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SPECIAL PAPER

Evolution of the second orangutan: phylogeny and biogeography of hominid origins

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ABSTRACT

Aim To resolve the phylogeny of humans and their fossil relatives (collectively, hominids), orangutans (*Pongo*) and various Miocene great apes and to present a biogeographical model for their differentiation in space and time.

Location Africa, northern Mediterranean, Asia.

Methods Maximum parsimony analysis was used to assess phylogenetic relationships among living large-bodied hominoids (= humans, chimpanzees, bonobos, gorillas, orangutans), and various related African, Asian and European ape fossils. Biogeographical characteristics were analysed for vicariant replacement, main massings and nodes. A geomorphological correlation was identified for a clade we refer to as the 'dental hominoids', and this correlation was used to reconstruct their historical geography.

Results Our analyses support the following hypotheses: (1) the living large-bodied hominoids represent a monophyletic group comprising two sister clades: humans + orangutans, and chimpanzees (including bonobos) + gorillas (collectively, the African apes); and (2) the human–orangutan clade (dental hominoids) includes fossil hominids (*Homo*, australopiths, *Orrorin*) and the Miocene-age apes *Hispanopithecus*, *Ouranopithecus*, *Ankarapithecus*, *Sivapithecus*, *Lufengpithecus*, *Khoratpithecus* and *Gigantopithecus* (also Plio-Pleistocene of eastern Asia). We also demonstrate that the distributions of living and fossil genera are largely vicariant, with nodes of geographical overlap or proximity between *Gigantopithecus* and *Sivapithecus* in Central Asia, and between *Pongo*, *Gigantopithecus*, *Lufengpithecus* and *Khoratpithecus* in East Asia. The main massing is represented by five genera and eight species in East Asia. The dental hominoid track is spatially correlated with the East African Rift System (EARS) and the Tethys Orogenic Collage (TOC).

Main conclusions Humans and orangutans share a common ancestor that excludes the extant African apes. Molecular analyses are compromised by phenetic procedures such as alignment and are probably based on primitive retentions. We infer that the human–orangutan common ancestor had established a widespread distribution by at least 13 Ma. Vicariant differentiation resulted in the ancestors of hominids in East Africa and various primarily Miocene apes distributed between Spain and Southeast Asia (and possibly also parts of East Africa). The geographical disjunction between early hominids and Asian *Pongo* is attributed to local extinctions between Europe and Central Asia. The EARS and TOC correlations suggest that these geomorphological features mediated establishment of the ancestral range.

Keywords
Hominid, hominoid, human origin, orangutan, panbiogeography, *Sivapithecus*, systematics, Tethys, vicariance.

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INTRODUCTION

The order Primates subsumes three major groups: prosimians (broadly, lemurs, lorises and bushbabies), anthropoids (monkeys, apes and humans) and tarsiers, with conflicting evidence for the grouping of the latter with prosimians rather than anthropoids (Schwartz, 1986; Groves, 1991, 2006). Anthropoids are traditionally subdivided into Platyrrhini (New World monkeys) and Catarrhini (Old World monkeys, apes and humans). The catarrhine superfamily Hominoidea includes the large-bodied hominoids or great apes (hominids, orangutans and African apes) as well as the small-bodied hominoids or lesser apes (Hylobatidae, i.e. gibbons and siamangs; Schwartz, 1986). For over a century the great apes, which were thought to be closely related, were allocated to the family Pongidae, but the last three decades have witnessed a shift in favour of interpreting overall molecular similarity as indicating that the African apes (chimpanzees, bonobos and gorillas) and now chimpanzees and bonobos alone are most closely related to humans (Marks, 2003; Schwartz, 2007; Schwartz & Maresca, 2007; Senut, 2007). The latter presumption has led some biologists to refer to humans as a third chimpanzee (Diamond, 1993) and others to place chimpanzees and all hominids in the same genus, *Homo* (Goodman *et al.*, 1998).

Most palaeoanthropologists taxonomically accommodate a human–African ape relationship either by restricting Pongidae to the orangutan and its fossil relatives while placing African ape and hominid genera within Hominidae, or by including all large-bodied hominoids in Hominidae (Andrews & Bernor, 1999) within which humans and their fossil relatives are placed in either the subfamily Homininae or the tribe Hominini (e.g. Goodman, 1996; Cameron, 1997; Begun & Güleç, 1998; Leakey *et al.*, 2001; Begun, 2004; Pilbeam & Young, 2004; Andrews & Harrison, 2005; Folinsbee & Brooks, 2007). Here we follow an alternative protocol that restricts the family Hominidae to include only humans and their fossil relatives to the exclusion of their closest living great ape relative(s) (cf. Schwartz, 1986, 2007; Hill & Ward, 1988; Strait & Grine, 2004; Tuttle, 2006; Strait *et al.*, 2007).

Pilbeam & Young's (2004) assertions notwithstanding, a presumed human–African ape relationship is phylogenetically quite problematic. Neither of two oft-cited morphological studies claiming to corroborate the interpretation of molecular data as supporting a close relationship between chimpanzees and humans (Shoshani *et al.*, 1996; Begun *et al.*, 1997) took into consideration or provided justification for excluding most of the morphological features that have been documented as being shared uniquely by humans and orangutans (see discussions in Schwartz, 2005; Grehan, 2006a). Of further note, the studies by Begun *et al.* (1997) and Cameron (1997) claiming support for a human–chimpanzee relationship did not include any extinct species of *Homo*. Clearly, however, given the considerable morphological evidence in support of it, the hypothesis of a closer relationship between humans and orangutans than between humans and either extant African ape genus has major implications for evaluating both the molecularly based theory of the relationship among large-bodied hominoids and the biogeography of these primates (Schwartz, 1987, 2005; Grehan, 2006b).

Biogeographical reconstructions of a common African origin of hominids and African apes have been dominated by Darwin's (1859) assumption that vicariant (spatially disjunct) fossil localities are historically connected by a series of discrete migrations from common centres of origin, as well as by Matthew's (1915) assumption that centres of origin and migration can be read – literally – from the fossil record (Heads, 2005). Localities with older fossils or basal lineages are generally assumed to represent actual sites of earlier occurrence, and multiple area relationships are attributed to multiple migrations or reciprocal migrations back and forth according to theoretical parsimony criteria (e.g. Beard, 2006; Fleagle & Gilbert, 2006; Heesy *et al.*, 2006; Folinsbee & Brooks, 2007).

The fossil record of modern African apes is limited to a few putative chimpanzee teeth dated to *c.* 0.5 Ma (McBrearty & Jablonski, 2005). In the absence of older fossils either of any African ape or of a presumed common African ape–hominid ancestor, hominoid systematists have attempted to link the origin of early fossil hominids in Africa with various Miocene fossil apes in Eurasia through a series of hypothetical dispersals that Begun (2001) characterized as 'very complicated'. Begun (2001) himself theorized an initial dispersal of hominoids into Europe where they diverged to give rise to the Asian apes as well as to a hypothetical common ancestor of humans and African apes that migrated back into Africa *c.* 9 Ma. Several similar biogeographical scenarios have been proposed according to differing parsimony hypotheses about the historical interrelationships between centres of origin and dispersal, phylogeny and area (Moyà Solà & Köhler, 1993; Begun *et al.*, 1997, 2003; Begun & Güleç, 1998; Miyamoto & Young, 1998; Stewart & Disotell, 1998, 1999; Moyà Solà & Köhler M., 1999; Begun & Nargolwalla, 2004; Cote, 2004; Begun, 2005; Harrison, 2005; Pickford & Senut, 2005; Pickford, 2006; Folinsbee & Brooks, 2007). Recently discovered fossils have been interpreted as providing evidence of African ape-like hominoids in Africa *c.* 12.5–10 Ma (Pickford & Senut, 2005; Suwa *et al.*, 2007) but their lack of African ape synapomorphies brings this interpretation into serious question.

