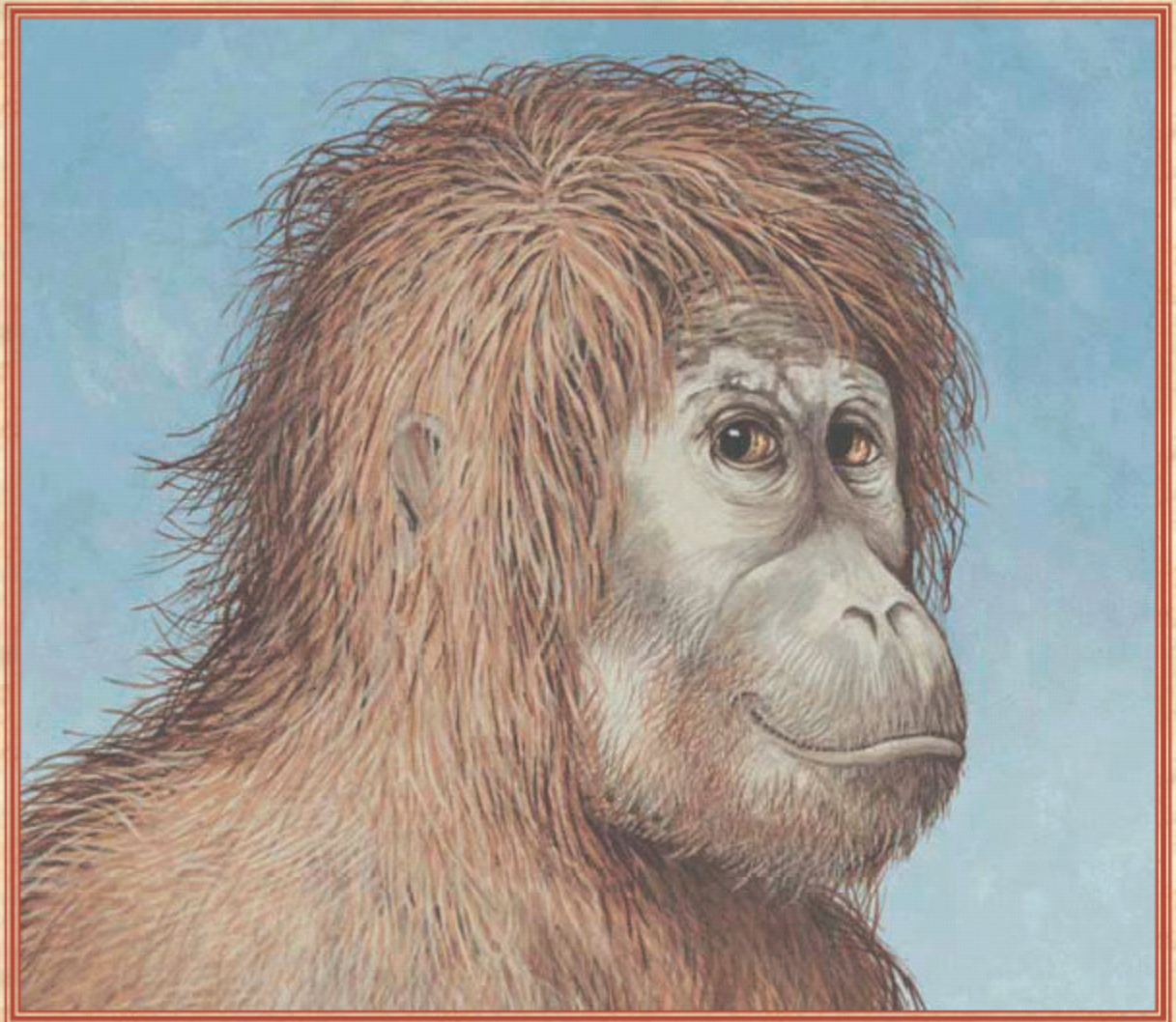


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Mona Lisa Smile: The Morphological Enigma of Human and Great Ape Evolution

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Mona Lisa Smile: The Morphological Enigma of Human and Great Ape Evolution

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The science of human evolution is confronted with the popular chimpanzee theory and the earlier but largely ignored orangutan theory. The quality and scope of published documentation and verification of morphological features suggests there is very little in morphology to support a unique common ancestor for humans and chimpanzees. A close relationship between humans and African apes is currently supported by only eight unproblematic characters. The orangutan relationship is supported by about 28 well-supported characters, and it is also corroborated by the presence of orangutan-related features in early hominids. The uniquely shared morphology of humans and orangutans raises doubts about the almost universal belief that DNA sequence similarities necessarily demonstrate a closer evolutionary relationship between humans and chimpanzees. A new evolutionary reconstruction is proposed for the soft tissue anatomy, physiology, and behavioral biology of the first hominids that includes concealed ovulation, male beard and mustache, prolonged mating, extended pair-bonding, “house” construction, mechanical “genius,” and artistic expression. *Anat Rec (Part B: New Anat)* 289B:139–157, 2006. © 2006 Wiley-Liss, Inc.

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INTRODUCTION

Primate evolutionists have looked to Africa as the home of our nearest living great ape relatives from the time Charles Darwin first speculated on the geographic coincidence between apes and what he believed were “primitive” humans in this region (Schwartz, 1987). It is now widely accepted that DNA sequence similarities not only support the African ape connection, but also demonstrate that we share a unique common ancestor with chim-

panzees, followed by the gorilla, and lastly by the orangutan (Goodman et al., 1983; Ruvolo, 1997; Wildman et al., 2002; Genome Sequencing and Analysis Consortium, 2005; McBrearty and Jablonski, 2005). Some evolutionary biologists even consider humans to be little more than an unusual “third” chimpanzee (Diamond, 1993; Goodman et al., 1998). There remains, however, a paradoxical problem lurking within the wealth of DNA data: our morphology and physiology have very little, if anything, uniquely in common with chimpanzees to corroborate a unique common ancestor. Most of the characters we do share with chimpanzees also occur in other primates, and in sexual biology and reproduction we could hardly be more different (Schwartz, 2004a, 2005). It would be an understatement to think of this as an evolutionary puzzle (Grehan, 2006a). The usual solution is to invoke the loss of the African ape features following our divergence from the common ancestor (Povinelli and Cant, 1995; de Waal, 2002; Pusey, 2002; Richmond and Strait, 2003). This ad hoc solution might be plausible if it were not for the incongruous fact that humans share many unique

features with the orangutan. This ape is not only the least similar to humans in DNA sequence similarity, but the very ape nearly universally considered the most primitive of all living great apes.

The orangutan first became a serious contender in the human evolutionary stakes when Schwartz (1984a) identified various “human” features that turn up only in the orangutan. Over the last 2 decades, the number has increased to about 40 anatomical, physiological, skeletal, and behavioral characteristics (Schwartz, 2005). This similarity is double the 17 that Groves (1986) proposed for the chimpanzee: a total he has since reduced to as little as 7 (Shoshani et al., 1996). The evolutionary implications for the genetic evolution of humans have never been fully examined by proponents of the chimpanzee theory. Responses by Goodman et al. (1994), Begun (1999), and Groves (2004) did appeal to falsification from molecular and morphological studies, but their sources were either published prior to the theory (Andrews and Cronin, 1982; Ciochon, 1983), never addressed the orangutan evidence (Groves, 1986; Ruvolo, 1994; Eastal et

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al., 1995), or questioned only a few characters (Andrews and Martin, 1987).

Resolution of the morphological evidence is vital for the study of primate evolution because the early fossil record relies exclusively on morphology, and molecular systematics looks to morphology to link fossils with living taxa and calibrate molecular clocks. The following sections review three principal human-African ape research programs that incorporate original observations along with broad outgroup comparisons (Andrews and Martin, 1987; Begun, 1992, 1999; Shoshani et al., 1996; Begun et al., 1997). Recent uncritical literature searches limited to humans and apes are excluded (Collard and Wood, 2000; Gibbs et al., 2002). Derived features linking humans and orangutans are those proposed by Schwartz (1984a, 1987, 1988, 2005). All characters are reviewed to verify published sources and discuss the evolutionary implications for currently popular DNA sequence models of human origin as well as reconstructions of hominid (humans and their closest fossil relatives) ancestral anatomy and biology.

HUMAN-CHIMPANZEE/AFRICAN APE EVIDENCE

Andrews (1987) and Andrews and Martin (1987)

Human-African ape

Of 12 proposed characters, 3 (few apocrine glands, many eccrine glands, small single larynx tuberculum) are not currently contested (Schwartz, 2005):

Supraorbital tori continuous: The African ape infraorbital torus with posterior sulcus does not characterize humans, or any fossil hominid with the exception of some specimens traditionally allocated to *Homo erectus* (Schwartz, 1997; Schwartz and Tattersall, 2002, 2003, 2005).

Postorbital sulcus developed: Incorrect, as above.

Frontal sinus derived from expansion of the ethmoid: A variety of Oligocene and Miocene fossils, including *Aegyptopithecus*, *Ankarapithecus*, *Morotpithecus*, *Oreopithecus*, *Otaviipithecus*, *Proconsul*, and *Turkanapithecus*, also have a frontal sinus (Rossie, 2004), and ethmofrontal sinuses may

not be unique to humans and African apes (Rossie et al., 2002). Frontal sinuses are also absent from *Homo floresiensis* (as illustrated by Brown et al., 2004) and they are usually small or absent in bonobos (also later overlooked by Strait and Grine, 2004). Frontal sinuses do occur in orangutans as extensions of the maxillary sinuses (Schwartz, 1984b), and CT scans of australopiths StW 505 and Sts 5 also appear to show the maxillary sinus extending up through the interorbital region, as in orangutans and *Sivapithecus* rather than humans or African apes (J.H. Schwartz, personal communication).

