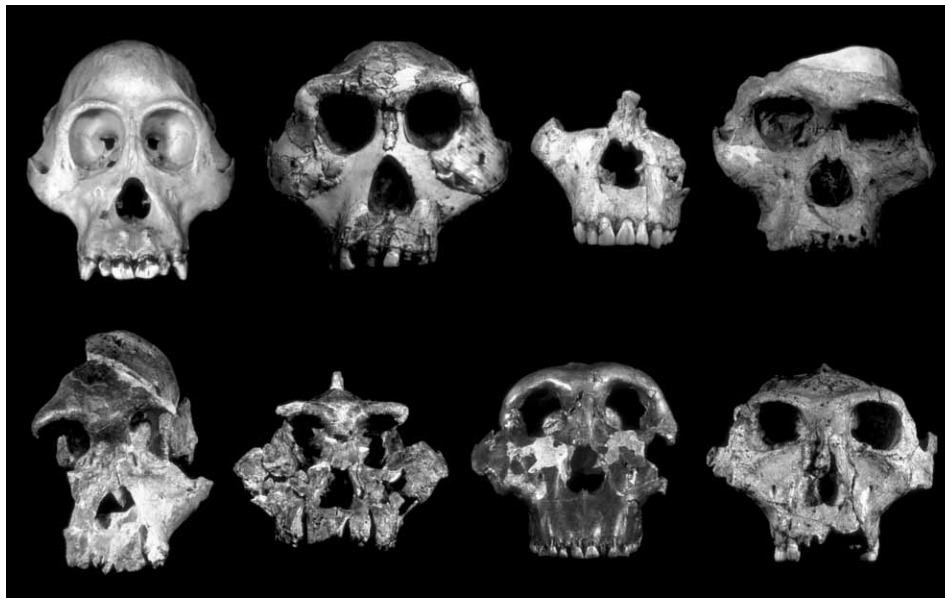

Fig. 4. Top (left to right): Pongo *(AMNH L.246, Q.10); Hadar Al 444-1 (reconstruction); Sterkfontein Sts 52a; Sts 5. Bottom (left to right): Sterkfontein StW 505; West Turkana, KNM-WT 17000; Olduvai Gorge OH5; Swartkrans SK 48. Although differing in facial width and flatness, the australopiths display* Sivapithecus-Pongo *cranial apomorphies, e.g mounded supraorbital rims (not bar-like tori), inwardly angled facial pillars that rise from the regions of the canines, and tall, forwardly facing, somewhat vertical infraorbital planes. Also, australopiths have subovoid-ovoid shaped orbits. Not to scale.*

Fig. 5. Top (left to right): Pongo *(as in Figure 4); Hadar Al 444-1; Sterkfontein Sts 5. Middle (left to right): West Turkana KNM-ER 17000; Swartkrans SK 48; Sterkfontein StW 505. Bottom (left to right): Drimolen DNH 7; Olduvai Gorge OH5; Sterkfontein StW 183a. Although differing in degree of facial flattening, the australopiths display* Sivapithecus-Pongo *apomorphies, e.g. mounded supraorbital rims (not bar-like tori with posttoral sulci), some amount of airorhynchy (as especially noted in the curvature of the tooth row), and tall, forwardly facing, somewhat vertical infraorbital planes. Not to scale.*

orbital outline in specimens allocated to the genus *Homo* can be subsquare (e.g. *Homo sapiens*) or »aviator-glass«-shaped (e.g. *Homo neanderthalensis*), ovoid orbits are also noted in various specimens (e.g. Koobi Fora KNM-ER 1813 and KNM-ER 1470, and West Turkana KNM-WT 15000). In australopiths, orbital shape may be subcircular (e.g. Koobi Fora KNM-ER 406 and Swartkrans SK 48), but it is also often ovoid (e.g. Sterkfontein Sts 5 and StW 505, Makapansgat MLD 6, Drimolen DNH 7, Koobi Fora KNM-ER 732 and ER 23000, Olduvai OH 5, and Hadar AL 333-105 and AL 444-2) (Figures 4 and 5).

