

Lufengpithecus and Hominoid Phylogeny

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Problems in Delineating and Evaluating Phylogenetically Relevant Characters

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Introduction

In the 1970s, the first specimens of the large-bodied hominoid now referred to as *Lufengpithecus lufengensis* (Fig. 1) were discovered in the southern Chinese province of Yunnan, at the Shihuiba colliery site, which lies 9 km north of the town of Lufeng. The site, which is characterized by lignite deposits, is late Miocene (ca. 8 Ma) and thus approximately coeval with *Sivapithecus* sites in Turkey (Andrews and Tekkaya, 1980) and Indo-Pakistan (Pilbeam, 1982) and perhaps a few million years younger than the *Dryopithecus* sites in Hungary (Kordos, 1987; Kretzoi, 1975) and Spain (Moyà-Solà and Köhler, 1993).

Two virtually complete mandibles (both recovered in 1975), differing primarily in size, were referred to different taxa: a smaller *Ramapithecus lufengensis* and a larger *Sivapithecus yunnanensis* (Xu *et al.*, 1978; Xu and Lu, 1979). The latter differed from Indo-Pakistani *Sivapithecus* in having a wider and flatter digastric fossa and strongly wrinkled molar enamel. A partial,

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Fig. 1. Partial skull of apparent male *Lufengpithecus lufengensis* (PA 644) (not to scale). The nasal bones are missing, thereby making the nasal aperture appear taller than it actually is. For other details, see text. (©Jeffrey H. Schwartz)

somewhat crushed skull (PA 644) discovered in 1978 was referred to *S. yunnanensis*, which Lu *et al.* (1981) argued had been ancestral to *Pongo*, a link between *Proconsul africanus* and *Pongo*, and also related to *Paranthropus boisei*. In 1981, a smaller more complete skull (PA 677) was referred to *R. lufengensis* (Wu *et al.*, 1983). Although the site of Lufeng has so far yielded hundreds of teeth and jaws, cranial and even postcranial fragments, the two partial crania and the two original mandibles remain the most informative specimens.

In 1983 Wu *et al.* suggested that the larger and smaller Lufeng hominoids represented, respectively, male and female individuals of the same taxon, the proper designation of which would be *Sivapithecus lufengensis*; the hypothesis of extreme sexual dimorphism has since been further developed morphologically and metrically by Kelley and Eler (1989; also Kelley and Xu, 1991). Wu *et al.* (1983, pp. 9–10) also argued that all *Sivapithecus* were related to *Pongo* because they shared the following features: upturned premaxillary region [apparently correlated with airorhynchy (e.g., see Brown and Ward, 1988)]; concave midfacial skeleton; marked temporal ridges emanating from the lateral portion of the supraorbital margin and paralleling the margin prior to angling posteriorly; orbits with supraorbital margins not confluent across

glabella; narrow nasal aperture; deep canine fossae; laterally divergent upper canines and markedly curved upper central incisor roots with prominent jugae; moderately high-crowned cheek teeth; thick-enameled, occlusally crenulated molars lacking cingula.

But Wu *et al.* (1983) also delineated features that distinguished the Lufeng hominoid from other *Sivapithecus* as well as from *Pongo*: subrounded orbits; extremely wide interorbital region; concave interorbital and glabellar regions; concave to rounded nasoalveolar clivus; sub-"U"-shaped and slightly posteriorly divergent palate. Such distinctions later prompted Wu (1987, p. 271) to refer this hominoid to its own genus, *Lufengpithecus lufengensis*, to the diagnosis of which he added: face broad and short; hard palate broad, short, and shallow; orbits ovoid with somewhat angled outer corners and horizontal dimensions longest; posteriorly divergent dental arcade; molars with higher cusps and more occlusal wrinkling.

Although Wu did not address the potential phylogenetic relationships of this new genus, it would follow that if the craniodental features cited when *Lufengpithecus* was thought to be a species of *Sivapithecus* are both accurate and indicative of a close relationship with *Pongo*, then these features still are and do. The consequence of recognizing *Lufengpithecus* is that features hypothesized as being synapomorphic for *Sivapithecus* and *Pongo* cannot be derived at the level of the last common ancestor of these latter two taxa alone. Rather, these features would be synapomorphic at the level of a hypothetical ancestor shared by *Lufengpithecus*, *Sivapithecus*, and *Pongo*. And it is within this hypothesized clade that one must test the three alternative phylogenies: (1) *Sivapithecus* and *Pongo* are sister taxa; (2) *Lufengpithecus* and *Pongo* are sister taxa; (3) *Lufengpithecus* and *Sivapithecus* are sister taxa. As such, the issue then is not whether *Lufengpithecus* belongs to a *Sivapithecus*-*Pongo* clade, but whether, within this clade, *Sivapithecus* and *Pongo* are sister taxa. However, inasmuch as *Lufengpithecus* is not always included in phylogenetic analyses of hominoid relationships (e.g., Begun, 1992, 1994), or when it is, conflict remains about either its phylogenetic relationships or even if such can be determined (cf. Andrews, 1992; Kelley and Etler, 1988; Kordos, 1988), it seems necessary to address the basic phylogenetic question: To which hominoid(s) is *Lufengpithecus* most closely related?

Given the states of preservation of the specimens and the number of earlier contributions that refer to them (e.g., see review by Schwartz, 1990), little new description can be added here. However, the interpretation of the potential phylogenetic relationships of *Lufengpithecus* hinges on the determination of the polarity of the character states of its preserved morphologies. These features will be discussed comparatively among anthropoids by category, with the description of the feature in *Lufengpithecus* presented first. The comparative data derive in part from the literature, but primarily from study of more than 300 specimens of a diverse taxonomic array of nonhuman anthropoid primates, 500 modern human specimens, and either the originals or casts of relevant fossil material. With regard to extant taxa, ontogenetic

series were studied whenever possible. For the sake of simplicity, representative taxa will be discussed throughout.

Comparative Morphology

1. *Circumorbital region (including supraorbital torus and glabella): Lufengpithecus has low, mounded orbital rims and the orbits are separated by a broad but sunken glabellar region: it does not have a supraorbital sulcus.*

Prior to discussing morphology in detail, it is important to make two points. First, neonates of a species typically do not display the supraorbital configuration or glabellar distension that might ontogenetically come to characterize the adults. Even in species with the most marked supraorbital distension [e.g., *Mandrillus* (Fig. 2), *Gorilla* (Fig. 5)], development of this region is not evident in extremely young individuals (e.g., prior to the eruption of M1). In taxa that ultimately attain less marked supraorbital distension (e.g., *Cercopithecus*), development is also often minimal in subadult individuals.