Fusion of os centrale with scaphoid: Also occurs in orangutans and gibbons (Schwartz and Yamada, 1998). Developmental studies of bone formation show a prenatal reduction of separate carpals through fusion or absence of the cartilaginous anlage of the os central in humans, while postnatal mineralization of the soft connective tissue between the os centrale and scaphoid occurs in other hominoids (Cihák, 1972). Absence of the os centrale in humans is not developmentally homologous with other hominoids.

Greater middle ear depth (8.5–12.5 mm): Not scaled to body or skull size or compared with other primates.

Subdivision of prostrate: No documentation or comparison with other primates.

Large uterus: Not scaled to body size. Linear dimensions group humans (52–55 mm) with gorillas (52 mm) rather than chimpanzees (37–40 mm) or orangutans (28 mm) (Schwartz, 2005).

Large axillary organ: Apocrine glands in humans are mostly restricted to the arm pit, where they comprise a “lavishly developed” axillary organ while the gorilla, chimpanzee, and, “to a lesser extent,” the orangutan also have an axillary organ (Montagna and Ellis, 1963). If the axillary organ is a uniquely shared feature for great apes and humans, a larger size for humans and African apes could be derived or primitive for large bodied hominoids while the orangutan size is derived. At this time, there is no evidence to support the human and African ape condition as a shared derived condition to the exclusion of the orangutan.

Low proportion of type I aorta (3%–21% vs. 63%–100% in other hominoids): Groves (1986) documented 3%–11% for humans, 21% for chimpanzees, 11% for gorillas, 94% for orangutans, 100% for gibbons, and 63%–88% for monkeys. These values would place gorillas closer to humans than chimpanzees and monkeys closer to humans and African apes than orangutans.

Human-chimpanzee

According to Andrews (1987), there is no morphological evidence for a cladistic relationship between humans and chimpanzees. The following characters are from Andrews and Martin (1987):

First and second incisors similar in shape: Undocumented. This linear comparison links taxa with teeth that are otherwise morphologically different (Schwartz, personal communication).

Obliteration of the premaxilla in adults: The premaxilla of the human fetus is already united with the maxilla through ossification of a maxillary isthmus, across which there is mesenchymal continuity from the onset of facial development (Schwartz, 1995).

Earbone axis of ear bones over 90°: Overlaps the range for monkeys (88–100°). Gibbons (80°) are more similar in this feature to humans than gorillas (79°) or orangutans (75°) (Groves, 1986).

Reduction of lower molar protocristid grooves: Undocumented, and not supported by Groves' (1986: appendix) characterization of the human and monkey protocristid as “fair” compared with “slight or absent” in chimpanzees, and “tiny or absent” in orangutans.

Shoshani et al. (1996)

Human-African ape

Of 27 proposed characters, 8 are not currently in dispute (Schwartz, 2005). Three that comprise linear or area measurements are not directly comparable because they are not scaled to body size: middle ear depth over 8.5 mm² (character 102), inner ear area over 50 mm² (character 104), and uterus size over 37 mm (character

231). Problems raised by Schwartz (2005) for the remaining characters are as follows:

Downward flexing of the face (character 106): Also occurs in all Old World and most New World monkeys and is evident in fossil apes such as *Aegyptopithecus* and *Afropithecus* (Leakey et al., 1991).

Frontal sinus (character 111): Also present in a variety of fossil apes (see above for Andrews and Martin, 1987).

Prominent trochlear keel (character 155): This feature may be applicable to all large-bodied hominoids and it is largest in gorillas.

Separation of a short ulnar styloid process from the carpal bones (character 65): Also applies to gibbons and orangutans as acknowledged by Shoshani et al. (1996: p. 134).

Separation of the recurrens ulnaris artery into anterior and posterior branches (character 219): No comparisons with nonhominoid primates to validate a derived state within hominoids.

Conjunct rotation of the carpus (character 137): No documentation for humans to confirm spiral groove on the hamate (unciform) and constriction on the capitate (magnum) that guides the distal carpals into a stable lock (Shoshani et al., 1996), and not observed in humans by Schwartz (2005).

Dorsal transverse ridges on the metacarpal heads (character 139): No documentation of these knuckle walking elements in humans, and not observed by Schwartz (2005).

Fusion of the os centrale (character 138): Not applicable to humans (see above for Andrews and Martin 1987).

Greater development of the protocrista (character 175): No documentation. The feature is poorly developed in all hominoids.

Lengthened small intestine as a percentage of head and body length (character 197): Groves (1986: appendix) records humans at 6.2%–10.4%, chimpanzees at 6.3%–6.8%, gorilla at 9.4%, orangutan at about 4.5%, gibbons at 3.8%–5.9%, and monkeys at 2.9%–8.4%. The gorilla is most derived while chimpanzees fall within the range of monkeys, orangutans, and gibbons.

Caudal position of heart lower than the sixth rib (character 216): The po-

sition in monkeys (ribs 6/8) and orangutans (rib 6) recorded by Groves (1986: appendix, p. 213) suggests the feature has a wider distribution.

Human-chimpanzee

Similar size of first and second premolars in mesiodistal occlusal view for males (character 48): An undocumented linear dimension. Chimpanzee teeth are morphologically more like gorillas than humans, so the linear similarity may be uninformative. The linear characteristics would also exclude hominids such as *Australopithecus afarensis*, where the size of the first and second premolar is dissimilar (Schwartz, personal communication). A similar premolar size shared by female orangutans and humans was acknowledged, but excluded (Shoshani et al., 1996).

Adult obliteration of the premaxillary suture (character 130): Although supported by Groves (1986) and Strait and Grine (2004), it is not applicable to humans (see above for Andrews and Martin 1987).

Fusion of the ankle epiphyses preceding fusion of the elbow and hip epiphyses (character 154): Attributed to Schultz (1944), but his Figure 20 identified human fusion patterns as elbow-hip-ankle (shared with orangutans, gorillas, gibbons, and monkeys) and elbow-ankle-hip sequence. Neither of these corresponds to the elbow (in part)-hip (in part) and elbow-hip overlapping the chimpanzee ankle sequence.

Digastric muscle attachment to the inside lower jaw (character 187): Uninformative for the orangutan, where the inferior belly of the digastric is absent.

Brain-to-body weight ratio greater than 11 (character 220): Documented only for hominoids. Gibbons (ratio 10–11) are closer to humans than chimpanzee (11.41), followed by the orangutan (8.48) and finally gorilla (8.37).

Delay of puberty at least 7 years (character 224): Greater than other hominoids (Groves, 1986: Table 4a, character 7), but overlaps the range for gorillas (6–7 years) and orangutans (6–8 years) (Groves, 1986: appendix, p. 214). Onset of male orangutan puberty is recorded as 7–9 years

by Maggioncalda and Sapolsky (2003). Male urinary testosterone levels suggest a similar pattern of puberty in orangutans, gorillas, chimpanzees, and humans (Kingsley, 1988). Minimal onset of puberty as a uniquely shared feature for humans and chimpanzees is not corroborated at this time (accepted by Groves, personal communication).

Erect penis length exceeding 80 mm (character 235): Based on a single orangutan measurement of 40 mm (Short, 1978), but another paper listed by Groves (1986) recorded 120 mm in another orangutan (Hill, 1958, citing Hill, 1953). The only other citation given by Shoshani et al. (1996) was Pocock (1918), but this article did not address hominoids. The erect penis length of orangutans is closer to that of the chimpanzee than gorilla (Nadler, 1995), and Dahl (1988) recorded 94 mm for an erect orangutan penis and 85 mm for an unspecified number of nonerect penises. Current records do not support penis length as a synapomorphy for humans and chimpanzees to the exclusion of orangutans (accepted by Groves, personal communication).

Begun et al. (1997)

Analysis of 240 characters in 13 taxa comprising living apes, 8 fossil hominoids, and 1 hominid (*Australopithecus afarensis*; Begun, personal communication) identified eight characters unique to *A. afarensis* and African apes, and four unique to *A. afarensis* and chimpanzees. The monophyly of humans and chimpanzees was not addressed, but the authors explicitly began with that assumption.

Australopithecus-African apes

Concavo-convex centrale facet on the capitate (character 57): No descriptive comparison.

Angled long axis of the posterior talar facet (character 101): No descriptive comparison for plane of orientation to distinguish from an "aligned" position in other primates.

Supraorbital torus (character 150): Not documented, and acknowledged to be problematic (see above for Andrews and Martin 1987). Australopithecus supraorbital margins may be thin or moderately to quite tall superoinferiorly (Schwartz, 2004b), but they do not

conform to the African ape configuration. The supraorbital configuration reconstructed for *Australopithecus afarensis* by Kimbal et al. (2004) is more like orangutans than African apes (Schwartz and Tattersall, 2005).

Broad supraorbital sulcus (character 152): Not applicable to *A. afarensis*, humans, and most hominids (see above for Andrews and Martin, 1987).

Large frontal sinus (character 154). Not documented, and apparently invalid as described above for Andrews and Martin (1987).

Inferior surface attachment for nuchal muscles (character 160): Not measured (Begun, personal communication) in comparison with a more posterior position for orangutans and *Dryopithecus*, and a superior position in other primates.

Maxilla containing alveoli of teeth inflated (character 198): No comparative documentation to contrast with alveoli being "collapsed or solid" around the roots of other primates. Feature not recognizable by J.H. Schwartz (personal communication).