In orangutans, *Sivapithecus*, *Ankarapithecus*, *Lufengpithecus*, *Dryopithecus* from Can Llobatares, and *Ouranopithecus*, the anterior root of the zygomatic arch faces forward, and the infraorbital plane is fairly-to-very wide, flat, and vertically oriented[36]. In this regard, infraorbital plane configuration and zygomatic orientation in australopiths becomes in-

teresting. In all australopith crania the anterior root of the zygomatic arch is anteriorly facing and the infraorbital plane broad and relatively tall (e.g. Taung 1; Swartkrans SK 46 SK 48, Drimolen DNH 7; Sterkfontein Sts 5, Sts 71, StW 13, and StW 505; Kromdraii TM 1517a; Makapansgat MLD 6; Olduvai OH 5; Koobi Fora KNM-ER 406 and ER 732; West Turkana KNM-WT 17000; Hadar AL 333-1, AL 333-86, AL 333-105, AL 417-1a, AL 444-2) (see descriptions and illustrations in ref. 23) (Figures 4 and 5). In most of these specimens, the infraorbital plane is also flat and fairly vertical. However, in some [e.g. SK 46, KNM-ER 406, KNM-WT 17000 (Figures 4 and 5)], as seen in side profile, the superior portion of the anterior root of the zygomatic arch arches posteriorly, facing more or less upward. In comparison to all other primates, this is surely a highly derived condition.

»Facial« or »canine pillars« of various degrees of expression that extend from the regions of the upper canines can be described for all large-bodied apes as well as many australopiths[23,24,37]. In chimpanzees and gorillas, pillars that are defined primarily on their lateral sides proceed essentially straight up from the alveolar regions of the canines, thereby staying quite lateral distant from the nasal aperture. In orangutans, the pillars are typically more clearly delineated and angle medially to course alongside and above the nasal aperture, creating somewhat of a pinched snout as a result of the fossa behind the pillar. *Sivapithecus*, *Ankarapithecus*, *Lufengpithecus*, and *Ouranopithecus* as well as *Dryopithecus* from Can Llobatares can be similarly described[24]. When pillars are visible (even faintly) on australopith faces (e.g. Taung 1, Sterkfontein Sts 5, Makapansgat MLD 6 and MLD 9, Drimolen DNH 7, Olduvai OH 5, Hadar AL 333-1, AL 333-86, AL 333-105, AL 417-1a, AL 444-2, and even Kromdraii TM 1517a), they conform to the configuration seen in orangutans and these Miocene taxa at least with regard to their orientation relative to the nasal aperture (Figures 4 and 5). In some specimens, such as OH 5 and KNM-ER 406, the lower face is extraordinarily broad and flat and lacks the »snout« otherwise seen in other specimens of australopith.

The long, slit-like single incisive foramen seen in orangutans, *Sivapithecus*, and *Ankarapithecus* – or any incisive foramen for that matter – cannot be identified in *Dryopithecus* from Can Llobatares, *Ouranopithecus*, or *Lufengpithecus*[24]. There may have been a large single incisive foramen in Rudabanyan *Dryopithecus* (= *Rudapithecus*)[24]. Interestingly, the Taung child clearly preserves a long, slit-like single incisive foramen. Nevertheless, when preserved, the common configuration in australopiths, as in hominids in general, is the presence of a medium-to-large single incisive foramen[23,32,34]. Juvenile chimpanzees and gorillas retain the primitive condition of two incisive foramina emerging through the palate (most consistently retained in adult gorillas, but sometimes remodeled in adult chimpanzees)[24,34]. The enigma of the Taung child aside, it is clear that, while a single incisive foramen is a derived condition among large-bodied hominoids, a long, slit-like single incisive foramen is even more derived (ibid.).