Second, although a depression or "dip" behind or above the orbits is created either when the supraorbital region is vertically distended or when the frontal is elevated to any degree above the level of the superior orbital margin, the resultant "sulci" are not equivalent. One could describe the slight curve in the transition from the superior orbital rims to the frontal in *Lufengpithecus* [as well as, e.g., *Turkanapithecus*, *Sivapithecus*, *Pongo*, *Homo neanderthalensis*, some *H. erectus* (e.g., Sangiran 17, the Solo skulls), *Paranthropus*, *Australopithecus*, *Cercopithecus*, *Presbytis*, *Colobus*, hylobatids, and most platyrrhines] as a "supraorbital sulcus" because it is a depression, albeit a slight one, situated above (even if slightly above) the highest level of the superior orbital rim. Thus, a supraorbital sulcus can be identified whether the superior orbital margins bear mounded rims, are distended anteriorly into a barlike torus (in which case it could be identified as a supratoral sulcus), or are almost featureless. On the other hand, in taxa [e.g., adult African apes, *Macaca*, *Mandrillus*, *Papio*, some *H. erectus* (e.g., Zhoukoudian), *H. ergaster*] in which the superior orbital margin is distended such that it rises above the floor of a depression behind it, the term "posttoral sulcus" is appropriate, especially because a vertically enlarged superior orbital rim can be classified as a torus. The anteroposterior length of a posttoral sulcus and its vertical depth are affected by the relative degrees of horizontal versus vertical distension of the supraorbital torus as well as elevation of the frontal. One can discuss the disposition of sulci relative to glabella similarly, i.e., in defining a "supraglabellar" or a "postglabellar" sulcus. Bearing these points in mind, we can turn to specifics of orbital rim development.

In contrast, for example, to *Gorilla*, which often develops a continuous, barlike supraorbital torus, *Cebus*, *Colobus*, *Cercopithecus*, and *Homo sapiens* acquire with growth little, if any, orbital distension. At most, the supraorbital



Fig. 2. *Mandillus sphinx*. Infant (left; AMNH 99.1/1288); M1 erupted. Subadult (middle; AMNH 99.1/2776); M3s but not permanent canines erupting. Adult (right; AMNH 99.1/2049); M3s erupted. Scale in mm. ©Jeffrey H. Schwartz

margin of adult *Colobus* and *Cercopithecus* is a thin, minimally anteriorly distended rim. Superficially, adult *Cebus* (Fig. 3) appear to display some circum-orbital distension. However, this is an artifact induced by the temporal muscle, which leaves an elevated muscle scar around the perimeter of the orbit as a result of extreme midsagittal convergence; the midsagittally convergent temporal muscles create a sagittal crest that originates close to the region of glabella. As in African cercopithecines, the supraorbital–frontal region subtended between the temporal lines is in *Cebus* elevated or swollen to the height of the lines rather than forming the more commonplace supraorbital trigon, in which the temporal lines rise (even if slightly) above the level of the bone they subtend (e.g., as in *Turkanapithecus*, *Proconsul*, *Ankarapithecus*, *Dryopithecus*, *Victoriapithecus*, *Aegyptopithecus*, *Pongo*, *Gorilla*, *Paranthropus*). Otherwise in *Cebus* and African cercopithecines, the supraorbital configuration in midsagittal profile is convexly arcuate, with the curve flowing into the arc of the frontal bone. *Colobus*, *Cercopithecus*, and *Cebus* either do not, or only minimally, develop swelling in the region of glabella. *Proconsul* and *Cebus* may present similar midsagittal profiles (cf. Begun, 1994), but the similarity lies in both taxa developing a swollen glabellar region and not in the details of supra- or superolateral orbital morphology.

Among the Old World monkeys sampled, *Papio*, *Macaca*, and *Mandrillus*, for example, develop a barlike supraorbital torus that incorporates a distended or swollen glabellar region; in *Papio* glabella may be flexed superiorly. Supraorbital development may occur earlier ontogenetically (at least relative to the eruption of the first permanent molar) in *Macaca* than in the other two taxa, but this needs to be investigated further. Supraorbital toral development, especially in *Papio* and *Mandrillus*, tends to straighten the superior orbital margin (such that the orbit looks like a “D” lying on its side with the straight side up) (Fig. 2). Thus, the supraorbital torus of these cercopithecids can be described as barlike in that not only is it horizontally oriented but it is also relatively uniformly thick from side to side. In these cercopithecids, the supraorbital torus projects noticeably anteriorly, but rises only slightly above the sulcus behind it. Because there is also little vertical elevation of the frontal, the posttoral sulcus is anteroposteriorly long but shallow.

Hylobatids are distinct in their development of thin, anteriorly protruding orbital rims. In juveniles, the medial portions of the rims do not project beyond the broad, flat glabellar region. Ontogenetically, however, the medial margins often become distended and thus in the adult project farther anteriorly than the somewhat domed glabellar region. Apparently in concert with the almost telescopic enlargement of the entire orbital rim, the hylobatid zygoma (which forms the lateral wall of the orbit) increases in size disproportionately and thus autapomorphically. Hylobatids do not have a supraorbital sulcus.

The African apes are distinguished among extant large-bodied hominoids by development of a relatively uniformly thick supraorbital torus that is

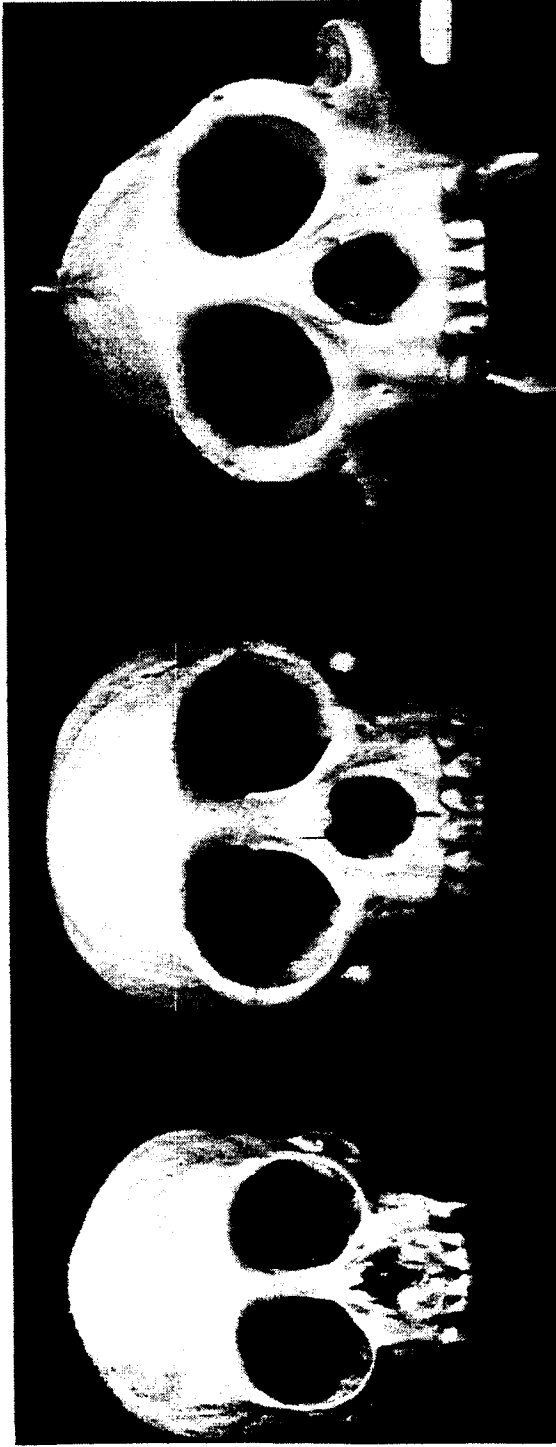


Fig. 3. *Cerbus* sp. Infant (left; AMNH L. 85): dm3s erupted. Juvenile (middle; AMNH 99.1/2074): permanent canines half-erupted, M2s erupted, M3s not yet erupting. Adult (right; AMNH L. 41): M3s worn. Scale in mm. ©Jeffrey H. Schwartz