These complicated and convoluted dispersal models are not grounded in empirical evidence, but rather on preconceived notions about the existence and locations of centres of origin. Following Darwin (1859), the underlying assumption is that an ancestor's distribution is geographically narrow with respect to the distributions of presumed descendants located in different (vicariant) geographical areas. The problem with this preconception, however, is that the very ability of individual descendants to move between different locations obviates the very criterion – geographical isolation – that is also invoked as essential for their differentiation and speciation. An alternative model of vicariant differentiation (Croizat, 1958) suggests that ancestral dispersal occurs before the differentiation of descendant taxa, with the ancestor establishing a widespread geographical distribution that encompasses the combined ranges of all vicariant descendants (Craw *et al.*, 1999).

We take the position that integrating theories of relatedness between fossil and living taxa with those concerning biogeography can be accomplished only if shared–derived morphological similarities are first delineated and then used to generate and subsequently test theories of relatedness (Schwartz, 1987, 2005). Here we present a morphological analysis of living and various fossil large-bodied hominoids in order to test alternative theories of relationship among and between them. We then integrate the resulting hypothesis of relatedness into a historical biogeographical model that considers the extent of vicariant replacement among member taxa as a predictor of the geographical range of the most recent common ancestor. We also examine possible tectonic correlations with the ancestral hominid range as a biogeographical calibration of the minimal age of origin and dispersal of the ancestor of a hypothesized common ancestor of hominids, orangutans and their closest fossil ape relatives.

MATERIALS AND METHODS

Taxonomic groups

Accepted hominids are represented here by *Homo* (Schwartz & Tattersall, 2001, 2003, 2005) and the australopiths (*Australopithecus*, *Paranthropus*; Schwartz & Tattersall, 2005). We also include in our analysis four other proposed hominids: *Orrorin* (Senut *et al.*, 2001), *Kenyanthropus* (Leakey *et al.*, 2001), *Ardipithecus* (White *et al.*, 1994, 1995) and *Sahelanthropus* (Brunet *et al.*, 2002). We do so primarily because of the publicity they have received and the claims made for their hominid status. But for the latter three, we do so with the caveat that only when their discoverers make at least the type specimens available for scrutiny by others can independent verification of the published descriptions and interpretations be possible (see commentaries by Schwartz, 2004b; Schwartz & Tattersall, 2005).

Our sample of fossil apes includes only those taxa for which substantial morphological evidence has already been provided in support of their cladistic membership within a large-bodied hominoid clade: *Hispanopithecus*, *Ouranopithecus*, *Ankarapithecus*, *Sivapithecus*, *Gigantopithecus*, *Lufengpithecus*, *Khoratpithecus* and *Dryopithecus* (e.g. Schwartz, 1990, 1997; Moyà Solà & Köhler, 1993; Stewart & Disotell, 1998; Begun, 2005). Other extinct large-bodied hominoids are either apparently more basal to these groups or insufficiently known skeletally to adequately resolve their phyletic position (see Begun, 2001). The fossil taxa *Langsonia* from Vietnam (Schwartz *et al.*, 1995) and '*Sivapithecus*' from Nepal (Munthe *et al.*, 1983) are not included here because they lack diagnostic features that can potentially suggest relationships beyond their membership within a hypothesized clade of dentally thick-enamelled apes. Extant ingroup taxa in our analysis are the species *Homo sapiens* and the great ape genera *Gorilla*, *Pan*, and *Pongo*.

Characters and phylogenetic analysis

Our analysis of potential phylogenetic relationships among extant large-bodied hominoids is based on a character matrix (see Appendix S1 in Supporting Information) comprising structural, behavioural and physiological features (Schwartz, 1987, 1988, 2004a, 2005, 2007; Grehan, 2006a). In contrast to more commonly published approaches, e.g. Strait & Grine (2004) in which purported cladistic analysis often claims synapomorphy within the ingroup in spite of the fact that the feature is also common in the outgroup, the vast majority of the features we propose as potential synapomorphies between humans and orangutans are not represented in any outgroup species. Only for enamel thickness (character 59 for living taxa, character 1 for all taxa) was a feature also present in the outgroup considered sufficiently rare as to represent an independent origin (see Appendices S1 & S2).

As much as possible, and in contrast to the practice in primate molecular studies (e.g. Ruvolo, 1997) and increasingly so in morphological studies (e.g. Begun & Güleç, 1998; Lockwood *et al.*, 2004; Strait & Grine, 2004), we included whenever possible a significant number if not all taxa in the outgroup, rather than only a few selected taxa. Where character states involved quantitative differences (such as in relative or absolute size and volume or angle and orientation), we limited the informative state to the two most derived conditions shared by any two taxa. The values for the other taxa are documented for each character in Appendices S1 and S2. For some characters we accepted a threshold value as proposed in other studies in support of derived states shared between humans and chimpanzees or humans and African apes.

Our analysis of relationships between living and fossil taxa is based on a character matrix limited to hard-tissue characters that have been sufficiently well described in the literature to permit verification, and whose claimed character states as well as unique occurrence within a large-bodied hominoid clade we could corroborate via a broad outgroup comparison (see Appendix S2). Our treatment of some hominid taxa with multiple species (e.g. *Australopithecus*) as single taxonomic units was sufficient to address their relationship to extant great apes while not precluding the possibility that they may be paraphyletic, or even polyphyletic, with respect to *Homo*. For the purposes of our analysis we accept the following hypotheses: Anthropoidea (New and Old World 'higher' primates) constitutes a monophyletic group that subsumes the monophyletic groups Platyrrhini (New World monkeys) and Catarrhini (Old World monkeys and hominoids), and that among the hominoids the monophyletic Hylobatidae (gibbons and siamangs) is the sister group of large-bodied hominoids. These hypotheses have withstood continual testing and are highly corroborated (e.g. Delson & Andrews, 1975; Groves, 1986; Schwartz, 1986; Shoshani *et al.*, 1996; Schwartz & Yamada, 1998), although relationships of taxa within any clade may be contested.

Characters used in our analyses emerged from a collation that initially consisted of hundreds of features generated for, and used in, various studies of human–great ape relationships. Most of these features, however, were found to be irrelevant to the question of relationships among the large-bodied hominoids (e.g. they appeared to be plesiomorphic), incorrectly identified or unverifiable (Schwartz, 1987, 1988, 2005; Grehan, 2006a; see Appendices S3–S5), even after requests for clarification addressed to the original authors. Elsewhere we have proposed up to 42 characters as uniquely shared between humans and orangutans, but of these only 28 are included here as particularly well corroborated at this time (see Appendix S1). This total does not include an additional seven characters proposed by other researchers for humans and orangutans that require further exploration (Grehan, 2006a). Of the 28 human–orangutan characters supported here, 15 have been accepted by various authors who embrace a human–chimpanzee relationship (Andrews, 1987; Groves, 1986, 1987; personal communication; Graham, 1988; Thiranagama *et al.*, 1991; Shoshani *et al.*, 1996; Strait & Grine, 2004). The other 13 characters have essentially been dismissed out of hand or ignored without proper evaluation by others (Grehan, 2006a). We acknowledge that some primate biologists and systematists object to using characters with a presumed functional role because they may be the result of selection independent of phylogeny. In the absence of empirical evidence, this objection is rhetorical. We take the view that such assumptions are not relevant to phylogenetic analysis [because they incorrectly embody use–disuse arguments in which the assumption 'form follows function' predominates (Croizat, 1964; Schwartz, 2005)] and that the most highly corroborated hierarchically nested set of derived characters yields the most probable phylogenetic relationship (Nelson & Platnick, 1981).

In order to maintain analytical comparability between our analyses and other studies on large-bodied hominoid relationships, we used maximum parsimony analysis with PAUP* 4.0b10 (Swofford, 2005) and TNT (sponsored by the Willi Hennig Society; Goloboff *et al.*, 2008) to identify diagnostic synapomorphies. We included bootstrap (50% majority rule) and Bremer support analysis as two widely used measures of tree viability. An exhaustive search was made for extant taxa (humans and the great apes) in Analysis A, and between extant taxa and unproblematic fossil hominids (australopiths and *Homo*) in Analysis B. A heuristic search was made in Analysis C for all extant and fossil taxa considered in this study. In each analysis, characters exclusive to small- and large-bodied hominoids were included to illustrate their monophyly in relation to monkeys. The same analysis was also carried out in Analysis D where only those fossil taxa with sufficient informative characters to provide resolution of relationships within the 'dental hominoid clade' (defined in Results) were included. This technique recognizes that missing data may increase the number of equally parsimonious trees as well as result in the production of spurious cladograms (Ebach & Ahyong, 2001). Unresolved relationships in Analyses C and D were identified by strict consensus.