More horizontal zygomatic arch angle (character 184): Undocumented, and not measured (Begun, personal communication) to distinguish from a more inclined angle for monkeys and gibbons, and a more vertical angle in orangutans.

Australopithecus-chimpanzee

Fossa distal to upper third premolar (character 140): This feature refers to the incisive foramina (Begun, personal communication), but in no hominoid are they distal to the upper third premolar.

Inion vertically below glabella (character 158): No measurements given to distinguish position from that of other primates.

Lesser palatine foramen larger than other primates (character 202): No comparative documentation.

Upper second incisor spatulate (character 225): No documentation to compare with "peg-shaped" incisor of other primates. This linear measurement also links morphologically distinct teeth (see above for Andrews and Martin 1987).

Human-chimpanzee (Begun, 1999)

An additional seven characters were identified as synapomorphies even

though they were also attributed to other unspecified fossil apes:

Short nasal premaxilla: Applicable to many monkeys (Schwartz, personal communication).

Reduction of upper third molar: Size parameter undefined and undocumented.

Absence of molar cingula: Also applicable to orangutans and gibbons (Andrews, 1987), with the orangutan cingula being reduced more than in other apes (Schwartz, 1988; Swindler and Olshan, 1988).

Elongated nasopalveolar clivus: Undocumented. The anterior part of the orangutan clivus is more forwardly sloping and the posterior pole of nasopalveolar clivus extends farther back into the nasal cavity so the incisive fossae are farther back in the nasal cavity than African apes. When scaled to body size, the orangutan nasopalveolar clivus should be longer than other hominoids and most other catarrhines (Schwartz, personal communication).

Reduction of the caliber of patent incisive canals: Undocumented.

Narrow lateral orbital pillar at the frontozygomatic: Undocumented.

Flared upper premolar and upper molar crowns: Undocumented.

ORANGUTAN-HUMAN CHARACTERS

Limb Development and Morphology

Scapula: Shortest (shoulder joint to vertebral border) and deepest (from top to bottom along vertebral border) in shape (character 1), greatest reduction of the supraspinous fossa (character 2), most horizontal orientation of the scapula spine (character 3), and greatest upward deflection of the coracoid (character 4) (Oxnard, 1983; Groves, 1987; Schwartz, 1988; Young, 2003).

Minimal ossification at birth: Documented for the proximal humerus (character 5) and distal radius (character 6) in a small sample of individual apes and three monkey species (Schultz, 1944). Although possibly correct (Andrews, 1987; Groves, 1987), lack of secondary ossification recorded for the distal radius of some chimpanzees and gorillas, and the

presence of secondary ossification in one newborn orangutan (Winkler, 1996), suggests further sampling is required for corroboration.

Fusion of the proximal ulna as the second fusion event (character 7), and fusion of the humerus head after fusion of the epicondyle (character 8): Recorded by Schultz (1944, 1968) for hominoids, lemurs, and only six New and Old World monkey species.

Skull Morphology

Contact between the ethmoid and sphenoid bones: Almost always 100% in orangutans (94 skulls) and humans (1,016 skulls; character 9) compared with only 77% in chimpanzees (86 skulls), 50% in gorillas (50 skulls), 0% in hylobatids (48 skulls), 0–3% in Old World monkeys (341 skulls), and 23% in New World monkeys (63 skulls) (Schultz, 1965; Groves, 1986; Strait and Grine, 2004).

Single incisive foramen in juvenile (character 10) and adult (character 11) humans and orangutans: African apes have two foramina while all other primates have two fenestrae. The juvenile and adult stages are distinguished as separate characters because some adult chimpanzee specimens appear to have a single foramen while juveniles always display two openings. Through subsequent growth, these openings sometimes appear to coalesce. Even where an adult chimpanzee has an apparently single incisive foramen, the juvenile state is clearly double and so the adult condition represents a closer alignment of two foramina rather than an originally fused foramen as in juvenile hominids and orangutans (Schwartz, 1983).

Foramen lacerum (character 12): Basal margin of the petrosal bone separated from basicranium by an irregular-sized foramen filled with connective tissue and traversed by blood vessels and nerves (Groves, 1986; Andrews, 1987; Schwartz, 2005). Visible in some australopith fossils (Schwartz and Tattersall, 2005), and occasionally absent in humans through extended ossification of the petrosal (Schwartz, 2007).

Thick posterior upper palate (character 13): Thickened in orangutans and fossil relatives and thick in hu-

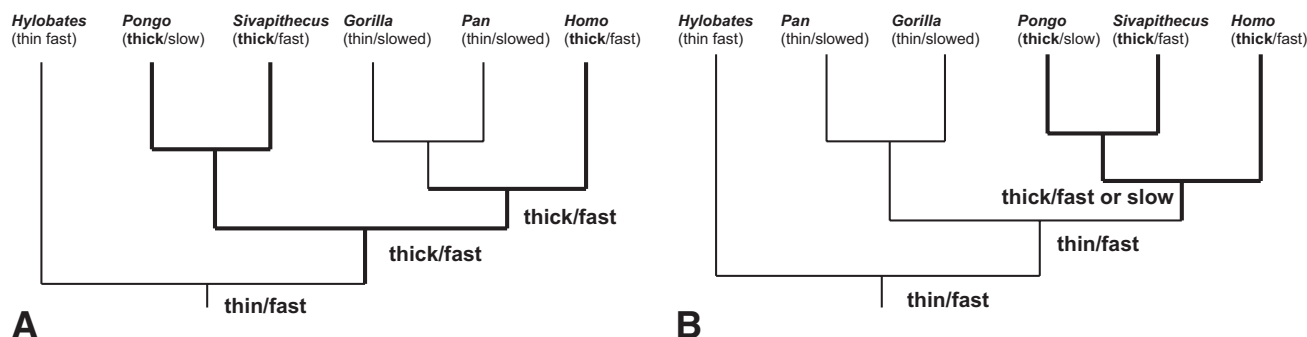


Figure 1. Phylogenetic distribution of molar enamel thickness and enamel deposition rates proposed by Martin (1985) mapped onto (a) the chimpanzee theory of relationship and (b) the orangutan theory of relationship. The chimpanzee theory requires reversion of the African apes (twice if chimpanzees are considered more closely related to humans than gorillas), while the orangutan theory requires no such reversion.

mans compared with African apes (Schwartz, 2004b). Posterior thickening is recorded in longitudinal cross-sections of australopith fossils with the possible exception of a slightly oblique section in *A. afarensis* (AL 200-1a) (Schwartz, 2004b; Schwartz and Tattersall, 2005).

Molar Morphology

Extant hominoids have a lower cusp relief than most other primates, although it is highest in the gorilla and lowest in humans and orangutans (Schwartz, 1984a, 1984b). This similarity of human and orangutan cusp relief is not currently treated as a synapomorphy because higher cusps are found in some fossil hominoids (Schwartz, personal communication). Derived molar cusp morphology includes the following features:

Anterior protocone higher than paracone for the deciduous upper molars (character 14).

Short trigonid on the lower posterior deciduous molar (character 15).

Upper molar lingual surface more oval than square in occlusal outline (character 16) (Swindler and Olshan, 1988).

On the lower anterior deciduous molars, the protoconid is anterior rather than central (character 17), the paracristid is angled rather than straight (character 18), and the talonid basin is closed (character 19). The lower anterior deciduous molar features are recorded by Swartz (1988) for hominoids and 12 species in 6 genera of Old World monkeys, and 17 species in 12 genera of New World monkeys.

Molar enamel of orangutans, humans, and hominoids (*Homo*, *Australopithecus*) is thick (character 20): Molar enamel of African apes, gibbons, and monkeys is thin with the exception of *Cebus apella* (Martin et al., 2003) and *Cercocebus* (Kay, 1983), which are treated as autapomorphies (Pilbeam and Simons, 1965; Schwartz, 1987). Thin enamel and rates of enamel deposition in chimpanzees and gorillas were attributed by Martin (1985) to secondary reversion in order to accommodate the sister-group relationship of humans and chimpanzees (Fig. 1a). This assumption later became evidence (Pilbeam, 1986; Andrews, 1987), but the enamel distribution is also congruent with a human-orangutan relationship (Fig. 1b) where thin enamel and fast deposition represent the ancestral condition for large-bodied hominoids (Schwartz, 1987). Martin's (1985) model was rejected by Shellis et al. (1998), who proposed an average enamel thickness for the common ancestor of large bodied hominoids, although they were uncertain about precise definitions of thickness. Studies on hominoids have generated contradictory positions between the presence of thick (Pilbeam, 1986) or thin enamel in the common ancestor of humans and chimpanzees (Pilbeam and Simons, 1965; Pilbeam, 1996; Brunet, 2005).

External Morphology

Absence of ischial callosities (character 21): Humans and orangutans, along with New World monkeys and prosimians, lack keratinized callosity-like thickenings over the ischial tuberosity region of the buttocks. Ischial

callosities of Old World monkeys and gibbons comprise skin and subdermal tissue overlying the pelvic ischial tuberosity (Rose, 1974). Gibbon callosities are small and appear late in life, while chimpanzees develop callosities more frequently than gorillas. Schultz (1936) found ischial callosities in 38% of chimpanzees (110 specimens). Straus (1950) did not report any callosity formation for a young female gorilla, and although Schultz (1936) did not observe callosities in 21 gorillas, he acknowledged Lönnberg's (1917) description of thickened skin with a horny layer present in gorillas. Schultz (1936) found callosities in only 5% of orangutans (61 specimens) and all were unkeratinized. The complete absence of keratinized callosities was treated as a shared derived condition for humans and orangutans by Schwartz (1988). The frequency of callosities in gorillas requires further clarification.