continuous across glabella (Figs. 4 and 5). However, whereas in male *Gorilla* the supraorbital torus is often straight across from side to side and barlike (as described by Andrews, 1992; see Fig. 5), in *Pan* (Fig. 4) and female *Gorilla* it typically follows the rounded contour of the superior margin of the orbit. At glabella, the torus is typically straighter across in *Gorilla*; it often "dips" downward in *Pan*. Although the glabellar region broadens ontogenetically in both African apes, it tends to remain flatter in *Pan*. In both apes, the supraorbital torus projects anteriorly and is also variably distended vertically, albeit more noticeably in *Pan* than in *Gorilla*. Thus, the posttoral/postglabellar sulci of these hominoids can be variably shallow to moderately deep (Figs. 4 and 5). The depth of the sulcus is also affected by frontal elevation, which is most marked in *Pan* and female *Gorilla*.

Although it has been suggested that certain fossil taxa share similar supraorbital configurations with one or both African apes (e.g., Andrews, 1992; Begun, 1992, 1994; Dean and Delson, 1992), this is not the case in detail. For example, *Ouranopithecus* may have had a broad and swollen glabellar region, but it lacked a vertically distended or barlike torus and thus a posttoral sulcus (cf. Bonis and Koufos, 1993, p. 470). Descriptively, the superior orbital margins of *Ouranopithecus* are surmounted by moderately tall, uniformly thick but low moundlike rims that are confluent across a downwardly flexed glabellar region; there is also a sulcus above. The glabellar region of *Dryopithecus* may also have been broad, but it and the supraorbital regions were only slightly swollen and delineated above by merely faint sulci (cf. Begun 1992, 1994; Kordos, 1987; Moyà-Solà and Köhler, 1993). Frontal elevation and glabellar swelling are remarkably similar in *Dryopithecus* and *Proconsul* (cf. Begun, 1994; Walker *et al.*, 1983), although, in the former, the more medially arcuate temporal lines create a more restricted, shallow supraorbital trigon. Rather than being presumptively or incipiently toral, the superior orbital margins of *Dryopithecus* simply bear low moundlike rims (cf. Begun, 1994; Moyà-Solà and Köhler, 1993).

Orangutan orbital margins are apomorphic for extant anthropoids (including hylobatids) in that they bear low, mounded rims that are most prominent superiorly (Fig. 6). In further contrast to hylobatids, adults retain the juvenile configuration. Because orangutans also retain into adulthood the narrow interorbital region characteristic of the juvenile, the orbital rims (apomorphically) abut one another at the midline.

The orbital rims of *Sivapithecus*, *Ankarapithecus*, and *Lufengpithecus* are similar in detail to *Pongo* (e.g., Andrews and Cronin, 1982; Kelley and Pilbeam, 1986; Schwartz, 1990; Wu *et al.*, 1986). Thus, regardless of any hypothesis of primitiveness versus derivedness in catarrhine supraorbital toral development (e.g., no torus versus an anteriorly projecting versus a vertically distended bar), *Lufengpithecus*, *Ankarapithecus*, *Sivapithecus* and *Pongo* appear to be synapomorphic in circumorbital configuration. The sunken glabellar region of *Lufengpithecus* is certainly autapomorphic among extant and known fossil anthropoids, although the primitiveness or derivedness of other config-



Fig. 4. *Pan troglodytes*. Infant (left; AMNH L. 19/ Ch. 7); dm2s erupted. Adult (right; AMNH L. 211/Ch. 14); M3s erupted. Scale in mm. (©Jeffrey H. Schwartz)

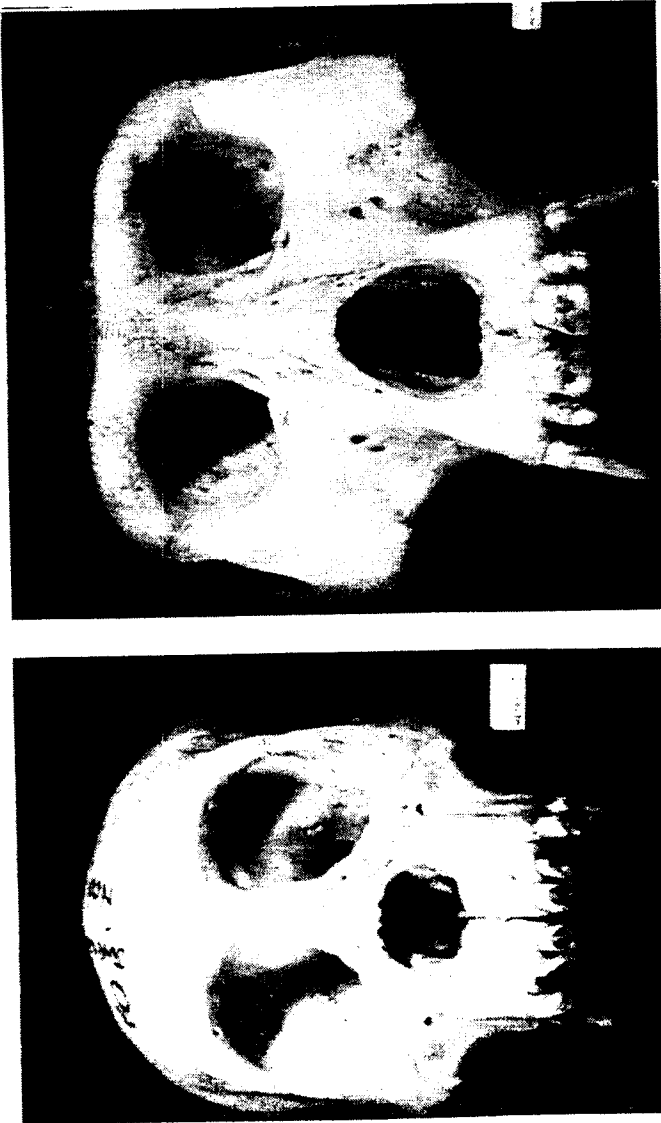


Fig. 5. *Gorilla gorilla*. Juvenile (left; AMNH 99.1/2251): dm2s and M1s erupting. Adult (right; AMNH 99.1/2044): M3s worn. (©Jeffrey H. Schwartz)



Fig. 6. *Pongo pygmaeus*. Infant (left; AMNH L. 28); M1s erupting. Adult (right; AMNH 140426); M3s worn. Not to scale (©Jeffrey H. Schwartz)

urations is unclear: for example, a rounded but somewhat low (as in *Proconsul*, *Dryopithecus*, various New and Old World monkeys, and apparently *Turkanapithecus* and *Afropithecus*) or depressed (as in *Ankarapithecus*) glabellar region, versus a more swollen one (as in other New and Old World monkeys). Seemingly synapomorphically, the glabellar regions of *Pongo* and *Sivapithecus* are obscured by the appression of right and left orbital rims.