Biogeographical analysis

The minimum-spanning tree (track) method (Craw *et al.*, 1999) was used to reconstruct the spatial connection between the disjunct and vicariant distributions of hominids and non-hominid members of the dental hominoid clade. Disjunct localities of each taxon, whether living or fossil, were linked together as a minimal spanning tree, and these tracks were then connected to each other by additional minimal spanning links between nearest localities. The spatial structure of the track was characterized with respect to the vicariant replacement of taxa, the intersection of two or more individual tracks (nodes) and main massings (geographical concentrations of diversity whether genetic, morphological, taxonomic, etc.). These spatial features are used to provide an evolutionary model for the differentiation of hominids and their nearest living and fossil relatives.

Spatial overlap (geological correlation) with tectonic or geomorphological features was examined in order to generate a historical model for estimating the minimum divergence age and distribution range of the last common ancestor. The distribution beyond Africa of species of *Homo* is generally considered to have resulted from one or more range expansions following an African origin of the genus. Since *Homo* is widespread and sympatric with respect to all other members of the dental hominoid clade, the biogeography of *Homo* lies outside the scope of the present analysis.

Taxa

(1) Ankarapithecus

Known from a single species, formerly known as *Sivapithecus meteai* Ozansoy, 1957, from 10.7 to 10.6 Ma in the Sinap Formation north of Yassiören in central Turkey (Fig. 1a; Andrews & Tekkaya, 1980; Alpagut *et al.*, 1996; Lunkka *et al.*, 1999). The specimens comprise a mandible and skull fragments that present a tall, wide and anteriorly facing zygoma (cheekbone), marked alveolar prognathism combined with a short upper face, tall, ovoid, superiorly rimmed but not widely separated orbits, and a long, slit-like incisive foramen situated anteriorly in the palate – all of which suggest affinity with the orangutan (Andrews & Cronin, 1982).

(2) Ardipithecus

Two species from the Middle Awash region of Ethiopia (Fig. 1a). The holotype of *Ardipithecus ramidus* (White *et al.*, 1994) comprises a set of 'associated teeth from one individual' and the paratype series has various associated cranial fragments, two partial cranial bases, a juvenile mandible and associated and isolated teeth dated *c.* 4.4 Ma. Molars are characterized as having absolutely and relatively thinner enamel than those in *Australopithecus* (White *et al.*, 1994, 1995). The holotype of *Ardipithecus kadabba* Haile-Selassie,

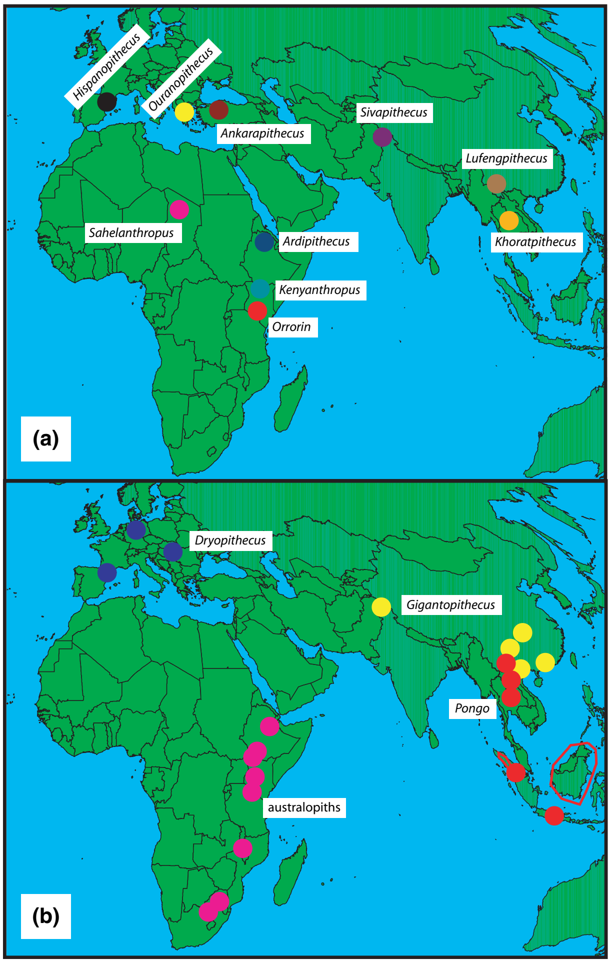

Figure 1 Generalized distribution localities for fossil and living hominoids (excluding *Homo*, *Pan* and *Gorilla*) included in this study. (a) Fossil hominoids *Hispanopithecus* (Spain), *Ouranopithecus* (Greece), *Ankarapithecus* (Turkey), *Sivapithecus* (Indo-Pakistan), *Lufengpithecus* (southern China), *Khoratpithecus* (Thailand), *Sahelanthropus* (Chad), *Ardipithecus* (Ethiopia), *Kenyanthropus* (Kenya) and *Orrorin* (Kenya). (b) Distribution of extant (outline) and fossil *Pongo* in Southeast Asia, and fossil hominoids *Dryopithecus* (Europe), *Gigantopithecus* (Indo-Pakistan and eastern Asia) and the australopith hominids (East Africa).

Suwa & White, 2004 comprises part of a right mandible with associated teeth, and various isolated teeth and postcranial fragments, some from the same site as the holotype; dated to *c.* 5.2–5.8 Ma (Haile-Selassie, 2001; Haile-Selassie *et al.*, 2004).

(3) *Australopithecus–Paranthropus*

At least 10 species in East and South Africa (Fig. 1b) *c.* 4.5–2.0 Ma (Schwartz & Tattersall, 2005). The relationships of australopiths to one another are very uncertain (Schwartz, 2004a), and some australopiths appear to be more closely related to *Homo* than others (Tattersall & Schwartz, 2000; Strait & Grine, 2004). Brunet *et al.* (1995) did not delineate derived features supporting their claim that *Australopithecus bahrelghazali* Brunet *et al.*, 1995 from Chad is a hominid; because independent study of the holotype was not permitted (Schwartz, 2005), this taxon is not recognized here. Australopiths share many derived postcranial features with humans, particularly with respect to bipedal locomotion (see review in Schwartz, 2007), but many of their derived craniodental features also characterize orangutans and their potential extinct relatives (Schwartz, 2004a). If australopiths are more closely related to humans than to any living great ape, the features they share with the orangutan may represent primitive retentions from the ancestor of a larger clade that subsumes them all.

(4) *Dryopithecus*

Three species from Europe (Fig. 1b) *c.* 9–12 Ma. Characterized by the unique development of narrow, tall-crowned upper central incisors and thin-enamelled molars with high dentine penetrance. *Dryopithecus fontani* Lartet, 1856 from France and Austria is represented by fragmentary mandibles (the holotype is a mandible), isolated teeth and a humeral shaft (Begun, 1994). *Dryopithecus brancoi* Schlosser, 1901 from Rudabánya, Hungary is represented by the holotype (a left M_3) plus additional material, including a partial cranium (RUD 77), tooth-bearing mandibles and maxillae and isolated teeth. The holotype of *Dryopithecus crusafonti* Begun, 1992 from Can Ponsic and El Firal, Spain comprises a poorly preserved left maxilla and a separate but apparently associated left canine fragment. In addition, 15 isolated teeth and a mandible have recently been allocated to this taxon (Begun, 2002). Begun & Kordos (1997) and Begun *et al.* (1997) have proposed *Dryopithecus* as the sister taxon of an australopith–African ape clade.