Largest distance between nipples (character 22): As an average percentage of chest width, the distance is greater in humans (71%) and orangutans (90%) compared with chimpanzees (52%), gorillas (46%), gibbons (32%), siamangs (8%), and macaques (40%). The hylobatid species were not specified, and although Schultz (1936) measured only one monkey group, the human-great ape comparison is probably robust since monkeys have a narrower rib cage than hominoids.

Uniquely shared features of the head include a hairline receded from the eyebrows (character 23), anterior cranial hair with forward orientation over forehead (character 24), and

male with a well-developed beard and mustache (character 25; cf. illustrations of all primates in Rowe, 1996).

Longest hair length (character 26): For the orangutan body and human head (cf. illustrations of all primates in Rowe, 1996).

Capacity for closed-mouth smile (character 27): Produces dimpling of the cheek in humans and orangutans (Kaplan and Rogers, 2000) and is either absent or extremely rare in other primates, with only one instance of a "mock-smile" (that may or may not be homologous) reported for the chimpanzee (Van Lawick-Goodall, 1968).

Reproductive Biology

Estrogen production profile (character 28): In a survey of urinary estrogen for two humans, a single capuchin monkey, a langur, a bonobo, and an orangutan (*Pongo pygmeus abelii*), Czekala et al. (1981) found a steep and continuous rise in orangutan urinary estrogen from 20%–30% of gestation until near-term, with maximum concentrations of 20–24 $\mu\text{g}/\text{mg}$ after 80% of the pregnancy in orangutans humans. Bonobos produced 8 $\mu\text{g}/\text{mg}$, and the langur produced 9 $\mu\text{g}/\text{mg}$ at 65% gestation. The capuchin profile was altogether different, with two peaks of 24 $\mu\text{g}/\text{mg}$ at 20% and 43 $\mu\text{g}/\text{mg}$ at 80% of total pregnancy. Czekala et al. (1983) recorded 3.88 ± 0.91 $\mu\text{g}/\text{mg}$ after 70% of pregnancy in the gorilla, and the common chimpanzee was found to produce similar (unspecified) quantities (Czekala et al., 1988: Fig. 8.4).

Highest production of estriol (character 29): Hominoids are unique among primates in their ability to produce large amounts of estriol (Bonney and Kingsley, 1982). Humans produce about 22.15 ± 6.49 $\mu\text{g}/\text{mg}$ late-pregnancy estriol compared with 14.28 ± 2.95 $\mu\text{g}/\text{mg}$ for the orangutan, 4.10 ± 2.4 $\mu\text{g}/\text{mg}$ for the bonobo, 1.46 ± 0.17 $\mu\text{g}/\text{mg}$ for the capuchin, and 1.06 ± 0.20 $\mu\text{g}/\text{mg}$ for the langur (Czekala et al. 1981). A further study (Czekala et al., 1983) reported values of 24.8 ± 6.78 for three humans, 16.27 ± 6.2 $\mu\text{g}/\text{mg}$ for one orangutan, and 1.13 ± 0.07 $\mu\text{g}/\text{mg}$ for five gorillas.

Absence of anogenital tumescence during ovulation (character 30): Orangutans do not show any swelling or

color change in the genitalia during ovulation, although they are unique for swelling during pregnancy (Schürmann and van Hooff, 1986). Genital swelling is slight in gibbons and gorillas, and prominent in common chimpanzees and bonobos (Nadler and Dahl, 1989; Dahl and Nadler, 1992a, 1992b). Reduced swelling (coded "1") was incorrectly attributed to African apes by Shoshani et al. (1996: character 241), while large and prominent swellings (coded "0") were attributed to humans and other primates (cf. Shoshani et al., 1996: appendix definition 241). Various combinations of color intensity and/or swelling are reported for most monkey and prosimian genera (cf. Butler, 1974; Graham, 1981; Hrdy and Whitten, 1987; Nishida and Hiraiwa-Hasegawa, 1987; Nadler and Dahl, 1989; Dahl and Nadler, 1992a, 1992b), but many species are not characterized and some descriptions may be erroneous. Genital swelling is reported in almost all Old World monkey genera and may be present in most species. Some New World monkey genera appear to lack swelling or color change. Sillén-Tullberg and Møller (1993) argued that concealed ovulation is a derived character for several primate lineages, including hominoids.

Females may mount and provide pelvic thrusting after first manipulating the penis to produce an erection (character 31): This may occur even when the male is passive (Schürmann, 1981; Nadler, 1988). The behavior is precluded in most monkeys and prosimians, where ventrodorsal mounting occurs, and it is absent for ventroventral mounting in Japanese macaques (Wolfe, 1984). The combination of manipulation and mounting by the female is not documented for African apes, although genital "inspection" or manipulation occurs in chimpanzees and bonobos (Van Lawick-Goodall, 1968; Nadler and Dahl, 1989; Wrangham, 1993), and female gorillas will straddle the male (Schaller, 1963). Female chimpanzees will occasionally back onto an already erect penis and achieve intromission (Goodall, 1986).

Sustained copulation with intromission (character 32): Mating in the wild orangutan ranges from 3 to 28 min, with an average of 10 min (MacKinnon, 1974; Rijksen, 1978;

Galdikas, 1979, 1981). In captivity, the range is 1–46 min, with an average of 9 or 15 min (Nadler, 1978; Maple, 1980). Copulation times in other hominoids are 1.5–1.6 min (gorilla), 7 sec (chimpanzee), 13–15 sec (bonobo), and 15 sec for at least one species of gibbon (Ellefson, 1974; Harcourt and Stewart, 1978; Kano, 1992; de Waal, 1995). Copulation is poorly documented for most other primate species. Prolonged copulation in some prosimians and monkeys involves a genital locking mechanism that is absent in hominoids (Dewsbury and Pierce, 1989; Dixon, 1998). New World monkey encounters are usually less than 10 min, with about three species lasting 15 or 25 min. Copulations in Old World monkeys generally last no more than a few minutes, with one species reported as up to 14 min (Carpenter, 1964; Nishida, 1988; Rowe, 1996).

Internal Anatomy

Gall bladder shape (character 33): Slightly bent in humans and nearly straight in orangutans compared with a more angled shape in other primates. This distinction was made by Groves (1986: p. 213) in reference to Lipp's (1958) illustrations of one prosimian, two genera and species of New World monkeys, three genera and four species of Old World monkeys, one gibbon, and one each of the great apes, but no distinguishing measurements were given.

Small accessory lobe of the parotid (character 34): Schneider (1958a) records a large accessory lobe in three prosimians, five New World monkeys, and three Old World monkeys, while the chimpanzee and gibbon lack the accessory lobe, and the lobe of the gorilla is very large. Humans and orangutans uniquely share a small lobe. Lobe size in chimpanzees and gibbons may represent autapomorphies. Further taxonomic sampling is desirable.

Vallate papillae of tongue (character 35): Humans and orangutans have 7–12 papillae compared with less than 5 in monkeys and gibbons, and possibly less than 8 in African apes (Sonntag, 1921; Schneider, 1958b). Some early publications suggest as

many as 15 for the chimpanzee (Sonntag, 1921), so further documentation is required.

Adrenal gland fetal zone (character 36): In humans at birth, this region occupies about 80% of the total gland volume (Serón-Ferré and Jaffe, 1981). The fetal zone of orangutans is not significantly different from humans, and both are significantly different from chimpanzees ($P = 0.05$) and gorillas ($P = 0.002$) (Czekala et al., 1988; Graham, 1988).

Deep head of pedal flexor digitorum rare (character 37): This feature is not well documented and requires corroboration (cf. Anderton, 1988).

Superficial radial forelimb vein (character 38): Unique for humans and orangutans in a survey of apes, six Old World monkeys, three New World monkeys, and four prosimians (Thirangama et al., 1991).

Frontal and occipital asymmetry (character 39): Common in great apes while monkeys show no significant differences (Hopkins and Marino, 2000). Hominoid asymmetries are also correlated with greater leftward asymmetry of the planum temporale (Pilcher et al., 2001). A slightly greater frequency of right frontal asymmetry was found in a sample of 12 endocranial casts of each great ape, 1 gibbon, and 43 casts for various Old World and New World monkey genera (LeMay et al., 1982). The measurements and sample sizes require further statistical corroboration.

Terminal deflection of right Sylvian sulcus (character 40): The point of deflection is higher in great apes and humans compared with other primates (Cantalupo et al., 2003), with the orangutan deflection being more similar to the human condition. In scaled photographic comparisons of 9 New World Monkeys, 12 Old World monkeys, 19 gibbons and 1 siamang (species not identified), 12 orangutans, 9 chimpanzees, and 7 gorillas, LeMay and Geshwind (1975) found the right Sylvian point to be more than 5 mm higher than the left in 5 orangutans and 2 chimpanzees and between 3 and 5 mm higher in 5 orangutans and 3 chimpanzees. LeMay (1976) found deflections of the right sulcus reached 10 mm in orangutans compared with 4 mm in chimpanzees in a survey of 69 nonhuman primates

comprising 3 New World monkeys, 5 Old World monkeys, 2 lesser apes, and the 3 great ape genera (one species each). Subsequent studies have generally focused on comparisons between humans and great apes, or chimpanzees and humans (Gannon et al., 1998; Hopkins et al., 2000; Freeman et al., 2004), with recent attention to the size of the planum temporale (PT) that was previously inferred by size differences in the Sylvian sulcus. Gannon et al. (1998) found the chimpanzee left PT to be larger than the right in 17 of 18 brains, therefore similar to humans. In four gorilla brains, three were found to have a significantly ($P < 0.005$) larger left PT, while a preliminary study of five orangutan brains found the left PT to be larger by $53\% \pm 46\%$ in three individuals, and symmetrical or 32% larger on the right in the other two (Gannon et al., 2001). MRI scans by Hopkins et al. (1998) found the left PT to be larger in 10 of 12 chimpanzees, 2 of 3 bonobos, 2 gorillas, and 2 of 4 orangutans, while in the coronal plane, the left PT was larger in 8 of 11 chimpanzees, 1 of 3 bonobos, 1 of 2 gorillas, and 1 of 4 orangutans. Since the Sylvian sulcus and PT are both variable in asymmetry, it would be desirable to have more sampling of the different ape species. Gannon et al. (2005) also recently recorded rightward asymmetry of the planum parietale in a survey of 23 chimpanzees and 4 orangutans.