2. *Thickening of lateral orbital margin:* In *Lufengpithecus* the orbital rim is continuous with the frontal process of the zygoma; the zygoma broadens inferiorly alongside the orbit; an appearance of superolateral thickening is created by a distinct, raised, thick, and ridgelike temporal line that courses up, around, and over the lateral orbital margin.

In general among catarrhines, and in contrast to prosimians and platyrrhines, the zygoma broadens inferiorly with differences between taxa being in the breadth of the zygoma inferiorly (e.g., compare the broad inferior zygoma of *Victoriapithecus* with the narrower inferior zygoma of *Cercopithecus*). Within the broader comparison among primates, the catarrhine configuration may represent another potential synapomorphy of this anthropoid clade. The development of lateral orbital margin thickening, however, is different in different taxa. It can be absolute (ontogenetic), expanded as a wall to the temporal muscle behind it, or built up via the surmounting of the rim by the temporal line superolaterally.

For example, in *Cebus* the lateral and superior portions of the orbital rim expand proportionately as a shelf anterior to the temporal muscle. The wider or broader adult lateral orbital margin maintains the characteristic shape of the juvenile, in which the outer edge follows the curvature of orbital shape. Thus, a superolateral "corner" is not thickened (there is no corner) and the base of the frontal process of the zygoma does not expand at the level of the inferior orbital rim (Fig. 3). In *Pongo*, on the other hand, the orbital margin superolaterally and especially superiorly thickens and the frontal process of the zygoma tends to broaden as it proceeds down the side of the orbit (Fig. 6). The amount of superolateral marginal thickening in *Pongo* is related to the degree to which the temporal lines are enlarged and expand up and around this part of the orbital rim (see also discussion of supraorbital costae in Clarke, 1977). For example, the temporal lines of some male *Pongo* extend as crestlike structures for much of the length of the supraorbital rims. *Dryopithecus*, *Ouranopithecus*, *Ankarapithecus*, *Sivapithecus*, and *Lufengpithecus* are similar to *Pongo* in lateral orbital morphology, including the superolateral course of the thickened temporal line along the supraorbital margin. *Lufengpithecus* is the most distinctive in temporal line prominence.

In *Victoriapithecus*, *Turkanapithecus*, *Afropithecus*, *Pan*, and *Gorilla*, as well as some New And Old World monkeys and hominids, the temporal lines may appear to thicken the superolateral margin of the orbit, but the position of these muscle scars remains posterior (even if slightly) to the supraorbital margin. In taxa with an anteriorly protruding supraorbital torus [and thus also a

posttoral sulcus, e.g., *Papio*, *Mandrillus*, *Macaca*, *Pan*, and *Gorilla* (Figs. 2, 4, and 5)], the lateral margin of the torus (and thus the superolateral margin of the orbit) is accentuated from behind by the sulcus. In some *Gorilla*, the supraorbital torus is thickened medial to the downward turn of the zygomatic process of the frontal and/or just at the superolateral "corner" of the orbit.

Given the above, it appears that a hominid/African ape/*Ouranopithecus* clade within Anthropoidea cannot be delineated on the basis of thickening of the lateral orbital margin (cf. Andrews, 1992). In contrast, the possession by *Dryopithecus*, *Ouranopithecus*, *Ankarapithecus*, *Lufengpithecus*, *Sivapithecus*, and *Pongo* of a thickened temporal line that courses up and around the superolateral margin of the orbit (which also bears a low moundlike rim) emerges as potentially phylogenetically significant. *Ouranopithecus*, in which the thickness of the supraorbital mound continues around and down the side of the orbit, may be uniquely derived in this regard.

3. *Orbital shape: The orbits of Lufengpithecus are horizontally ovoid/rectangular.*

In most juvenile anthropoids the orbital margins are rounded or arced and are either vertically ovoid (taller than wide) or subcircular (height and width subequal). In many anthropoids, orbits become longer or wider ontogenetically, therefore changing from vertically ovoid to subcircular [e.g., *Cebus*, *Pan*, *Gorilla* (Figs. 3–5)], or from subcircular to longitudinally rectangular or elliptical (e.g., *Colobus*, *Papio*). In other anthropoids, however, the juvenile orbital shape is retained into the adult: subcircular (e.g., *Hylobates*, *Macaca*), vertically ovoid (*Pongo*; Fig. 6), or square or rectangular (humans). With regard to other shapes and changes, mandrills, for example, have natively longitudinally ovoid orbits that become rectangular in the adult.

The orbits of *Afropithecus* were taller than wide and bean-shaped (Leakey *et al.*, 1988b); *Sivapithecus*, tall and vertically ovoid (Pilbeam, 1982); *Ouranopithecus*, wide and horizontally rectangular (Bonis and Koufos, 1993); *Turkanapithecus*, square (Leakey *et al.*, 1988a); Rudabányan *Dryopithecus*, taller than wide and "D"-shaped (Kordos, 1987, 1991) and *Ankarapithecus*, about subequal in height and width (Alpagut *et al.*, 1996) and possibly "D"-shaped. The orbits of Can Llobateren *Dryopithecus* also look "D"-shaped but have been reconstructed as either taller than wide (Moyà-Solà and Köhler, 1993) or slightly wider than tall (Begun, 1994).

Although it seems reasonable to conclude in the absence of an ontogenetic series that adults with vertically ovoid or tall orbits or with horizontally rectangular or wide orbits possess differently derived configurations, it is difficult, in light of the above, to use orbital shape in the generation of any particular theory of relatedness. Thus, for example, the tall and vertically ovoid orbits of *Sivapithecus* and *Pongo* can be argued as synapomorphic for the two, but only after their relationship has been hypothesized on the basis of other, more clearly discernible potential synapomorphies. With regard to *Lufengpithecus*, the shape of the orbits are best interpreted as autapomorphic for it.

4. *Interorbital distance: It is (extremely?) broad in Lufengpithecus.*

With the exception of hylobatids and humans, extant anthropoid neonates typically have narrow interorbital regions. In some anthropoids (e.g., *Pongo*, cercopithecines, and some platyrrhines), the narrow neonatal configuration is retained into the adult (Figs. 2 and 6). In other anthropoids (e.g., the African apes, colobines, *Cebus*, and other platyrrhines), the interorbital region broadens ontogenetically (Fig. 3–5).

The broader comparison among extant anthropoids leads to the interpretations that: (1) humans and gibbons are derived (presumably independently so) in retaining the neonatally broad interorbital region into the adult; (2) the African apes and cercopithecines are primitively anthropoid in ontogenetically broadening the interorbital region; (3) *Pongo* and colobines are derived (presumably autapomorphically so) in retaining the neonatally narrow interorbital region into the adult (see also Delson, 1975, for Old World monkeys). Only if hylobatids are defined *a priori* as primitive relative to extant large-bodied hominoids (as is often the case, in morphological and molecular studies) could the retention into the adult of a neonatally broad interorbital region be conceived of as being primitive for the clade.