(5) *Gigantopithecus*

A few incomplete lower jaws and numerous isolated teeth allocated to three species: *Gigantopithecus blacki* von Koenigswald, 1935 from south-eastern China and northern Southeast Asia between 2.0 and 0.3 Ma (Pei & Woo, 1956; Simons & Ettel, 1970; Ciochon *et al.*, 1990, 1996; Huang *et al.*, 1995; Schwartz *et al.*, 1995; Zhao *et al.*, 2006), *Gigantopithecus bilaspurensis* Simons & Chopra, 1969 (Simons & Chopra, 1968, 1969; Patnaik *et al.*, 2005) and *Gigantopithecus giganteus* (Simons & Chopra, 1968, 1969; Cameron, 1997, 2001, 2003) from Indo-Pakistan (Fig. 1b) *c.* 7.5–7.8 Ma. The holotypes comprise a right lower third molar for *G. blacki*, a right lower second or third lower molar for *G. giganteus* (Kelley, 2002) and a lower jaw lacking ascending rami for *G. bilaspurensis* (Simons & Chopra, 1968, 1969). The genus *Indopithecus* was resurrected for the Indo-Pakistan species by Cameron (1997, 2001, 2003) because of perceived dental differences with *G. blacki*. Aside from a partial mandible for *G. blacki* and *G. bilaspurensis*, *Gigantopithecus* is known primarily from isolated, often highly worn teeth.

(6) *Hispanopithecus*

A single species, *Hispanopithecus laietanus* Villalta & Crusafont, 1944 represented by fragments of skull, upper and lower jaw and partial postcranial skeleton and isolated teeth recorded from the Valles-Penédes region of north-eastern Spain at La Tarumba, Can Llobatéres, Palinyá and Can Mata (Fig. 1a), with fossil ages ranging between 9.5 and 10 Ma (Agustí *et al.*, 1996). The holotype comprises a set of associated lower premolars and molars (Ribot *et al.*, 1996; Begun, 2002). The forelimbs and hands are 'extremely' long relative to femoral length (Begun *et al.*, 1990; Moyà Solà & Köhler, 1993; Begun, 1994, 2002; Ribot *et al.*, 1996). Moyà Solà & Köhler (1993) suggested that this taxon was basal to an orangutan clade that included the fossils *Ouranopithecus*, *Lufengpithecus* and *Sivapithecus*. Cameron *et al.* (1997) also concluded that this taxon was related to an orangutan clade. In their revision of Dryopithecinae, Simons & Pilbeam (1965) reduced *Hispanopithecus* to a junior synonym of *Dryopithecus*, but without justification. In the absence of any evidence to the contrary, we regard *Hispanopithecus* as a valid taxon (see also comments by Cameron, 1998, 1999).

(7) *Kenyanthropus*

A single species, *Kenyanthropus platyops* Leakey *et al.*, 2001 represented by a largely complete but distorted cranium (holotype), a partial left maxilla and a variety of other cranial fragments (paratypes) from sites along the Lomekwi and Topernawi rivers of the Turkana district, northern Kenya (Fig. 1a). The holotype, paratypes and other fragments are from different sites: LO-6N, LO-5, LO-4, 5 and 9, respectively. The cranium lacks most of the cranial base, premolar and anterior tooth crowns, and the entire right incisor. The upper second molar crown has been characterized as having enamel thickness comparable to that in *Australopithecus anamensis* and *Australopithecus afarensis* (Leakey *et al.*, 2001).

(8) *Khoratpithecus*

Two species: *Khoratpithecus chiangmuanensis* Chaimanee *et al.*, 2003 represented by isolated teeth from Chiang Muan Basin, northern Thailand at 10–12.5 or 13 Ma and *Khoratpithecus piriyai* Chaimanee *et al.*, 2004 represented by a lower jaw (holotype) with thick-enamelled and low-cusped molars from Nakorin Ratchasima, eastern Thailand (Fig. 1a; Chaimanee *et al.*, 2003, 2004, 2006; Pickford *et al.*, 2004; Kunimatsu *et al.*, 2005; Suganuma *et al.*, 2006). The absence of digastric fossae (indicating the absence of the anterior belly of the digastric muscles) along the anteroinferior margin of the mandible in *K. piriyai* is cited as a synapomorphy with the orangutan (Chaimanee *et al.*, 2004), but this feature is also absent in *Ankarapithecus* (J.H.S., personal observation). Kunimatsu *et al.* (2005) expressed uncertainty about the phylogenetic status of *K. chiangmuanensis*, and Pickford *et al.* (2004) regard *K. chiangmuanensis* (as *Lufengpithecus chiangmuanensis* as originally designated by Chaimanee *et al.*, 2003) as a synonym of ?*Lufengpithecus keiyuanensis*.

(9) *Lufengpithecus*

At least two species from southern Yunnan Province, China: *Lufengpithecus lufengensis* Xu *et al.*, 1987 (holotype mandible with right and left lower second incisor and third molar) from Shihuiba near Lufeng at 8 Ma (Wu & Xu, 1985; Lu, 2004), and *Lufengpithecus keiyuanensis* Woo, 1957 (isolated teeth, maxillary and mandibular fragments) from Xiaolongtan and Yuanmou *c.* 7–9 Ma (Fig. 1a; Zheng & Zhang, 1997; Harrison *et al.*, 2002; Ni & Qiu, 2002). Harrison *et al.* (2002) cite an undescribed mandibular fragment from Yangyi at 2–5 Ma in Yunnan Province, which may represent another *Lufengpithecus* locality. The genus shares with *Pongo* and *Sivapithecus* rim-like supraorbital margins, a small and triangular nasal aperture, tall, anteriorly facing and flattened zygomas, a broadly spatulate first upper incisor that is markedly larger than the subconical second upper incisor, and a superiorly expanded maxillary sinus (Schwartz, 1990, 1997). The configuration of the region of the incisive foramen/foramina remains unknown for *Lufengpithecus* because of damage to the anterior palate of skulls PA 644 and 677 (*L. lufengensis*) (Schwartz, 1990) and inadequate clarity illustrated for skull YV 0999 of *L. keiyuanensis* (Zheng & Zhang, 1997). Isolated teeth from northern Thailand that have been linked with *Lufengpithecus* are of uncertain status (Kunimatsu *et al.*, 2005).

(10) *Orrorin*

A single species, *Orrorin tugenensis* Senut *et al.*, 2001 from Lukeino, Kenya (Fig. 1a) *c.* 5.7–6.0 Ma (Sawada *et al.*, 2006) is represented by two mandibular fragments (BAR 1000'00a, b as the holotype), along with four isolated teeth and various postcranial fragments treated as conspecific with the holotype (Schwartz & Tattersall, 2005). Senut *et al.* (2001) concluded that features of the femoral fragments are consistent with those in australopiths and *Homo* that are associated with bipedalism. Galik *et al.* (2004) subsequently CT-scanned the better-preserved partial femur and interpreted the relatively greater thickness of cortical bone along the inferior vs. superior extent of the femoral neck as indicative of a load-bearing stress response seen in australopiths and *Homo*. Exposed sections of molar enamel appear to be moderately thick (Schwartz & Tattersall, 2005). Pickford & Senut (2001, 2005) stated that the molars recall those of australopiths and *Homo* in overall crown shape, bunodonty, cusp inflation and restriction of the talonid basin. Pickford *et al.* (2002) suggested that the affinities of *Orrorin* lie closer to *Homo* than to *Australopithecus*.