Behavior

Mechanical ability (character 41): Orangutans are the “mechanical geniuses” of the nonhuman primate world, and their interest and ability in solving mechanical problems is second only to humans (Russon, 2000). Orangutans enjoy fiddling with locks and bolts longer than other apes (Parker, 1996). They show high degrees of patience and persistence with solving mechanical problems and they are sometimes more interested in the mechanical challenge than the experimental goal (Russon, 2000). Captive and ex-captive orangutans may be the most sophisticated tool-makers of all nonhuman primates (Russon, 2000), and the ability of orangutans to escape from locked cages is almost legendary (Kaplan and Rogers, 2000).

Shelter (character 42): Great apes and humans are the only animals to sleep in a bed reconstructed each day, and this behavior is predicted for ancestral hominids (Van Schaik, 2004). Orangutans occasionally reuse the same bed, which may also be repaired or relined (MacKinnon, 1974; Rijksen, 1978). Orangutans and humans are the only primates habitually to construct shelters incorporating roofs. A single example is reported for the chimpanzee (MacKinnon, 1974). Roofs are constructed by orangutans to provide shelter from rain or sun, as camouflage or apparently just for fun, and they will sometimes place fronds over the sides forming walls (MacKinnon, 1974; Van Schaik, 2004; Van Noordwijk and Van Schaik, 2005).

Other Characters of Phylogenetic Interest

These features require further corroboration, either as uniquely possessed characters or as shared derived features of humans and orangutans within the hominoids.

Navicular tubercle shape: Unpublished comparisons by Henry McHenry (personal communication) suggest a greater similarity in shape between humans and orangutans, although the navicular tubercle of the hominid OH8 was found to overlap that of African apes. The sample comprised 28 humans, 18 bonobos, 23 chimpanzees, 24 gorillas, and 16 orangutans. Further measurements are needed for gibbons, monkeys, and fossil taxa.

Pituitary gland histology: Bundles of gomori-positive fibers within the periphery of the stem in orangutans may represent a uniquely shared feature with humans (Hanström, 1958).

Female genitalia: Arrangement of the labia majora, labia minora, and associated prepuce of immature female orangutans may be more similar to that of humans than African apes (Dahl, 1988), while the configuration of external genitalia in female bonobos represents an autapomorphy within the large-bodied hominoids (Dahl, 1985).

Ventroventral mating: Most nonhominoid primates have dorsoventral mating (Dixon, 1998). Japanese macaques are one of the few exceptions, where a ventroventral orientation oc-

curs in 30% of heterosexual encounters (Wolfe, 1984). Ventroventral postures are recorded in siamangs, although the dorsoventral orientation is the most common pattern for hylobatids (Chivers, 1978; Dixson, 1998). Ventroventral postures are occasionally found in wild gorillas (Schaller, 1963; Harcourt and Stewart, 1978), in 30% of heterosexual bonobo encounters in the wild (Kano, 1992; de Waal, 2002) and 52% in captivity (Savage and Bakeman, 1978). The common chimpanzee orientation is limited to dorsoventral mating (Dixson, 1998). Ventroventral mating represents the majority of orientations in humans and orangutans (MacKinnon, 1971, 1974; Nadler, 1977; Galdikas, 1979, 1981), and it comprises 70%–80% of cooperative orangutan encounters in captivity (Maple, 1980). Ventroventral mating may represent a shared primitive retention for hominoids (Kano, 1992), while increased frequency may be more derived, with humans and orangutans being more similar to each other in this respect.

Artificial genital stimulation: Hand-held objects separated from the substrate as a source of genital stimulation is recorded in orangutans using objects such as sticks (MacKinnon, 1974; Rijksen, 1978; Van Schaik et al., 2003a; Van Schaik, 2004). Only fixed substrates are currently recorded for other hominoids (Van Lawick-Goodall, 1968; Wolfe, 1984).

Behavioral mimicry/imitation: Orangutans readily imitate human and orangutan individuals with whom they have the most intense relationships. They rarely imitate strange humans (Galdikas, 1995a). Use of human tools (e.g., axes, saws, and hoes) and duplication of human activities (e.g., washing clothes, fire-lighting, cooking recipes, and canoeing) suggests a very human-like cognitive process (Speidel and Nelson, 1989; Russon and Galdikas, 1995; Russon, 1996).

Longevity: Orangutans have the slowest rate of maturation of all the great apes (Parker, 1999) and perhaps the greatest longevity in the wild (Wich et al., 2004). Male orangutans reach at least 58 years and females 53 years—the latter probably an underestimate due to incomplete life history tracking. The oldest record for wild

chimpanzees is 55 (female) and 46 years (male). The expected age of death for orangutans at 15 years is 46 (male) and 40 (female) years compared with 24 and 41 years for male and female chimpanzees, although the estimate rises to 33 and 41 years for captive chimpanzees (Wich et al., 2004). Van Schaik (2004) noted that orangutans are generally healthy into their 50s while chimpanzees begin to look visibly aged after 35. The estimated maximum age at death for chimpanzees at Gombe is 33 years for males and 37 years for females. In the wild, very few chimpanzee individuals appear to survive into old age (defined by Huffman, 1990, as 33–41 years). Adult gorillas have a comparably short life expectancy. One wild male was estimated to have lived 43–46 years. Expected average age of death at 13 years is 27 years for female gorillas and 20 years for male gorillas (Groves and Meder, 2002). Pusey (2002) drew attention to the similarity of chimpanzee longevity to humans, but the comparison appears to be more applicable to orangutans and humans. The extended life history of orangutans suggests the evolution of increased longevity in hominids has been less than traditionally assumed (Wich et al., 2004).

Absence of infanticide: The constant threat of infanticide involving unfamiliar orangutan males is either absent or so rare as to be currently unobserved in orangutans (Van Schaik and Dunbar, 1990; Galdikas, 1995a; Van Hooff, 1995; Fox, 1998; Wich et al., 1999; Delgado and Van Schaik, 2000; Van Schaik, 2004). Bonobos (de Waal, 1997) and orangutans are more similar to humans in this respect than chimpanzees, although infanticide by unfamiliar males is a sporadic threat in humans under particular social and political circumstances (Van Schaik and Janson, 2000).

Mother-infant bond: The seemingly unique bond between the human mother and juvenile offspring may apply even more strongly to orangutans. Van Schaik (2004) found it impossible not to be struck by the human-like qualities of female orangutan protectiveness toward their children and he suggested orangutan mothers are perhaps closer than human mothers to the Platonic ideal of perfect mother-

hood. Kaplan and Rogers (2000) characterized orangutans as the best mothers in the primate world. These inferences require critical evaluation in comparison with other primates.

Aesthetics: Adolescent and subadult male orangutans sometimes carry fresh branches or vines when approaching another individual, usually draping the vegetation around the neck or head (Rijksen, 1978). Self-decoration is also reported for gorillas (Schaller, 1963) and chimpanzees (Van Hooff, 1973), although not in the context of approaching another individual. Orangutans may line their nests with regularly spaced twigs and sometimes construct and sleep with rolled bundles of leaves called “leaf dolls” (Van Schaik et al., 2003a). One orangutan was observed by Kaplan and Rogers (2000) to paste clay on its face in what appeared to be an act of adornment.

Private and elaborate sex: Mating in private has been described as a uniquely human characteristic (Diamond, 1992; Van Schaik, 2004), although some humans will sometimes mate in public view. While the human preference for private mating contrasts with African apes, it may not be all that different from orangutans (Kaplan and Rogers, 2000). If private sex in orangutans is not solely an artifact of dispersed populations, it will represent another seemingly unique human characteristic shared only with orangutans. As with various other primates, orangutan and human females can mate at any time during the estrus cycle, and female choice increases the frequency of copulation closer to ovulation (Hrdy, 1981; Nadler, 1988, 1995; Wallen, 2001) or maximum tumescence in the case of bonobos (Wrangham, 1993). Copulation during pregnancy occurs in both orangutans and humans (Van Schaik, 2004). Orangutans have a fuzzy sense of species boundaries with respect to humans (Russon, 2000), and orangutan males have forcibly mated with human females while female orangutans have made the same physical attempt on human males (Galdikas, 1995a; Russon, 2000).

Pair-bonding: Female orangutans have long-term pair bonds where they pair up with the same male between child-rearing intervals. Adolescent fe-

males and subadult males sometimes establish long-term “affiliative” relationships that anticipate future consortships (Schürman and Van Hoof, 1986; Galdikas, 1995b). Chimpanzees do not appear to establish individual long-term pair bonds between particular males and females that extend between consortships (cf. Nishida and Hiraiwa-Hasegawa, 1986). Like humans, female orangutans will employ positive and negative mate choice in the absence of direct male-male competition, a rare behavior among non-human primates (Fox, 2002).