In the absence of relevant juvenile specimens, phylogenetic hypotheses concerning fossil taxa would be restricted to those in which adults possess one of two potentially apomorphic states: either a narrow interorbital region or one that is relatively broader than is typical of anthropoid primates. Thus, “narrow interorbital region” reemerges as a potential synapomorphy linking *Ankarapithecus*, *Sivapithecus*, and *Pongo* (cf. Alpagut *et al.*, 1996; Andrews and Cronin, 1982; Brown and Ward, 1988; Kelley and Pilbeam, 1986). The narrow interorbital region of *Victoriapithecus* must also be interpreted as apomorphic (at some hierarchical level within Anthroidea) and not indicative of the primitive catarrhine state (cf. Benefit and McCrossin, 1991). On the other hand, such taxa as *Aegyptopithecus*, *Dryopithecus*, *Afropithecus*, *Turkana-pithecus*, and *Ouranopithecus*, with their broad, but not excessively broad, interorbital regions remain primitive in this regard. Only if the interorbital region of *Lufengpithecus* is excessively broad (e.g., Wu *et al.*, 1983)—but it may not be (e.g., compared to *Pan*; Schwartz, 1990)—would it be (aut)apomorphic.

5. *Nasal aperture: It is small and piriform in Lufengpithecus.*

In most anthropoids (as well as prosimians) the nasal aperture of juveniles and adults is thin and tall in outline and is at least as narrow inferiorly as superiorly. Specific, common configurations are an upside-down triangle (e.g., *Macaca*, *Colobus*) or an ellipse [e.g., *Mandrillus*, *Cebus* (Figs. 2 and 3)]. *Proconsul* and *Victoriapithecus* retain this basic primitive configuration, but the nasal aperture is more diamond-shaped in outline.

In juvenile and adult hylobatids, the nasal aperture is primitively broader superiorly than inferiorly, but it is broader (i.e., less narrow) overall than is typical of nonhominoid anthropoids. From what is preserved (the inferior

portion is missing), nasal aperture shape in *Turkanapithecus* appears similar to hylobatids.

In contrast to other extant anthropoids, extant large-bodied hominoids—from the juvenile to the adult—are distinctive in having a nasal aperture of different proportions: it is noticeably narrower superiorly than inferiorly and the wide inferior margin is relatively straight across. In *Pan*, *Gorilla*, and hominids, the nasal aperture is either roundly triangular or trapezoidal (Figs. 4 and 5), while in *Pongo* it is small and roundedly triangular [and often referred to as piriform (= pear-shaped)] (Fig. 6).

With regard to fossils, *Afropithecus* has been described as having a small, piriform nasal aperture (Leakey *et al.*, 1988b). Indeed, its nasal aperture is actually more pear-shaped compared with *Pongo* in that the superior portion is constricted relative to the base, which is slightly distended inferiorly at the midline; qualitatively, as in *Ankarapithecus*, the nasal aperture of *Afropithecus* appears relatively larger (especially taller relative to lower facial height) than the orangutan's. Within the confines of the comparisons here, *Afropithecus* might be synapomorphic with extant large-bodied hominoids in overall nasal aperture shape (i.e., narrower superiorly than inferiorly), but autapomorphic among anthropoids in having a truly pear-shaped nasal aperture. The shape and vacuity of the nasal aperture in *Ouranopithecus* and apparently Rudabányan *Dryopithecus* (only the floor of the nasal aperture is known) may be similar to *Pan* and *Gorilla*. In *Sivapithecus* and *Lufengpithecus*, the size and shape of the nasal aperture approximate those of *Pongo*. If we posit that a large, roundedly triangular or trapezoidal nasal aperture (typical of the majority of large-bodied hominoids) is primitive for the clade, then the small aperture of *Sivapithecus*, *Lufengpithecus*, and *Pongo* emerges as derived and potentially synapomorphic for them.

6. *Lower facial triangle: The canine fossa is deep in Lufengpithecus and the markedly midsagittally angled canine "root" pillars delineate a triangular snout.*

Depending on the length of the snout, and the height and robustness of the upper canine root, a diversity of anthropoids can be described as having a depression between the region of the canine root and the infraorbital region. The question is whether to identify this depression as a canine fossa. A consistent observation, however, is that in most anthropoids the canine roots (and/or the moderately stout pillars that continue up from the regions of the roots) do not veer or converge markedly toward the midline. Differences lie among the large-bodied hominoids.

Gorilla is similar to *Pan* in having relatively vertical canines (especially crowns) but root pillars that sometimes angle inward slightly (Fig. 4 and 5). These pillars do not course alongside the lateral margin of the nasal aperture and they do not set off the snout significantly from the rest of the lower facial skeleton. Juvenile *Pan* are similar to the adult, but in juvenile and the occasional adult *Gorilla* (e.g., see figure in Dean and Delson, 1992), a thickening

may course up from the region of the upper canine root, arc inward, and wrap around the side of the broad nasal aperture. In these latter cases the snout thus appears semicircular in configuration and "pinched" off from the facial skeleton behind by a broad canine fossa (Fig. 5).

In *Pongo* (Fig. 6), the canine roots and relatively straight, long, and stout root pillars converge noticeably, paralleling the sides of the small triangular nasal aperture and further emphasizing the triangularly shaped snout, which is set off from the facial skeleton by a fairly deep but not particularly broad canine fossa. These features are retained from the juvenile into the adult and would seem to be apomorphic within Anthroidea.

Ouranopithecus has a shallow canine fossa of moderate size. This hominoid, as well as *Turkanapithecus*, *Proconsul*, and apparently *Dryopithecus*, are also similar—but primitively so—to *Pan* and *Gorilla* as well as most anthropoids in having canine root pillars that neither converge markedly inward nor extend fully along the lateral margins of the nasal aperture (cf. Bonis and Koufos, 1993). A shallow to moderate fossa lies over the region of M¹ in *Turkanapithecus* and *Proconsul*, whereas *Dryopithecus* appears to have a true canine fossa. *Afropithecus* is interesting in that its canine roots/pillars are moderately convergent, but the pillars are neither markedly swollen nor do they extend fully along the sides of the nasal aperture. A restricted but relatively deep fossa lies over the region of the first molar, well back along the long snout. At present it is probably reasonable to conclude that *Afropithecus* is primitively anthropoid in root pillar stoutness, snout length, and (supramolar) fossa configuration, and presumably autapomorphic in canine root convergence. *Ankarapithecus* has slightly more medially convergent root pillars than *Afropithecus* that extend farther along the sides of the nasal aperture in the larger-canined MTA 2125 than in the smaller-canined AS 95-500 (cf. Alpagut *et al.*, 1996; Andrews and Tekkaya, 1980). Both specimens of *Ankarapithecus* have a pronounced canine fossa (*ibid.*). *Sivapithecus* and *Lufengpithecus*, however, are presumably synapomorphic with *Pongo* in having markedly convergent canine roots/stout pillars that parallel the margins of a small nasal aperture. These three taxa also have moderately deep but constricted canine fossae.

7. *Zygoma (maxillary/facial component) and maxilla (infraorbital component):* The zygomatic/maxillary plane is vertically flat and deep and anteriorly facing in *Lufengpithecus*.

The typical anthropoid zygoma can be characterized thusly: (1) when viewed from above, it arcs posteriorly away from the lateral margin (and thus the plane) of the orbit and (2) when viewed from the side, the inferior margin of the facial root of the zygoma lies posterior to the inferior margin of the orbit and thus the zygoma is inferoposteriorly arcuate. This is noted clearly in New and Old World monkeys as well as in hylobatids. Although *Afropithecus* is often depicted with its orbits facing rather superiorly, orienting the facial skeleton to the plane of the cribriform plate (and thus the Frankfort horizon-

tal) reveals that this hominoid had the primitive zygomatic configuration. *Turkanapithecus* retained both primitive states and *Proconsul* at least the first.