The interorbital region of orangutans (and more so in *Sivapithecus* than in *Ankarapithecus*) is narrow, while it is broad in Can Llobateres *Dryopithecus*, very broad in *Ouranopithecus*, and extraordinarily broad in *Lufengpithecus*[24]. It is narrow in australopith juveniles (e.g. Taung 1 and Hadar AL 333-105) but broad-to-very broad in australopith adults[23]. This developmental change is commonly seen in, and thus primitive for, anthropoid primates (ibid.) Juvenile Neanderthals and humans have somewhat wider interorbital regions than is typical of anthropoid

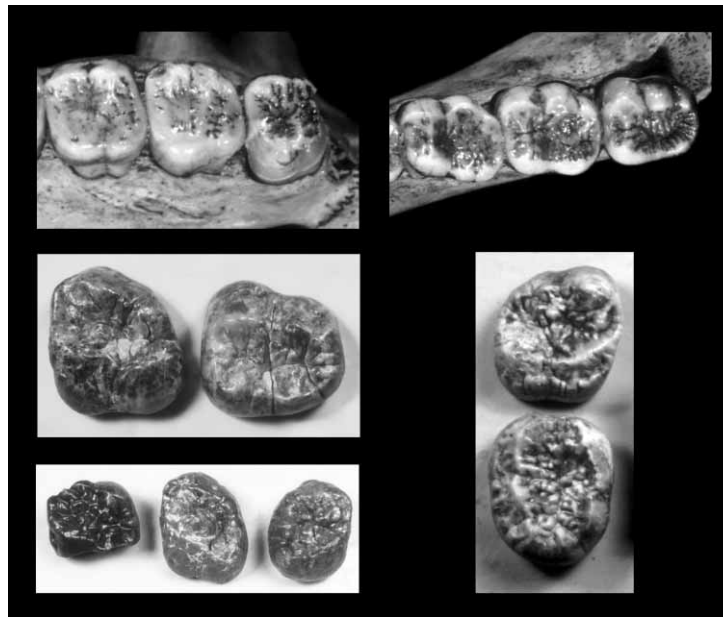

Fig. 6. Upper and lower molars of Pongo *(USNM 142180; left and right top), Sterkfontein StW 277 and 288 (left middle), Kanapoi KNM-KP 34725T and G (right lower), and Omo L51–5, L9–12, and L398–2608 (left lower). As in* Pongo*, these »australopith« teeth have cusps that are compressed and incorporated into the peripheral cresting systems around broad, shallow basins, and deep, thick enamel crenulation. Not to scale.*

juveniles (23; cf. illustrations in ref. 31), which would suggest that these hominids are apomorphic in this regard. Typically, adult specimens referred to the genus *Homo* have wide interorbital regions[32,33]. Regardless of interorbital breadth, however, the nasal bones of orangutans, *Sivapithecus*, *Ankarapithecus*, Can Llobatares *Dryopithecus*, *Ouranopithecus* and *Lufengpithecus* are long and in most cases relatively narrow[24]. They are also long and narrow in australopiths (see illustrations in ref. 23). To the contrary, and thus probably apomorphically, nasal bones are typically short in specimens referred to genus *Homo* (with the notable exception of the Bodo skull, in which, however, the nasal bones are also rather wide) (see illustrations in refs. 32 and 33).

Finally, it is worth noting that not only do potential members of the orangutan clade exhibit size and shape heteromorphy in the upper incisors, so, too, do some australopiths (e.g. StW 252, AL 200-1a), although their lateral incisor is not conical[23,24]. In other australopiths the anterior teeth are apomorphically tall and narrow mesiodistally.

Rethinking Australopiths in Light of an Orangutan Clade

The forgoing was not presented as a prelude to concluding that australopiths are more closely related to the orangutan clade than to the genus *Homo* (however many taxa that taxon unnaturally subsumes). What these comparisons do indicate, however, is that there is more potential apomorphy in common between australopiths and members of the orangutan clade than just low-cusped cheek

teeth and thick molar enamel, the latter of which characterize all hominids as well as members of the orangutan clade. Clearly, claims of synapomorphy between australopiths and *Pan*, if valid even minimally, are outweighed by the array of apomorphies shared by australopiths and members of the orangutan clade.