Consortships: Individual paired relationships in orangutans range from a few hours to at least 7 months (MacKinnon, 1974; Rijksen, 1978; Van Schaik, 2004). Chimpanzee consortships average 7 days and last no more than a month (Tutin and McGinnis, 1981). Adult orangutan males may be excluded from participating in longer consortships only by incompatible foraging needs (MacKinnon, 1978). Individual consensual relationships between adult female and subadult males were recorded by Rijksen (1978), but not Fox (1998).

Social organization: Orangutans and chimpanzees are both characterized by temporary associations lacking the spatially permanent or discrete groupings of humans (Van Schaik, 1999; Van Schaik et al., 2004). Orangutan and chimpanzee females both have predominantly solitary behavior, where dependant offspring are usually the only company (Wich et al., 1999; Van Noordwijk and van Schaik, 2005), although bonobo females normally travel with other adult females (Wrangham, 1993), and orangutan females are frequently followed by other age and sex classes (Galdikas, 1984). The relatively solitary behavior of orangutans (Rodman and Mitani, 1987; Van Schaik, 1999; Wich et al., 1999, 2006a) may be the result of ecological constraints preventing more continuous or frequent interactions (Mitani, 1989; Galdikas, 1995a). Dispersed and loosely cohesive subgroups of orangutans may be comparable to the wide-ranging and loosely bonded groupings of chimpanzees (MacKinnon, 1974). The lower range of grouping tendencies in chimpanzees almost overlaps the upper end for orangutan females (Wich et al., 1999).

Higher-density populations of orangutans may form loose communities comprising one or more female clusters and the adult male they all prefer to mate (Singleton and Van Schaik, 2002). Orangutans sometimes form travel associations that include sexual consortships and nursery groups of multiple females with offspring (Sugardjito et al., 1987). There are also links of familiarity and general tolerance between individuals ranging over the same area (MacKinnon, 1974). Adolescent females have been observed to form coalitions to drive away siamangs in fruit trees (Sugardjito et al., 1987). The more gregarious Sumatran orangutans of Suaq Balimbing (Delgado and van Schaik, 2000; Wich et al., 2006a, 2006b) and West Langkat (MacKinnon, 1974) coordinate their movements between food patches and they will often share food. Socially distinct orangutan communities based on preferential association may exist in the wild, but have yet to be observed (Van Schaik, 1999; Singleton and Van Schaik, 2002). Increased social interactions occur between adult males and juveniles under zoo conditions (Zucker and Thibaut, 1995). According to Van Schaik (Rogers, 2005), orangutans are “every bit as sociable, as technically adept and as culturally capable” as chimpanzees.

Tool use: Orangutans in captivity show a level of complexity in tool use equal to that of chimpanzees (Bard, 1993). Habitual tool use in the wild is more extensive in Sumatran populations, where greater gregariousness and higher social tolerance allows for increased social transmission of cultural innovations (Van Schaik et al., 2003b). The use of hammer and anvil techniques in chimpanzees is widely seen to have direct significance for human evolution, even though the behavior is also found in *Cebus* monkeys (Croizat, 1958; Urbani, 2002). Apparent absence of the technique in wild orangutans may be a consequence of their arboreal habit. A group of captive juvenile orangutans was observed to use cement chips to hammer out a half-meter hole in the concrete floor of their cage (Russon, 2000). The overall range and quality of chimpanzee imitative tool use are considered comparable to those recorded for orangu-

tans under more stringent methodological conditions (Russon, 1999).

Intelligence: Intellectual performance by chimpanzees and orangutans in various cognitive tests is among the highest of any primate. Shared abilities include the understanding of bartering, habitual use of feeding tools, causal and logical reasoning, mirror self-recognition, self-conception, role reversal, planning, intentional deception, and protolanguage (Maple, 1980; Povinelli and Cant, 1995; Hyatt and Hopkins, 1998; Delgado and Van Schaik, 2000; Call, 2003; Van Schaik et al., 2003a). Characterizing the orangutan as the “philosopher ape,” Van Schaik (2004) concluded: “There is no doubt about it: orangutans are smart, regardless of exactly how you define that term. Whether intelligence is defined as creative problem solving, uncanny memory, or thinking (mental stimulation), orangutans get high marks.”

FOSSIL EVIDENCE

Fossils continue to play a significant role in reconstructing human origins. Paleontologists initially believed that the 12 Ma *Ramapithecus* jaws were unequivocally hominid because of their thick enamel and low molar cusps (Pilbeam, 1972; Smith and Pilbeam, 1980; Kay, 1983; Simons, 1989). Once the skull was found to resemble the orangutan rather than the African ape, *Ramapithecus* was “defrocked” (Pilbeam, 1982, 1997; Simons, 1989) from its hominid status, and its name was also subsumed under *Sivapithecus* as an orangutan relative (Andrews and Cronin, 1982). Pilbeam (1978) resolved never again to cling quite so firmly to one particular evolutionary scheme, but he later found the DNA similarities between chimpanzees and humans too compelling for him to sustain that position (Pilbeam, 1982, 1984). Having accepted DNA similarity as the only source of phylogenetic evidence, he repudiated the ability of morphology to produce legitimate phylogenetic hypotheses (Pilbeam, 2000) except for fossil hominids (Brunet et al., 2005). These contradictory positions exemplify the modern dilemma for paleontology. If morphology is phylogenetically uninformative for living taxa, it

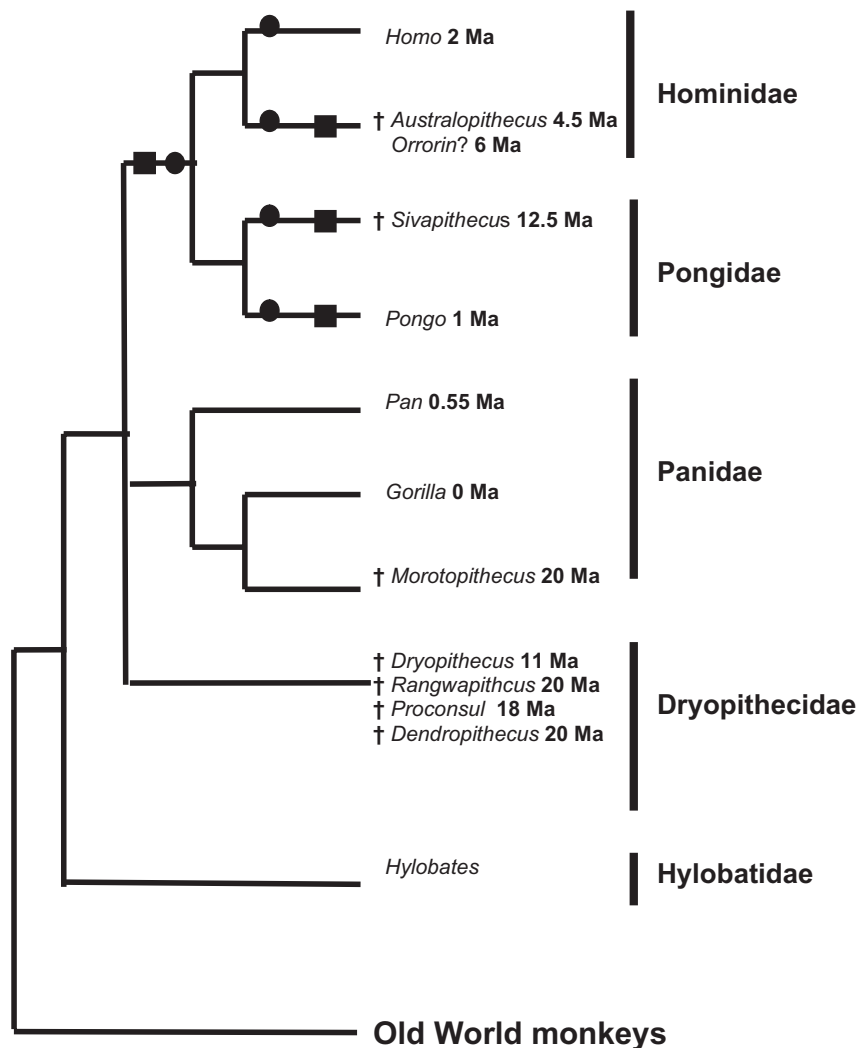


Figure 2. Phylogenetic and taxonomic implications of the human-orangutan relationship for selected fossil and living taxa (after Schwartz, 1986). The oldest fossil records for each genus are in bold. Daggers denote extinct taxa; solid circles, the approximately 40 uniquely shared features for humans and orangutans inherited by all hominid- and orangutan-related lineages; solid squares, primitive retentions of orangutan-like characters in early hominids that were later lost in *Homo*. Hominids (such as *Australopithecus*, *Homo*, and *Orrorin*) represent the sister group of orangutans and their fossil relatives (represented here by *Sivapithecus*). These taxa comprise the sister group living thin-enameled great apes along with potential fossil members such as *Morotopithecus* (Schwartz, 1983) comprising the family Panidae and various other thin-enameled fossil apes (Dryopithecidae). The lesser apes (Hylobatidae) and Old World monkeys comprise successively more distantly related anthropoid primates).

cannot be any more informative for fossils (Schwartz, 2005).