In general, the great ape zygoma faces anteriorly more than in most other anthropoids and that of *Pongo* is the most forwardly facing (Figs. 4 and 6). Viewed from the side, the inferior margin of the gorilla zygoma lies posterior to the plane of the inferior margin of the orbit. The inferior margin of the zygoma of *Pan* may be somewhat more anteriorly situated, but the bone retains the primitively inferoposteriorly arcing configuration. *Pongo* is unique among the great apes in that the inferior margin of its zygoma lies directly beneath or even slightly anterior to the inferior margin of the orbit. Thus, the anterior surface of its zygoma is flat and vertical and in the same plane as the orbit. Among anthropoids, the configuration of the orangutan zygoma would seem to be apomorphic.

Sivapithecus and *Lufengpithecus*, as well as *Ankarapithecus* (Alpagut *et al.*, 1996; Andrews and Tekkeya, 1980), (given what is preserved) *Ouranopithecus* (cf. Bonis and Koufos, 1993; Schwartz, 1990), and *Dryopithecus* (cf. Begun, 1994; Kordos, 1987; Moyà-Solà and Köhler, 1993) share, presumably synapomorphically with *Pongo*, a vertically flat and deep and anteriorly facing zygoma.

8. *Zygomaticofacial foramina (number and position): Lufengpithecus had at least one large foramen situated superior to the inferior margin of the orbit.*

Andrews and Cronin (1982) suggested that the possession by *Sivapithecus* and *Pongo* of multiple large zygomaticofacial foramina situated superior to the inferior margin of the orbit was synapomorphic for them. Schwartz (1990) pointed out that the male and female crania of *Lufengpithecus* as well as the female Rudabányan *Dryopithecus* could be described similarly, as later did Moyà-Solà and Köhler (1993) and Begun (1994) for Can Llobateren *Dryopithecus*.

Review here of the larger sample of anthropoids reveals, however, that the number of zygomaticofacial foramina is more variable from individual to individual than previously thought. The more consistent development of only one zygomaticofacial foramen appears to characterize only *Mandrillus* (Fig. 2) and *Colobus*. Thus, with regard to foramen number, neither can *Pan* and *Gorilla* be unequivocally distinguished from *Pongo* nor the latter united phylogenetically with *Sivapithecus* or any other taxon.

Foramen position is variable among New and Old World monkeys; i.e., in some individuals (of the same taxon) the foramen lies below, in others it is level with, and in yet other individuals it lies slightly above the inferior margin of the orbit (in these anthropoids, zygomaticofacial foramina should not be confused with another foramen that is often found in the zygomaticofrontal suture at the lateral margin of the orbital rim). In the African apes, however, the zygomaticofacial foramen (or foramina) more consistently lies below the inferior margin of the orbit, whereas in *Pongo* this foramen (or foramina)

more consistently lies above the inferior orbital margin (Figs. 4 and 6). Among extant hominoids, *Pongo* is apomorphic in developing a large foramen (or foramina). In terms of foramina position and size, *Sivapithecus*, *Lufengpithecus*, *Ankarapithecus*, and *Dryopithecus* (see above) emerge as potentially synapomorphic with *Pongo*. The region is insufficiently preserved in *Ouranopithecus* to be revealing.

9. *Subnasal region: Lufengpithecus may have had a flat nasal floor and upwardly rotated premaxilla.*

Brown and Ward (1988) and Kelley and Etler (1989) described the subnasal region of *Lufengpithecus* as similar to the African apes (stepped down nasoalveolar clivus; broad incisive fossa and canal in the floor of the nasal cavity), whereas Kordos (1988) concluded that it was synapomorphically like that of *Sivapithecus* and *Pongo* (extensive overlap of the maxilla by the posterior pole of the premaxilla; small incisive fossa and long, narrow incisive canal). Neither of these configurations is clearly evident in the specimens (Schwartz, 1990), but there are features of the upper incisors and the anterior margin of the premaxilla that contribute to a tentative partial reconstruction.

In the male *Lufeng* cranium, the upper central and lateral incisor crowns are oriented more orthally than procumbently, but the long roots of the central incisors are curved, paralleling the contour of the upper surface of the premaxilla. The preserved right lateral incisor and the alveoli of the other incisors in the female cranium present a similar picture. The curvature of the male's central incisor roots and the intact portions of the nasoalveolar region of the female indicate that the descent from this region into the floor of the nasal cavity was not steep. Although noted in the occasional chimpanzee (McCollum *et al.*, 1993), a relatively flat transition from the nasoalveolar clivus to the floor of the nasal cavity is typical of *Pongo* and apparently *Sivapithecus* (Ward and Kimbel, 1983). Recent cleaning of the *Ankarapithecus* specimen MTA 2125 (Begun and Gülec, 1995) revealed a mildly stepped nasoalveolar region (Alpagut *et al.*, 1996). If there is a correlation between having enlarged, curved upper incisor roots and a long, upwardly tilted premaxilla, as in *Ankarapithecus*, *Sivapithecus*, and *Pongo* (see Kelley and Pilbeam, 1986), then the same can be inferred for *Lufengpithecus*. Inasmuch as a markedly stepped down transition from the nasoalveolar clivus to the floor of the nasal cavity and an unrotated premaxilla [as in *Gorilla* (Ward and Kimbel, 1983) and apparently also *Ouranopithecus* (Bonis and Koufos, 1993; Bonis and Melentis, 1978, 1985)] appear to be primitive features for large-bodied hominoids (Martin, 1986; Schwartz, 1984), the configurations in *Ankarapithecus*, *Sivapithecus*, *Pongo*, and *Lufengpithecus* would be synapomorphic for them.

With regard to other aspects of the nasal region, the narrowness of the nasal aperture of *Lufengpithecus* mitigates against the presence of a broad or deep incisive fossa (= depression in the floor of the nasal cavity), as is seen in *Gorilla* (cf. Ward and Kimbel, 1983). But without evidence of the vomer it is difficult to place the "boundary" between the posterior pole of the premaxilla

and the maxilla and, thus, to locate the two openings in the floor of the nasal cavity (one on either side of the vomer) that represent the apertures of the incisive canals. In *Pongo* and *Sivapithecus*, these apertures are situated farther back in the nasal cavity than in *Pan* (Ward and Kimbel, 1983). On the oral cavity side of the Lufeng palates, it is impossible to determine if there was a single incisive foramen (and, if so, if it was long and slitlike, as in *Pongo* and *Sivapithecus*) or some version of two incisive foramina (as in *Gorilla* and *Pan*) (Schwartz, 1983, 1988). Until these various apertures are identified, one cannot be certain about the length or vacuity or the incisive canal(s).