(11) *Ouranopithecus*

Numerous mandibles (holotype is a mandible) and teeth, as well as two phalanges and a partial skull of *Ouranopithecus macedoniensis* de Bonis & Melentis, 1977 from Ravin de la

Plué, Xirochori and Nikiti in northern Greece (Fig. 1a) *c.* 9 Ma (de Bonis *et al.*, 1974; de Bonis & Melentis, 1977, 1978). The molars have low, broad cusps with very thick enamel (de Bonis *et al.*, 1990; Begun, 2002). *Ouranopithecus* shares with *Pongo*, *Sivapithecus* and *Lufengpithecus* marked upper incisor size heteromorphy, a subconical second upper incisor, an anteriorly facing zygoma and a superiorly expanded maxillary sinus (Schwartz, 1990). The anterior palate lacks sufficient detail to confirm whether one or two incisive foramina are present (J.H.S., personal observation, 2003). de Bonis *et al.* (1990) and Koufos & de Bonis (2004) suggested that the relatively reduced canines, absence of a honing wear facet on the mesial face of the lower anterior premolar, and rounded and swollen molar cusps represent derived features that place *Ouranopithecus* closer to hominids such as *Australopithecus* and *Homo* than to the African apes. A second species, *Ouranopithecus turkae* from central Anatolia, Turkey, is represented by a maxilla (holotype) and partial mandibles with thickly enamelled molars (Güleç *et al.*, 2007). The lack of clarity as to whether this fossil shares apomorphies with *Ouranopithecus* precludes inclusion of this species in our character analysis, although it would appear to be a member of a thick-enamelled hominoid clade.

(12) Pongo

Possibly two extant subspecies, *Pongo pygmaeus pygmaeus* (Linnaeus, 1760) in Borneo and *Pongo pygmaeus abelii* (Lesson, 1872) in northern Sumatra (Harrison *et al.*, 2006) and fossil records ranging from southern China to Indonesia (Kahlke, 1972; von Koenigswald, 1982) with localities in southern China *c.* 1.2–0.011 Ma (Hooijer, 1948; Colbert & Hooijer, 1953; Ho *et al.*, 1995; Wang *et al.*, 2007); Vietnam *c.* 0.3–0.02 Ma, including *Pongo hooijeri* Schwartz *et al.*, 1995; and four subspecies of *P. pygmaeus* (Schwartz *et al.*, 1995; Bacon & Long, 2001); Thailand *c.* 0.17 Ma (Chaimanee & Jaeger, 1993; Tougard *et al.*, 1998; Tougard & Ducrocq, 1999); Sarawak *c.* 0.04 Ma (Hooijer, 1960); Sumatra *c.* 0.08–0.06 Ma, including *Pongo pygmaeus paleosumatrensis* (Hooijer, 1948; de Vos, 1983); and Java *c.* 0.13–0.06 Ma (van den Bergh *et al.*, 2001; Westaway *et al.*, 2007) (Fig. 1b).

(13) Sahelanthropus

A single species, *Sahelanthropus tchadensis* Brunet *et al.*, 2002, *c.* 7 Ma from the western Djurab Desert, northern Chad (Fig. 1a), represented by a holotype comprising a nearly complete cranium preserving some teeth, and four paratypes comprising an isolated upper first incisor, a partial right mandible, an upper third molar and a portion of a mandibular symphysis. Molar enamel is characterized as 'intermediate' between *Pan* and *Australopithecus*. Its hominid status has been based on several supposedly derived features, including canines that are small and apically worn and intermediate postcanine enamel thickness (Brunet *et al.*, 2002). Similarities to later hominids, including *Kenyanthropus* and *Homo*, were identified as the length and horizontal orientation of the basicranium, the anterior position of the foramen magnum, reduced subnasal prognathism without a canine diastema and a large continuous supraporbital torus (Brunet *et al.*, 2002). We are unable to find support for any of these proposed character states as uniquely shared hominid features (see Appendix S4).

(14) Sivapithecus

Three species: *Sivapithecus indicus* (Pilgrim, 1910), *Sivapithecus sivalensis* (Lydekker, 1879) and *Sivapithecus parvada* Kelley, 1988 between 12.5 and 8 Ma from the Siwalik formation of Indo-Pakistan (Fig. 1a). Specimens comprise cranial and postcranial remains and molars with thick enamel and low cusps (Andrews & Cronin, 1982; Kelley, 1988; Kappelman *et al.*, 1991; Cameron *et al.*, 1997, 1999; Patnaik *et al.*, 2005; Pillans *et al.*, 2005), although crowns of unworn teeth of at least *S. sivalensis* may be tall (J.H.S., personal observations). The skull presents a narrow and single palatal incisive foramen and anteriorly oriented, tall, vertical and flat zygomas. The genus is generally regarded as a close orangutan relative (Schwartz, 2004b). The genus also subsumes *Ramapithecus*, which was once widely and unequivocally regarded as a close relative if not the ancestor of all later hominids (Simons & Pilbeam, 1965; Pilbeam, 1986; Simons, 1989; Benefit & McCrossin, 1995).

RESULTS

Analysis A resulted in a single most parsimonious tree (Fig. 2a) with a consistency index (CI) of 0.79 and a retention index (RI) of 0.76. There is strong bootstrap support (BS = 100%) for the monophyly of both a clade that subsumes humans (Hominidae) and orangutans (Pongidae) and a sister group comprising chimpanzees and gorillas (Panidae; see Schwartz, 1986, for taxonomic categories).

Analysis B resulted in three most parsimonious trees for the interrelationship between humans, fossil *Homo* and australopiths. A strict consensus analysis resulted in an unresolved relationship among humans, fossil *Homo* and australopiths, which collectively emerged as the sister group of *Pongo* (Fig. 2b). As in Analysis A, a bootstrap analysis also gave strong support (BS = 100%) for a monophyletic group consisting of a clade that subsumes living and fossil hominids (*Homo*, australopiths) and orangutans (Pongidae) that shared a common ancestor with the sister group *Pan–Gorilla*.

Analysis C for all taxa retrieved 20 trees of 75 steps; the consensus analysis placed the hominids in an unresolved relationship with the putative hominids *Kenyanthropus* and *Orrorin* along with the orangutan and various fossil Miocene–Pliocene apes (Fig. 2c), which we refer to as the 'dental hominoid clade' in reference to their relatively thick molar enamel. The putative hominids *Sahelanthropus* and *Ardipithecus* were placed in an unresolved relationship with the dental hominoid clade, the African apes and European *Dryopithecus*. Bootstrap support for the monophyly of all living and fossil