Contrary to expectations from the chimpanzee theory (Pilbeam, 1996; Wrangham and Pilbeam, 2001; de Waal, 2002), the earliest unequivocal hominids do not represent some kind of bipedal chimpanzee. Early hominids are characterized by anterior-facing zygomatic roots, a broad/relatively tall/mostly flat infraorbital plane, canine pillars that angle medially alongside and above the nasal aperture, and tall oval orbits with mounded superior

orbital rims (Ward and Kimbel, 1983). These are features otherwise unique to orangutans and their fossil relatives such as *Sivapithecus* (*Ramapithecus*), *Ankarapithecus*, *Lufengpithecus*, *Dryopithecus* of Can Llobatares and *Ou-ranopithecus* (Schwartz, 2004b). The nasal bones of australopiths are also long and narrow, as often found in orangutans, while heteromorphy in relative size and shape of upper incisors is similar to that of orangutans and orangutan relatives (Schwartz, 2004b). Since fossil hominids are con-

sidered to be most closely related to humans, those features shared with the orangutan clade would represent primitive retentions from a last common ancestor shared by the orangutan and hominids clades that have since been lost within *Homo* (Fig. 2).

Recent fossil reconstruction of *Australopithecus afarensis* (Al 444-2) (Kimbel et al., 2004) also exemplifies the tall, vertically inclined orbital region, broad cheek bones, as well as absence of the African ape brow ridge and sulcus. Combining these structural features with the uniquely shared soft tissue characters of humans and orangutans (Grehan, 2005, 2006b) leads to a new reconstruction of early hominid appearance. Fossil hominids such as the famous "Lucy" are predicted to have an exposed forehead, forwardly directed hair over the forehead (whether short as in orangutans or long as in humans), and a Mona Lisa smile (Fig. 3a). Unlike the clean "shaved" male hominids of the chimpanzee theory (cf. Stringer and Andrews, 2005), the male counterpart to Lucy also had a well-developed beard and mustache (Fig. 3b). These features would be expected throughout hominid evolution.

QUALITY OF EVIDENCE

Current morphological evidence indicates that humans are morphologically more similar to orangutans than other great apes in shared derived characters. Corroborated documentation of characters linking humans or hominids with African apes or chimpanzees (Table 1) is very poor compared with that linking humans and the orangutan (Table 2). None of the 13 African ape- and chimpanzee-related characters proposed by Andrews (1987) and Andrews and Martin (1987) are cladistically corroborated, and of these at least 9 appear to be incorrect. Three of the human-African ape characters proposed by Shoshani et al. (1996) lack proportional scaling, 4 could not be corroborated by Schwartz (2005), and 13 are invalid or problematic, leaving only 8 as currently valid. None of the seven chimpanzee-human characters (Shoshani et al., 1996) are corroborated and two are recognized as currently invalid by Groves (personal communication).

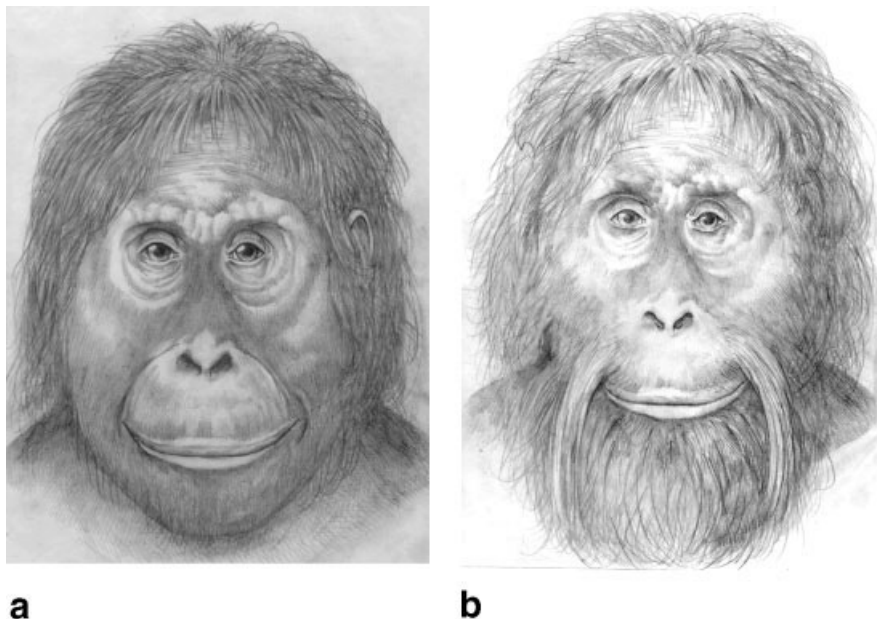


Figure 3. Soft tissue reconstruction for the fossil skull AI 444-2 (*Australopithecus afarensis*) showing (a for "Lucy") a receded hairline, forward facing cranial hair, low-mounded eyebrow ridges, and a generalized (primitive) nostril. b: Male counterpart ("Luke") with well-developed beard and mustache. Illustration by William Parsons.

Of the seven australopith-African ape characters proposed by Begun et al. (1997), three are invalid, three lack documentation, and one lacks outgroup comparison. None of the four australopith-chimpanzee characters are described or documented. Of the additional chimpanzee-australopith characters proposed by Begun (1999), three are invalid and four lack published documentation (Table 1). All may be invalid since Begun (1999) refers to their presence in one or more other unnamed fossil apes. In contrast, all but 1 of the proposed orangutan characters are supported by published sources, and 28 are strongly or completely corroborated. Broader taxonomic sampling and documenting are required to test the remaining 14 characters (Table 2).

EVOLUTIONARY IMPLICATIONS

Phylogenetic Significance of DNA Sequences

DNA sequences are widely seen to track hominoid evolutionary relationships (Diamond, 1988, 1992; Pilbeam, 2000; Curnoe, 2003; Gibbs et al., 2002; Lockwood et al., 2004; Strait and Grine, 2004). With DNA studies supporting a close relationship between humans and chimpanzees or African

apes, the orangutan theory is "inconceivable in this day and age of ample molecular evidence" according to molecular geneticist Maryellen Ruvolo (Small, 2005). At least one popular science journal (*Natural History*) will not allow publication of the orangutan theory because it challenges what appears to be "settled science" (editorial communication). Scientific justification for rejecting morphological evidence rests on the proposition that the smaller the genetic distance, the greater the probability of a shared phylogeny (Enard and Pääbo, 2004). According to Caccone and Powell (1989), "virtually all molecular phylogenetic studies . . . have a major underlying assumption: the genetic similarity or difference among taxa is an indication of phylogenetic relatedness." They accept the molecular assumption because the proposed relationships are in agreement with phylogenies deduced by other methodologies, even though they also acknowledge this is not quite the case because of the orangutan. And they cite morphologist David Pilbeam's opinion that the typical African ape features were lost in the human lineage even though this explanation is based on his acceptance of molecular

interpretations of phylogeny rather than morphological evidence.

Incongruence between morphological and molecular evidence is not unique to the orangutan. A morphologically incongruous result from albumin, myoglobin, and the prion protein sequence placed gibbons closer to African apes and humans than the orangutan. A study of opsin genes linking the chimpanzee with gorilla to the exclusion of the bonobo was rejected because it was not supported by morphology as well as other molecular data. Schwartz (2005) questioned why it should occasionally be acceptable to use morphology to support one molecular conclusion over another when morphology is considered an untrustworthy reflection of phylogeny in the first place. A consistent position would require morphology to be always phylogenetically uninformative once it is deemed unreliable. Schwartz (2005) notes that on an intuitive level, it would seem that the closer one gets to the genetic level of organisms, the closer one is to the answer to relatedness. Since individuals of the same species must be genetically more similar to one another than any are to individuals of another species, it would seem that closely related species are also the most genetically similar, and nothing would preclude equating genetic similarity with relatedness. Orangutans are therefore seen to be equally related to chimpanzees, gorillas, and humans because its genetic distance from each is almost the same (Saitou, 1991). The systematic problem is that similarity is not a de facto measure of evolutionary relationship because primitive retentions are not distinguished from derived novelties. The genetic distance of orangutans from humans and African apes, for example, may be the result of orangutan DNA having evolved while that of humans and African apes has not. Humans and African apes may be similar merely because they still share the same primitive DNA sequences.

Molecular studies have attempted to solve the problem of primitive and derived character states by using cladistic techniques and terminology. The original sequence data are retained, but those sequences in the assigned outgroup are made primitive by the cladistic algorithm. The out-

TABLE 1. Support for proposed African ape-hominid relationships

	supported	invalid?	untestable	total
Andrews (1987) and Andrews and Martin (1987)				
African ape-human	0	9	0	9
Chimpanzee-human	0	4	0	4
Totals	0	13	0	13
Shoshani et al 1996				
African ape-human (26)	8	16	3	27
Chimpanzee-human	0	7	0	7
	8	23	3	34
Begun 1999, Begun et al 1997				
African ape- <i>Australopithecus afarensis</i>	0	3	5	8
Chimpanzee- <i>Australopithecus afarensis</i>	0	0	4	4
Chimpanzee-human	0	3	4	7
	0	6	13	19