10. *Paranasal sinuses: Lufengpithecus had superiorly expanded maxillary sinuses.*

Brown and Ward (1988; see also Ward and Brown, 1986) suggested that *Lufengpithecus*, *Ouranopithecus*, and Rudabányan *Dryopithecus* (RUD-44) were similar to *Pongo* and *Sivapithecus* in having air cells in the interorbital region that derived from the maxillary rather than ethmoidal sinuses. Although Begun (1992) interpreted these air cells in RUD-44 as ethmoidal derivatives, and thus as "true" frontal sinuses (cf. Cave and Haines, 1940), Moyà-Solà and Köhler (1993) disagreed. For Can Llobateren *Dryopithecus* Begun (1994) described (p. 19) and illustrated (p. 21) a pair of large, symmetrical, unifocal air cells that are separated from one another by a midline bony septum that courses from nasion to a level below the supraorbital notch; at this point the air cells diverge and each courses over the medial portion of the supraorbital rim (the fully preserved left sinus tapers toward its end). Begun (p. 19) also suggested that, as judged from the right side, these sinuses communicated with the maxillary sinuses. And, indeed, these "frontal sinuses" are not dissimilar in their morphology and disposition to examples given by Schultz (1936, pp. 269–270) for superior maxillary sinus expansion in *Pongo*, but are dissimilar to the multifocal, asymmetrical air cells that constitute the frontal sinuses in the African apes and humans, in particular. In addition, Moyà-Solà and Köhler (1993) described a separate ethmoidal sinus in Can Llobateren *Dryopithecus*.

Since "superiorly expanded maxillary sinuses" has been proposed as a potential synapomorphy of *Pongo* and *Sivapithecus* (e.g., Ward and Kimbel, 1983), the issue of paranasal sinus development is not a trivial one: *Lufengpithecus* as well as *Ankarapithecus*, *Ouranopithecus*, and *Dryopithecus* could be united with *Pongo* and *Sivapithecus* by this character. Although Begun (1994) presents an interesting topographical argument for identifying a frontal sinus as an ethmoidal derivative (e.g., by its position relative to glabella), the criteria are not universally applicable to African apes or fossil hominids. On the basis of communicating drainage passages, however, humans and African apes develop ethmofrontal sinuses (Cave and Haines, 1940; Hershkovitz, 1977), apparently by primitive retention, as is further suggested by the presence of ethmofrontal air cells in *Proconsul africanus* (Walker and Teaford, 1989) and "*P. major*" [i.e., the upper jaw/lower facial specimen (UMP

62-11) from Moroto, Uganda (Pilbeam, 1969), which now seems to be referable to *Afropithecus* (e.g., Andrews, 1992), the most complete cranial specimen of which does have a sinus above the region of glabella (Leakey *et al.*, 1988b)]. If development of ethmofrontal sinuses (or at least ethmoidal air cells) is primitive for large-bodied hominoids and superiorly expanded maxillary sinuses apomorphic within this clade, the lack of a multifocular ethmoid in taxa with superiorly expanded maxillary sinuses could be interpreted not as a primitive retention, but as an apomorphic consequence of superior maxillary expansion.

11. The dentition.

Lufengpithecus shares with most large-bodied hominoids—but not *Dryopithecus*, *Proconsul*, or the extant African apes—the development of relatively thick molar enamel. In some features *Lufengpithecus* is most similar to *Pongo*; e.g., the upper central and all lower incisors are relatively high-crowned, molar occlusal foveae are less restricted (and cusp apices are situated at crown margins), molar crown relief is reduced, and enamel wrinkling dominates molar occlusal morphology (even in worn teeth) (Kelley and Pilbeam, 1986; Wu *et al.*, 1983).

Sivapithecus, *Lufengpithecus*, *Ankarapithecus*, and *Pongo* are similar in that, e.g., the upper incisors are strongly heteromorphic (in size and shape) with central incisors being somewhat spatulate, the upper canines are markedly angled outward (i.e., the root pillars converge midsagittally), and (with the apparent exception of *Ankarapithecus*) unworn molars are crenulated to some degree (Schwartz, 1990). *Dryopithecus* may have had relatively shorter and less laterally expanded upper central incisor crowns, but, as in *Sivapithecus*, *Lufengpithecus*, and *Pongo*, they bore strong lingual pillars (Begun, 1994). These four hominoids, as well as *Ankarapithecus* and *Ouranopithecus* lacked molar cingula.

Lufengpithecus appears to share dental apomorphies with at least *Sivapithecus* and *Pongo*, but finer phylogenetic resolution is not at present decipherable.

Conclusion

Clearly some of the problems attendant to unraveling the phylogenetic relationships of *Lufengpithecus* to other large-bodied hominoids—"large-bodied hominoid" itself being a phylogenetic hypothesis—are related to overwhelming autapomorphy, especially as reflected in its sunken superior interorbital, glabellar, and lower interorbital regions. No other known primates can be so described, including hylobatids. Also seemingly autapomorphic for *Lufengpithecus* is the development (in both male and female) of thickened, ridgelike, temporal lines, which, having coursed up and around the lateral

orbital margins, are perfectly straight as they proceed posteriorly along the cranium. When viewed in the context of an overall morphological pattern rather than in terms of individual character states, *Lufengpithecus* might appear to be at the same time generally similar to all large-bodied hominoids (because of primitive retention) and yet similar to none specifically (because of autapomorphy) (cf. Kelley and Eter, 1989; Kelley and Pilbeam, 1986).

The autapomorphies and plesiomorphies aside, *Lufengpithecus* shares specific features with extant *Pongo* and Miocene *Sivapithecus*: nasal aperture size (small), convergence (marked) and extent (along the nasal margins) of upper canine root pillars, canine fossa depth (relatively deep), incisor crown height (high), molar enamel surface (crenulated), and some aspects of the nasal floor (flat) and premaxilla (upwardly rotated). If these features are apomorphic for *Pongo* and *Sivapithecus*, they are as well for *Lufengpithecus* and thus are potentially synapomorphic at the level of a hypothetical ancestor shared by these three taxa. Other cited synapomorphies of *Pongo* and *Sivapithecus* are found in *Lufengpithecus*, *Ankarapithecus*, and either *Ouranopithecus* or *Dryopithecus*, or both. These include orbital rimming (superior, low, mounds), zygomaticofacial foramen size (large) and position (above inferior orbital margin), orientation of zygoma (anteriorly directed and vertical), upper incisor size and shape relationship (heteromorphic), and upper central incisor crown morphology (broadly spatulate, with lingual pillar).

Although these five taxa do indeed appear to constitute a clade, the incompleteness of specimens of *Ouranopithecus* and *Dryopithecus* makes difficult resolving the sister relations of one or the other to the hypothesized *Pongo*–*Sivapithecus*–*Lufengpithecus*–*Ankarapithecus* clade. Tentatively, *Ouranopithecus* may be the sister taxon of this clade and *Dryopithecus* the sister taxon of all (Moyà-Solà and Köhler, 1993; Schwartz, 1990). Of course, more complete specimens of these fossil taxa as well as specimens of new taxa could very well demonstrate a different set of hierarchical relationships within the larger hypothesized *Pongo* clade. But the potential phylogenetic viability of “a *Pongo* clade” (see also Begun and Gülec, 1995; Moyà-Solà and Köhler, 1993) provides some fodder for a functional discussion of the craniofacial features of *Lufengpithecus* and other hominoids.