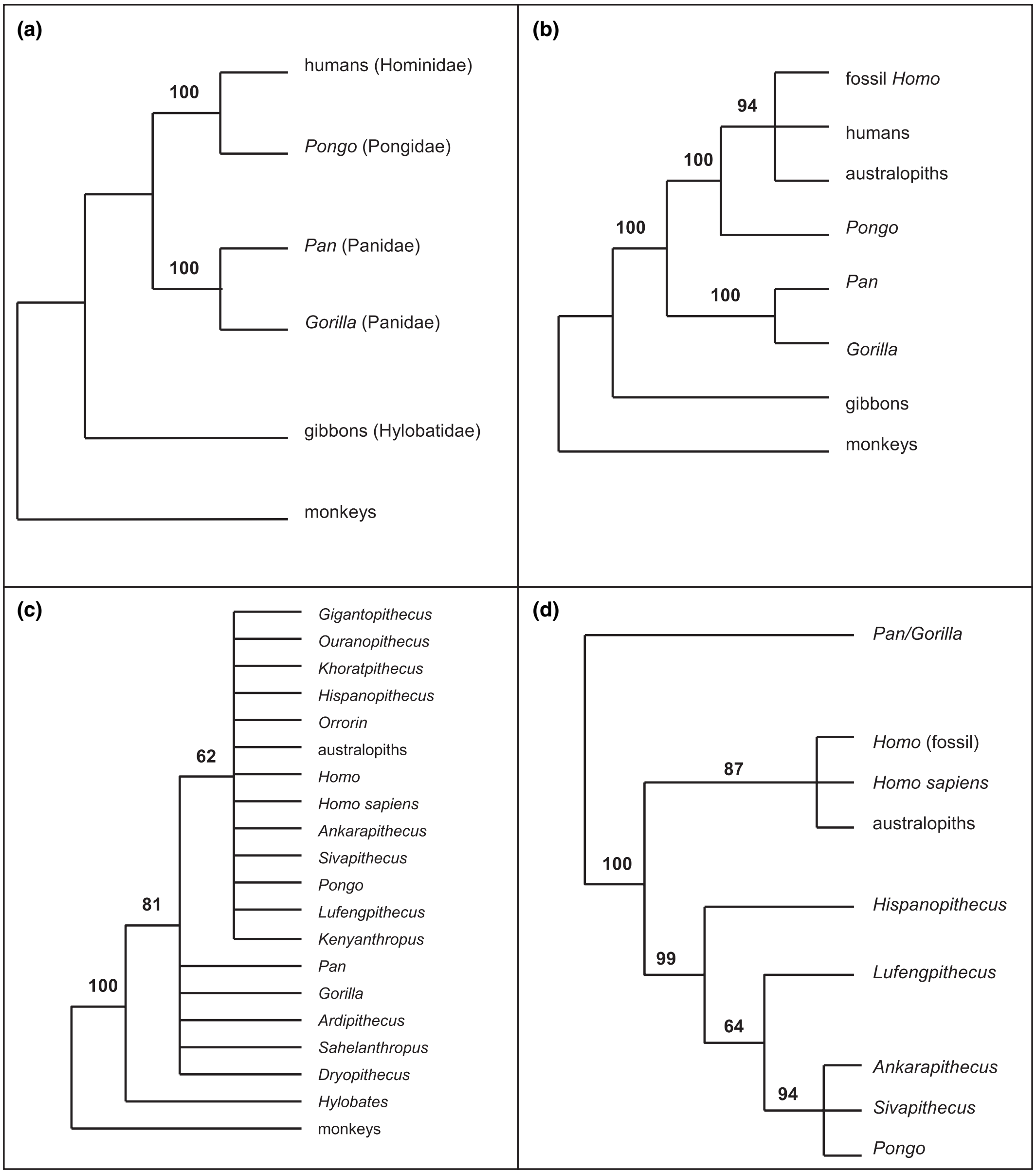

Figure 2 Phylogenetic relationships and bootstrap values for living and fossil large-bodied hominoids. (a) Single most parsimonious tree for extant large-bodied hominoids supporting the monophyly, respectively, of humans (Hominidae) and orangutans (Pongidae) and of the African apes (Panidae). (b) Consensus tree for large-bodied hominoids supporting the monophyly of living (humans) and fossil hominids (*Homo*, australopiths) as the sister-group to orangutans. (c) Consensus tree supporting the monophyly of hominids and various Miocene–Pliocene fossil apes and orangutans into a 'dental-hominoid clade', with the African apes as a sister clade along with the putative hominids *Ardipithecus* and *Sahelanthropus*. The heuristic search was made with a random seed = 100, replicates = 50,000, saved trees/replication = 10, tree bisection–reconnection (TBR) option and replacement of existing trees. (d) Consensus tree for fossil and living large-bodied hominoids with fossil taxa limited to those with 14 or more shared character states as the maximum number of taxa providing resolution of relationships within the dental-hominoid clade.

taxa was weak (BS = 62) and it was not possible to collapse any of the nodes using Bremer analysis.

Restricting the analysis of living and fossil relationships to eight fossil taxa with sufficient characters (14 or more) to resolve relationships within the dental hominoid clade resulted in a much higher level of support (BS = 100) for this clade (Fig. 2d). This latter analysis (Analysis D) also strongly supported the hominid clade (BS = 87) as the sister group of five dental hominoids (BS = 99) with variably unresolved relationships: *Pongo*, *Sivapithecus* and *Ankarapithecus*, followed by *Lufengpithecus* and *Hispanopithecus*, respectively. Bremer analysis could not collapse this tree further.

The geographical distribution of the dental hominoid clade is characterized by a track (Fig. 3a) comprising disjunct

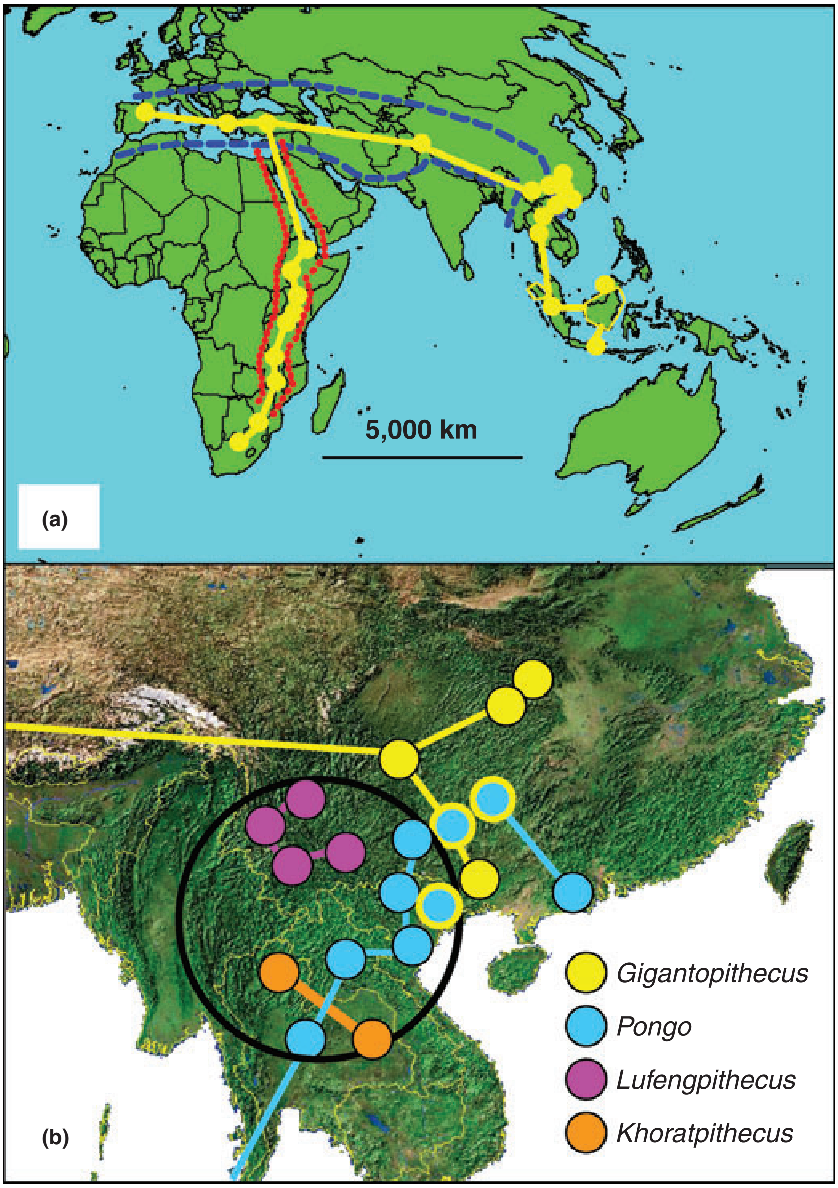

Figure 3 Geological and spatial correlations for dental hominoids. (a) Tectonic correlation of the dental hominoid track (yellow) with the East African Rift System (approximate boundary as red dotted lines) and Tethyan Orogenic Collage (approximate boundary as blue dashed lines). (b) East Asian Node (as open black circle) encompassing geographical proximity or overlap of tracks between four largely or entirely vicariant dental hominoid genera: *Lufengpithecus*, *Gigantopithecus*, *Khoratpithecus* and *Pongo* (with overlapping ranges of *Gigantopithecus* and *Pongo* indicated by blue circles with a yellow border).

distribution ranges for hominids (East Africa), *Hispanopithecus* (Spain), *Ouranopithecus* (Greece) and *Ankarapithecus* (Turkey). This dental hominoid clade track is spatially correlated with two major tectonic structures: the East African Rift System (EARS) and the Tethys Orogenic Collage (TOC). The wide-ranging *Gigantopithecus* and *Pongo* are vicariant for most of their respective ranges and their tracks only intersect in southern China, northern Thailand and Vietnam (Fig. 3b), where also are found *Lufengpithecus* (southern China), *Khoratpithecus* (northern Thailand), *Langsonia* (northern Vietnam) and possibly other as yet undescribed dental hominoid clade-related taxa (Kunimatsu *et al.*, 2005). The main massing of dental hominoid clade generic and species diversity is found in southern China–northern Southeast Asia (six taxa) and is centred on a southern China–northern Thailand–Vietnam node where the otherwise vicariant *Gigantopithecus*, *Pongo*, *Lufengpithecus* tracks intersect with each other. A second massing of about four genera and 11 hominid species is represented in East Africa, followed by a smaller Indo-Pakistan massing (about two genera, four species) represented by *Gigantopithecus bilaspurensis*, *Sivapithecus indicus*, *Sivapithecus sivalensis* and *Sivapithecus parvada*.