How might we incorporate these apparent synapomorphies into a theory of hominid – indeed hominoid – relationships (hominid being used here to refer to *Homo sapiens* and its fossil relatives)?

At present, these data suggest (to me, at least) not only that we must rethink the broader relationships of humans and apes, but also that we should probably rethink the question of »what constitutes an orangutan clade?«. In the context of a clade predicated on extant human and orangutan synapormophies (of which numerous can be delineated[4,38]), it might very well be that the relationships of some of the taxa that have been regarded as members of an orangutan clade actually lie outside this clade, perhaps as sister taxa to the larger human- orangutan clade. This might be the case for *Ouranopithecus* and even *Lufengpithecus*: e.g. the orbits of these hominoids, although bearing superior orbital mounding, are, however, subsquare in outline.

The relationships of australopiths may indeed lie closer to other hominids – those that currently constitute genus *Homo* – but the relationships of australopiths to one another is so uncertain that nothing more definitive than this obvious generalization can be made at this time[23]. Until an operational and testable definition of hominid is more clearly articulated and dealt with in rigorous systematic fashion, it would certainly be premature to proceed as if there was only a handful of hominid genera, with each supposedly being represented by not many more species. Indeed, until fossils that have been identified as hominid have been scrutinized further at the pre- alpha level of taxonomy, statements concerning »who's related to whom« are meaningless, especially because it is still unclear just how many morphs there might have been and how these morphs are related to one another (ibid.). The very fact that orangutan-like teeth pervade the drawers of specimens from supposed hominid sites of the Plio-Pleistocene of East and South African (e.g. from Sterkfontein, Kanapoi, Omo, Hadar) (ibid.) (Figure 6) should send a strong warning about this problem. The identification as hominid of specimens that, were they a few million years older, would undoubtedly be identified as fossil relatives of the orangutan should also signal that proclaimed early hominids that are either primitively chimpanzee--like (*Ardipithecus*) or surprisingly unchimpanzee-like (*Sahelanthropus*) are actually not hominids at all. Indeed, the presence of orangutan-like specimens in samples that have been identified as hominid not only strongly suggests that the chimpanzee is an inappropriate model on which to base interpretations of human origins, but also provides an answer to the longstanding question: What became of thick- enameled hominoids subsequent to the Miocene? The answer is: They have been identified as Plio-Pleistocene hominids.

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J. H. Schwartz

Departments of Anthropology and History and Philosophy of Science, University of Pittsburgh, Pittsburgh, PA 15260, USA
e-mail: jhs@pitt.edu

LOV NA POGREŠNOG ČOVJEKOLIKOG MAJMUNA – AUSTRALOPITECINI I POTRAGA ZA OSOBINAMA ČIMPANZI U FOSILIMA HOMINIDA

S A Ž E T A K

Potraga za osobinama čimpanzi u ranih hominida pojačala se nakon što tijekom 1980-tih godina dolazi do promjene u razmišljanjima o sličnosti od generalizirane sličnosti: čovjek-čovjekoliki majmun prema razlikovanju nivoa sličnosti orangutan-(gorila-(čimpanza-čovjek)). Rekonstrukcije ranih hominida postale su karikaturama čimpanzi, ne samo u karakteristikama mekih tkiva (npr. nosna regija), već i u pretpostavljenim koštanim strukturama (npr. anteriorno i naročito superiorno izbočen nadočni luk sa odvojenom brazdom iza luka). Unatoč naglašene »panofilije«, morfologija većine ranih hominida pokazuje zajedništvo sa linijom orangutana. Oni fosili koji pokazuju sličnosti sa čimpanzama, vjerojatno kladistički ne možemo ubrojiti u hominide.