Consider the condition of airorhynchy, which has been described as variably present in *Pongo*, *Sivapithecus*, hylobatids, some Old and New World monkeys, and possibly *Aegyptopithecus* and *Pliopithecus* (e.g., see reviews in Brown and Ward, 1988; Schultz, 1968; Shea, 1988). Shea (1988), for example, has argued that the lack of a supraorbital torus and sulcus in these taxa is reflective of their airorhynchous condition and that the distribution among anthropoids of airorhynchy implies that this condition is primitive for hominoids. As such, Shea (1988) interprets klinorhynchy and the development of a supraorbital torus and sulcus as correlated and synapomorphic of hominids and African apes. Brown and Ward (1988), however, argue that airorhynchy and the associated craniofacial features of *Pongo* and *Sivapithecus* are derived among anthropoids and thus reflective of the relatedness of the former two

taxa. Certainly, *Pongo* and *Sivapithecus* are very different craniofacially from virtually all other anthropoids (e.g., in frontal elevation, orbital rimming, interorbital distance, lower facial configuration, palatal thickening, upward premaxillary rotation and posterior distension). In addition, as illustrated here, one cannot generalize about supraorbital tori or sulci solely with regard to size or "presence" versus "absence." Thus, one should not conflate any amount of supraorbital thickening in conjunction with a shallow supraorbital sulcus (as, e.g., in *Turkanapithecus*, *Colobus*, *Paranthropus*) with a vertically distended supraorbital torus associated with a distinct posttoral sulcus (as, e.g., in *Mandrillus*, *Homo ergaster*, the African apes). This is relevant not only to claims of similarity in supraorbital torus and posttoral sulcus configuration in, for example, *Dryopithecus*, *Ouranopithecus*, African apes, and hominids (e.g., compare Andrews, 1992; Bonis and Koufos, 1993; Begun, 1992, 1994; Shea, 1988), but also to attempts to correlate supraorbital morphology with either klino- or airohynchy (e.g., Ravosa and Shea, 1994; Shea, 1988). It may be that airohynchous animals lack supraorbital tori and posttoral sulci, but so do many klinorhynchous animals, some of which lack any kind of supraorbital distension whatsoever [e.g., *Daubentonia*, marmosets, tamarins; see also Shea's (1988) illustration of *Cebus albifrons*]. In fact, very few klinorhynchous primates develop a true supraorbital torus and posttoral sulcus (*Mandrillus*, *Papio*, *Macaca*, *Pan*, *Gorilla*, *Homo ergaster*, some "*H. erectus*"), which suggests that such craniofacial hafting is not necessarily functionally correlated with the development of the torus and sulcus.

It appears that the only feature shared by all airohynchous primates is dorsal deflection of the palate. Other features, such as upwardly oriented orbits or premaxillae, are not universal but taxon specific and may exist in the absence of an airohynchous condition (e.g., the variably dorsally oriented orbits of *Nycticebus*). With regard to the features enumerated above that distinguish *Pongo* and *Sivapithecus* from other airohynchous primates, it would be tempting to conclude that they were interrelated and functional correlates of the specific type of airohynchy that these two hominoids develop. Palatal thickening and posterior premaxillary elongation may, however, be synapomorphies of large-bodied hominoids (Andrews, 1992; McCollum *et al.*, 1993; Schwartz, 1983) rather than a feature associated with airohynchy, but upward rotation of the premaxilla could still be so correlated as might also be other features of *Pongo* and *Sivapithecus* (such as low-mounded rimmed and tall, ovoid orbits, narrow interorbital region, lack of ethmoidally derived frontal sinuses, superior expansion through the interorbital region of the maxillary sinus, anteriorly facing and vertical infraorbital/maxillary plane, outwardly rotated upper canine with strongly convergent root pillars, and deep canine fossae).

But just because we find these features together does not mean that they are all functionally or developmentally correlated. And this is where other taxa, such as *Lufengpithecus*, become even more relevant. Does the fact that *Lufengpithecus* had superiorly expanded maxillary sinuses or an anteriorly

facing, deep, vertical infraorbital/maxillary plane mean that it, too, was airorhynchous? If upper canine root curvature is correlated with an upwardly rotated premaxilla, does this indicate that *Lufengpithecus* was airorhynchous? Clearly, the development of low-mounded rimmed orbits (as in *Lufengpithecus*, *Sivapithecus*, *Pongo*, as well as *Ankarapithecus*, *Ouranopithecus*, and *Dryopithecus*) is not correlated with the development of tall, ovoid orbits or the retention into the adult of a narrow interorbital region (*Sivapithecus*, *Pongo*). If *Lufengpithecus* was airorhynchous, then these latter features are not functional correlates of airorhynchous in (although they may be synapomorphies of) *Sivapithecus* and *Pongo*. Rather, *Pongo* and *Sivapithecus* happen to be airorhynchous hominoids which also happen to share the apomorphies of tall, ovoid orbits and paedomorphically narrow interorbital regions.

Even if we had more complete specimens of *Lufengpithecus*, and knew for certain that this hominoid had been airorhynchous, we would still have to try to sort out which features found together are functionally correlated and which just happen to be together, either because of a hierarchy of primitive retentions (including the apomorphies of the last common ancestor) or autapomorphy.

At present, the only clues to *Lufengpithecus* having been airorhynchous come from inferences about which features really are correlated with this configuration: a *Pongo*-like subnasal floor and curved upper incisor roots. If *Lufengpithecus* is the sister of (or at least a member of a clade that includes) *Pongo* and *Sivapithecus*, then, perhaps, (1) low-mounded rimmed orbits, (2) outwardly rotated upper canines with stout, medially convergent root pillars, (3) deep canine fossa, (4) anteriorly facing, flat and vertical infraorbital/maxillary plane, (5) superior maxillary sinus expansion, and (6) small, piriform nasal aperture are not just potential synapomorphies of these three hominoids, but also functional correlates of airorhynchous. However, characters 1, 2, and 3 describe not only these three taxa but also *Ouranopithecus* and *Ankarapithecus*, if not *Dryopithecus*, as well. If *Ouranopithecus* were klinorhynchous [but the claim was based on the assertion that this hominoid as well as the African apes and hominids possessed a barlike supraorbital torus and sulcus (Dean and Delson, 1992)], then features 4 and 5, although potentially synapomorphic for the hominoids that possess them, are only coincidentally (i.e., by way of primitive retention) associated with airorhynchous. However, the two preserved premaxillary regions of *Ouranopithecus* (Bonis and Melentis, 1978; Bonis and Koufos, 1993) appear to be upwardly rotated, suggesting that this feature might be a synapomorphy of *Ouranopithecus*, *Lufengpithecus*, *Sivapithecus*, and *Pongo* (to the exclusion of *Dryopithecus*), and, once more, begging the question of which morphology is functionally correlated with airorhynchous. Inasmuch as *Dryopithecus* appears not to have been airorhynchous, it would seem that little craniofacial morphology is specifically functionally correlated with dorsiflexion of the splanchnocranium.

Lufengpithecus is an important hominoid taxon. But its importance derives less from our ability to imbue it with scenarios of the functional significance of

its morphology than from its effect on our reconstructions of the phylogenetic relationships of the large-bodied hominoids. And, at least with regard to craniofacial morphology, it appears that the particular theory of relationship informs the interpretation of functional morphology.

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