DISCUSSION

Phylogenetic relationships

Morphological implications

Our results are phylogenetically interesting because we have taken into consideration an array of characters that have been published as similarities between hominids and apes, even though we found that most were problematic, lacked adequate documentation or could not be confirmed (see Schwartz, 2005; Grehan, 2006a; and see Appendices S3–S5). Although a range of morphological studies have claimed to support a closer relationship between humans and chimpanzees or African apes, these studies have relied on many of the characters that we found to be problematic, and thus demonstrate how entrenched error becomes as it is unquestioningly passed on from and incorporated into one study after another. While our morphological analysis of living taxa contradicts the interpretations of an array of recent studies based on molecular comparisons, the proposed monophyly of hominids (*Homo* and australopiths) and orangutans to the exclusion of the African apes is further corroborated by the analysis of fossil taxa – including several Miocene hominoids that have otherwise been largely marginalized in the biogeographical exploration of hominid origins and evolution – which collectively comprise a clade we descriptively refer to as 'dental hominoids'. Monophyly of a dental hominoid clade encompassing all living and fossil representatives is only weakly supported because many taxa are known only from partial remains and there is currently only one character state (thick molar enamel) represented in all fossil members.

A hominid clade was distinguished from, and shown to be more closely related to, the orangutan than to the African apes, when the analysis of fossil taxa was restricted to the relatively well-known australopiths and *Homo*. The result of Analysis D, which compared hominids to fossil taxa with 14 or more informative characters, is somewhat similar to one proposed by Begun (2007). However, a major difference in our analysis is the absence of Begun's purported African ape–australopith clade (the putative synapomorphies were found to be either incorrect or unverifiable; Grehan, 2006a). Exclusion of *Sahelanthropus* and *Ardipithecus* from the dental hominoid clade in the living-fossil comparisons further emphasizes the uncertainties of recognizing these taxa as hominids (Schwartz, 2007). Our results support the hypothesis that the African apes are not only less closely related to humans than are orangutans, but also less closely related to humans than are many Miocene hominoids. Claims of a close evolutionary relationship between African apes and various early Miocene taxa need to be re-evaluated without the analysis being constrained from the outset by assuming a close relationship between African apes and humans.

The numerous features that cannot be documented for many members of the dental hominoid clade represents the principal weakness of our (or any other) analysis encompassing all fossil and living hominoids considered in this study. Nevertheless, we have shown that there is indeed evidence to link human ancestry to various fossil Miocene apes and that it is possible to identify human–nearest living ape relatives (*contra* Andrews & Harrison, 2005). We predict that future fossil discoveries will confirm that many if not all missing character states will be compatible with our current findings.

Molecular implications

The most frequently raised objection to the human–orangutan relationship is that the molecular evidence supporting a closer relationship between humans and chimpanzees is said to be 'overwhelming' (e.g. Koop *et al.*, 1989; Ruvolo, 1997; Goodman, 1999; Bradley, 2008). But the widely accepted notion that 'greatest overall molecular similarity' is synonymous with 'most closely related' derives not from any empirical evidence but merely from the acceptance without question of the 'molecular assumption': namely, most recently divergent taxa will be most similar in their proteins and DNA because they will have shared a longer lineage of molecular change prior to their divergence and that the pace of molecular change was clocklike in nature (see discussion in Schwartz, 2005, and Schwartz & Maresca, 2007). Nevertheless, despite claims to the contrary, the demonstration of molecular similarity does not *a priori* equate with a demonstration of homology, which must precede any hypothesis of phylogenetic relationship (Patterson, 1982) because a demonstration of similarity alone is only phenetic and must be subject to rigorous phylogenetic enquiry (Williams & Ebach, 2008).

Molecular systematists originally validated the use of molecular data by claiming consistency in results with well-established relationships of taxa that derived from morphological studies. Curiously, although morphology was the key to validating the use of molecular data in hypothesizing phylogenetic relationships, the subsequent popularity of the intrinsically internally consistent, and therefore unfalsifiable, molecular assumption led to the widespread belief that demonstration of molecular similarity was always a more accurate reflection of phylogenetic propinquity than morphology, which was considered to be too malleable in the face of adaptive and selection pressures. Consequently, the intellectual tables got turned around with the theoretically and philosophically inconsistent result that molecularly based phylogenies were taken as revealing the 'true' evolutionary relationships, no matter what the phylogenetic conclusions based on analysis of morphology (Schwartz, 2005).

Further justification of the authority of molecular data came from the psychological effect of what became known as the 'law of large numbers' (Sibley & Ahlquist, 1984), which emphasizes the fact that in any molecular study one is comparing 'so many' molecular elements – in contrast to a mere few thousand soft and hard tissue anatomical features – that overall similarity must be a reflection of phylogenetic closeness (Rieppel & Kearney, 2007). It is beyond the scope of this discussion to provide a detailed critique (see Schwartz & Maresca, 2007), but our position is that the molecular assumption is problematic. We draw attention to four aspects of molecular similarity affecting the analysis of large-bodied hominoids which suggest that molecular similarity is not the final arbiter of phylogenetic relationship.

1. *Cladistic analysis*. Morphological data are not immune to the possibility of homoplasy, but neither are molecular data. In fact, the lack of a comprehensive theory of homology in molecular systematics is its main weakness. As with demonstrated morphological similarity, similarity between DNA sequences can be due to primitive retention, reversal, homoplasy or simply to being non-homologous (e.g. convergent). The only bases for claiming demonstration of molecular homology are the limited data set of four nucleotides and their positions relative to each other (sequence order). DNA sequences are further inherently ambiguous because a substitution event leaves no evidence of replacement, which would seem to be a critical element towards hypothesizing whether matching base pairs represent primitive retention, convergence, or unique derivation.

In addition, in order to compare supposedly homologous DNA sequences one must align sequences of different lengths, which is a procedure that requires assumptions about deletions or additions that underlie the observed disparity in nucleotide sequence order and length. In the end, there is no objective way to assess the relative phylogenetic value for the number of gaps and substitutions that are assumed in order to align sequences of different lengths (Marks, 2003). Thus, statements of sequence homology are not generated from individual comparative outgroup character analysis as they are in morphological analyses. Rather, the claim of sequence homology is the result of an overall best fit between an artificially reconstructed sequence and subsequent measures of phenetic similarity (Giribet *et al.*, 2002; De Laet, 2005; Redelings & Suchard, 2005; Phillips, 2006; Kjer *et al.*, 2007).

Earlier molecular comparisons such as DNA hybridization have since been recognized by molecular systematists as being non-cladistic, but the results continue to be cited in support of a close human–chimpanzee relationship (Ruvolo, 1997; Bradley, 2008). Other non-cladistic measures of overall similarity, such as distance measures (Nelson & Ladiges, 2009), also remain popular, in large part because of the seductive argument that they pass the 'test of reciprocity' (Sarich & Wilson, 1966). That is, if the anti-albumin, for example, from taxon A is cross-reacted with albumin from taxon B and the reverse experiment provides a similar percentage of similarity, then one is 'testing' the first hypothesis of 'distance' (= difference) between taxa A and B and demonstrating from two 'directions' relative phylogenetic propinquity. Further tests of reciprocity with additional taxa are interpreted in the same fashion. But this kind of comparison itself is not as objective as it might seem at first glance. Underlying it is the very basis of the 'molecular assumption' (Schwartz & Maresca, 2007) that informs all molecular comparisons: namely, that greater dissimilarity reflects longer periods of separation between continually changing lineages, while greater overall similarity reflects a more recent divergence of continually changing lineages (see Zuckerland & Pauling, 1962). This, of course, is the application of a Darwinian model of continually active change on a static observation of similarity. It is not the demonstration that overall similarity equates with phylogenetic propinquity (Schwartz, in press). So we are back to square one, wherein the data themselves do not resolve whether similarity is the result of primitive retention (no change), homoplasy or synapomorphy. In fact, since the test of reciprocity does not identify the basis of overall similarity – as at least comparing nucleotide sequences does – one does not know if the 'similarities' between different taxa are actually between similar molecular regions (Schwartz & Maresca, 2007).