TABLE 2. Proposed orangutan-human synapomorphies

	robust	limited sample	Other systematist support
scapula shape	1	1	Groves, pers. comm.
reduced suparspinous fossa	2	1	Groves, pers. comm.
scapula spine orientation	3	1	Groves, pers. comm.
coracoid deflection	4	1	Groves, pers. comm.
humerus ossification	5	1	Andrews 1987, Groves 1987
radius ossification	6	1	Andrews 1987, Groves 1987
fusion sequence ulna	7	1	Groves, pers. comm.
fusion sequence humerus	8	1	Groves, pers. comm.
ethmoid contact about 100%	9	1	Strait and Grine 2004
incisive foramen juvenile	10	1	Groves 1987
incisive foramen adult	11	1	Groves 1987
foramen lacerum	12	1	Groves 1987, Andrews 1987
thick posterior upper palate	13	1	
upper ant. decid. molar protocone high vs paracone	14	1	Shoshani et al 1996
lower posterior deciduous molar trigonid short	15	1	Shoshani et al 1996
upper molar lingual shape oval	16	1	
lower anterior deciduous molar protoconid anterior	17	1	Shoshani et al 1996
lower anterior deciduous molar paracristid angled	18	1	Shoshani et al 1996
lower anterior deciduous molar talonid basin closed	19	1	Shoshani et al 1996
thick molar enamel	20	1	Shoshani et al. 1996
ischial callosities unkeratonized	21	1	Andrews 1987
mammary spacing	22	1	
hairline receded	23	1	
forward oriented hair over forehead	24	1	
beard and mustache well developed	25	1	
longest hair	26	1	
smile with closed mouth	27	1	
estrogen production high	28	1	
estriol production high	29	1	Shoshani et al 1996
estrus swelling absent	30	1	Groves, 1986, 1987
female initiated mating	31	1	
sustained copulation	32	1	
gall bladder shape	33	1	Groves 1986, 1987
accessory lobes of parotid gland	34	1	Shoshani et al 1996
vallate papillae number	35	1	
fetal zone size	36	1	
Pedal flexor digitorum rare	37	1	Graham 1988
radial vein present	38	1	Thirangama et al 1991
brain asymmetry marked	39	1	
right sulcus of brain highest	40	1	
mechanical genius	41	1	
house construction	42	1	
Totals	42	28	26

group sequences are treated as primitive (unchanged) even though this procedure contradicts the molecular assumption of continually and randomly diverging sequences in all lineages. DNA analysis mimics cladistics while failing to separate out actual derived character states (Grehan, 2005), and the DNA synapomorphies are created as an artifact of the tree-building algorithm rather than prior comparative analysis of each character to limit character states to those that are uniquely shared (Schwartz, 2005). Compounding this discrepancy is the common practice of using grossly inadequate (by morphological standards) outgroups that are often limited to one or a few species of monkey or gibbon, or even just the orangutan, which is consequently removed from consideration as a possible nearest relative (Goodman et al., 1994; Janke et al., 1997; Ruvolo, 1997; Reyes et al., 2000; Satta et al., 2000; Lin et al., 2002).

Humans are consistently closer in overall morphological similarity to African apes, especially the gorilla (Schwartz 1987), so it would not be surprising to find a similar result for coding DNA sequences, whether or not cladistic algorithms are used. This correlation would not apply to randomly mutating noncoding sequences, but these are phylogenetically problematic because they have no necessary link with phylogenetic sequence other than through the assumption of correlated divergence. The status of molecular evidence is problematic for both molecular systematists and supporting morphologists. Molecular systematists reject DNA similarities that contradict accepted morphological evidence, and accurate phylogenetic relationships derived from morphology are accepted at face value for calibrating molecular clocks (Schwartz, 2005). Some molecular biologists will both accept (Goodman et al., 1994) and discount (Goodman, 1996) morphological evidence, and some morphologists will dismiss morphology for living taxa while accepting morphology alone for fossils (Pilbeam, 1982, 1984, 1997; Tuttle, 1988), or selectively reject genetic relationships (e.g., Shoshani et al., 1996, for the tarsier). Some molecular biologists have ar-

gued that the solution to the apparent incongruence of DNA and morphology lies in the integration of DNA sequences with genetic and epigenetic developmental process (Dover, 1999, 2000; Maresca and Schwartz, 2006). According to molecular biologist Jonathan Marks (1994), it is impossible to rank either genotype or morphology as inherently superior. He argues that where molecular and morphological data disagree, both must be reexamined carefully. It is the apparent incongruence between molecules and morphology (both living and fossil) that may be the most exciting problem for the study of hominid origins, whether or not the orangutan theory proves to be correct.

Ancestral Hominid Biology

The chimpanzee/African ape theory renders the evolutionary sexual and reproductive biology of humans wholly imaginary because African apes lack shared derived characters for these features (Johanson and Edey, 1980; Diamond, 1992; Wrangham, 2002). Paleoanthropologists end up expending a great deal of time and effort explaining away the contradictions that come from using chimpanzees as a model of early hominid behavior (Schwartz, 2004c). The shared derived characters identified by the orangutan theory predict that the biology of Lucy and her contemporaries included concealed ovulation, extended consort relationships, long-term male-female pair-bonding (continuous as in humans, or intermittent as in orangutans), prolonged copulation initiated by either the male or female, preference for face-to-face mating, and the option for females to mate during pregnancy or any time during the menstrual cycle. Sexual partnerships may have been polygamous, monogamous, or some other combination, and either aggressively male-initiated, mutually entered, or female-initiated, and a preference for sex in private and female choice would have strongly influenced the tempo and mode of sexual relationships. Pregnancy could be expected to last about 9 months and reproductive physiology included production of estradiol and total estrogen within the

range of modern humans and orangutans. MacKinnon (1978) regarded the orangutan as a much better model of human evolution than African apes, and his characterization of courtship where “young couples indulge in rather playful courtships with the young males trying to impress their initially shy pick-ups with their physical splendor, and such flirtations sometimes lead to lasting sexual consortships” could apply as much to the earliest hominids as modern humans.

The orangutan theory also predicts environmental interactions by the earliest hominids that included construction of tree canopy shelters with roofs and walls as the direct precursors of the shelters constructed when terrestrial living became dominant (Perry, 2005). As mechanical geniuses, the earliest hominids would have an elaborate and diverse tool kit culturally inherited at least 10 million years earlier from the mid-Miocene common ancestor of humans and orangutans (Van Schaik et al., 1996). A primitive sense of aesthetics may have been expressed in the construction of objects such as the orangutan “leaf dolls” as well as in artistic expressions of design symmetry as found in orangutan nest construction. Vegetation may have also been used for head or body coverings, artificial amplification of vocal communication, and enhancement of personal appearance as a social device as found in modern orangutans. Other aspects of early hominid biology such as greater community cohesion and intramale socialization in early hominids may represent primitive retentions shared with African apes while the orangutan lineage evolved a more solitary behavior.

CONCLUSIONS

Comparative Morphology

From my perspective as a systematist and evolutionary biologist, comparative primate morphology seems to be one of the most overlooked and understudied fields of modern biology, which has suffered a clear decline in scope and depth since the mid-20th century. It is probably not an exaggeration to say that there is far more morphology known for some obscure insect groups than there is for all

known primates. The science of morphology has become so degraded in hominid systematics that selective withholding of access to holotypes (e.g., *Ardipithecus*, *Australopithecus bahralghazali*, *A. garhi*, and *Kenyanthropus platyops*) (Schwartz and Tattersall, 2005) is a disgraceful problem contrary to the intent of the International Code of Zoological Nomenclature. Hominid taxonomy also often lacks corroborating outgroup and in-group documentation (Schwartz, 2004c; Schwartz and Tattersall, 2005), and perhaps primate morphology is "intractable" (Pilbeam, 2000) only because the necessary standards of comparative documentation and specimen access are so often lacking (see also Winkler, 1995).

Current morphological evidence does not justify recent claims by morphologists (Begun, 1999) or geneticists (Goodman et al., 1994) that morphology supports a close phylogenetic relationship between humans and chimpanzee or both African apes to the exclusion of the orangutan. Instead, it is the claim of DNA hegemony over morphology that may be in doubt. Comparative morphology supports a unique common ancestry for humans and orangutans as the only phylogenetic theory with substantial corroborated evidence. Even supporters of a unique common ancestry for humans and chimpanzees collectively support more (26) orangutan-related human characters than they do for chimpanzee-related human characters (Table 2). The morphological evidence supporting a unique common ancestry for humans and orangutans has critical implications for how fossil members of Hominidae are recognized (Schwartz, 2006), and it requires reallocation of African apes (Fig. 2) to their own family (Panidae), leaving only the orangutan within Pongidae as the sister group to hominids in the Hominidae (Schwartz, 1986).

Ramapithecus Revisited?

The combination of living and fossil morphological evidence for the orangutan relationship with humans suggests Pilbeam (1968) and Simons (1981) were more right than wrong in recognizing *Ramapithecus* and Plio-

Pleistocene hominids as the same or closely related lineages. Only a small number of evolutionary biologists such as Peter Andrews, H. James Birx, Malte Ebach, Gisela Kaplan, Judith Masters, Gary Nelson, Donald Perry, and Ian Tattersall (personal communications) are willing to recognize Schwartz's orangutan theory as a critical issue for understanding hominid origins. The orangutan theory warrants serious consideration because it is the only theory that anticipated the further discovery of features in hominids that were otherwise unique to orangutans and their fossil relatives (Grehan, 2005). In this respect, the orangutan theory represents a progressive research program (*sensu* Lakatos, 1978), while the DNA theory seems to generate confusion about human origins among at least some of its supporters (Wong, 2003).

It is exactly because we have invested so much in the chimpanzee relationship that it is important to better understand why they do not look like us, while in various unique ways orangutans do. The uniquely shared morphological similarities of humans and orangutans represent a very important spectrum of genetic material that chimpanzees either lack or fail to develop. Given the number of uniquely shared features, it is likely that humans and orangutans have similar regulatory pathways and it may be this level of genetics that should be the focus of evolutionary reconstruction (Schwartz, 1987, 2005). Perhaps more than anything else, the orangutan evidence gives substance to Marks's (1994) conclusion that molecular genetics needs "to be carefully weighted and integrated, not blindly obeyed." More conceptual and empirical research will need to be invested in the comparative morphology of fossil and living primates, as well as in their genetics and developmental biology, if we are to find an integrated genetic and morphological solution to why there are so many uniquely "human" features in the orangutan. This incongruence is to be explored rather than ignored. In the words of General George S. Patton: "If everyone is thinking alike, no one is thinking."

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