2. *Insufficient outgroup sampling*. If, for the moment, the alignment problem is ignored and similar nucleotide bases are accepted as representing shared derived, cladistically valid character states (which is the general assumption in sequence analysis), similar molecular sequences should be absent or rare in the outgroup. Corroboration thus requires adequate sampling of outgroup taxa, although ideally all taxa in the outgroup should be sampled. In our morphological study, the outgroup is most frequently represented by the lesser apes and all Old World monkeys. In some cases outgroup sampling for the morphological characters is more limited and we have drawn attention to these specific cases in the supporting information. By comparison, outgroup sampling in molecular analyses of human–chimpanzee relationships is extremely limited [e.g. within Primates, 12 species (Prasad *et al.* 2008), nine species (Cooper *et al.*, 2005; Steiper & Young, 2006), eight species (Bailey *et al.*, 1992), seven species (Koop *et al.*, 1989), five species (Patterson *et al.*, 2006), four species (Hayasaka *et al.*, 1988), one species (Ebersberger *et al.*, 2007)]. Consequences of the bias towards analysing only the taxa in which one is currently interested are not trivial. First, the result is at best tautological because the analysis can only result in a reiteration of that which is already assumed (such as chimpanzees being more closely related to humans than orangutans). Second, it adds an additional layer of superficial similarity by claiming demonstration of synapomorphy when in fact pursuing the analysis with a limited number of taxa from the outset precludes alternative hypotheses of character polarity (assuming that different nucleotides do indeed represent different character states and are thus cladistically equivalent to primitive vs. derived states of a morphological character or morphoclines of increasing derivation).

3. *Exclusion of the orangutan*. Many studies that claim support for the human–chimpanzee relationship are uninformative with regard to the orangutan because if they even include this hominoid in the analysis (which is usually not the case), these studies assume from the outset that the orangutan represents the primitive outgroup and thus its molecular sequence is primitive relative to other large-bodied hominoids (e.g. Ruvolo, 1997; Enard & Pääbo, 2004; Hobolth *et al.*, 2007). When the orangutan is excluded from an analysis, the justification given is that its distant relationship to other large-bodied hominoids has long been demonstrated by 'extensive' genetic data (Ruvolo, 1997). Clearly, these rationalizations are at best tautological.

4. *Molecular inconsistency*. An interesting, yet unscientific, contradiction exists in the molecular literature in terms of conflicts between morphologically and molecularly derived phylogenies. The overwhelming morphological evidence in support of a human–orangutan sister relationship is discounted as 'false' because it is not consistent with the interpretation of molecular similarity, but when molecular data yield phylogenies that are in conflict with traditional taxonomic groupings of primates, these molecular data are also rejected as 'false' (Ruvolo, 1997; Patterson *et al.*, 2006). In further tautology, the paltry morphological data in support of a human–chimpanzee sister relationship are imbued with greater valence than the morphological data supporting a human–orangutan sister relationship because the former are 'compatible' with an interpretation of molecular similarity (Ruvolo, 1996). Clearly, in the latter two examples, molecular systematists use morphology when it is useful to their objectives – which means that they are selectively using morphological data when it serves a purpose. We take the position that a rejection of a human–orangutan sister relationship on the basis of biased uses and interpretations of molecular data is arbitrary and inconsistent with a truly scientific hypothetico-deductive approach to phylogenetic reconstruction.

We believe the above points provide empirical reasons why molecular evidence may be called into question, even when the same answer emerges from different molecular studies and despite the fact that a claimed human–chimpanzee sister relationship often lies within a larger scheme of phylogenetic relationship that yields 'false' relationships among other taxa. Emphasis on the same result from different genes or from large data sets may seem to further corroborate the molecular result, but if the molecular comparisons are not actually between homologous derived character states, the large numbers of similarities may reflect a prevalence of primitive retentions, as is often the case in demonstrations of overall morphological similarity (Schwartz, 2005). Our study cannot resolve such questions, but we do show that if morphology is critically examined using the cladistic principle of restricting analysis to character states that are absent or very rare in the outgroup (Hennig, 1966; Kitching *et al.*, 1998), the preponderance of evidence not only supports a human–orangutan sister relationship among living taxa, but it is also congruent with a cladistic analysis of living and fossil taxa, which can be analysed only through the study of morphology. In this regard, we are compelled to point out that it is precisely when one incorporates fossil evidence into the analysis that the limits of molecular data become apparent, precisely because molecular data cannot speak to, much less falsify or corroborate, any morphological analysis of the relationships between extinct and extant taxa. We recognize that molecular systematists and many palaeoanthropologists will probably disagree with our position on these issues and we look forward to seeing future publications on human origins that explicitly address the challenge of incongruence between patterns of primate molecular and morphological similarity.

Given the results of our cladistic analysis of morphological comparisons between living taxa and between extant and fossil taxa, we conclude that the molecular similarities between humans and chimpanzees cannot all be potential synapomorphies and thus must represent to some (large) extent unidentified primitive retentions, the determination of which cannot derive from ingroup analysis alone. Robust morphological support for phylogenetic relationships that run counter to interpretations of molecular data (as we suggest is the case for humans and orangutans) represents a viable falsifier of molecular similarity, particularly when the morphological evidence of relationship among living taxa (as between human and orangutan) is not contradicted by (indeed is consistent with) hypothesized phylogenetic relationships between fossil and living taxa.

Biogeographical relationships

The largely vicariant distributions of *Gigantopithecus* and *Pongo*, together with their disjunct relationships with the vicariant ranges of australopiths/*Orrorin*, *Hispanopithecus*, *Ouranopithecus* and *Ankarapithecus*, are incongruent with a historical process whereby each taxon arrived at its respective location by independent chance dispersal, as is required by Darwin's (1859) centre-of-origin theory. The occupation of different areas by related taxa implies independent evolutionary histories, whereas chance dispersal connecting each area to a common centre-of-origin implies an absence of geographical isolation. This contradiction is often accommodated by theorizing barriers that are sufficient for isolation while also being occasionally permeable (Simpson, 1965; Rögl, 1999).

One need not, however, resort to hypothetical migrations and barriers once it is appreciated that vicariant distributions are congruent with their deriving from a common ancestor that was already widely distributed over a range that subsequently encompassed the combined distributions of its vicariant descendants (Craw *et al.*, 1999). That is, after the widespread ancestral range was established during a period of mobility when geographical and ecological conditions permitted range expansion, there was differentiation and origination of descendant taxa in different regions that might give the appearance of each descendant having migrated to establish its respective distributions (Croizat, 1964). But once the limits of ancestral range expansion are reached there is effectively a state of immobility where local differentiation may be further enhanced by geological, topographic and climatic disruption of the ancestral range (Croizat, 1964). The prevalence of vicariant distribution ranges within the dental hominoid clade suggests that the ancestral dental hominoid established a distribution that encompassed parts of Africa, Europe and Asia (Fig. 4a). Although the spatial correlation of this range with the EARS and TOC might be attributed to accidents of taphonomy, we suggest instead that this correlation indicates that these geological formations facilitated the geographical and ecological conditions that allowed/permitted the ancestral dental hominoid to establish a widespread ancestral range between Africa, Europe and Asia.

The spatial correlation of dental-hominoid clade apes with the TOC is historically significant because Darwinian models of primate biogeography treat the TOC between Africa and Europe as a barrier to, rather than a facilitator of, dispersal, whereby dispersal across the barrier periodically takes place through the formation of hypothesized land bridges of some uncertainty (Kingston & Hill, 1999; van der Made, 1999; Rögl, 1999). The EARS comprises a series of rift valleys and associated synclines and anticlines between southern Africa and the Middle East with hominid fossils in the African sector

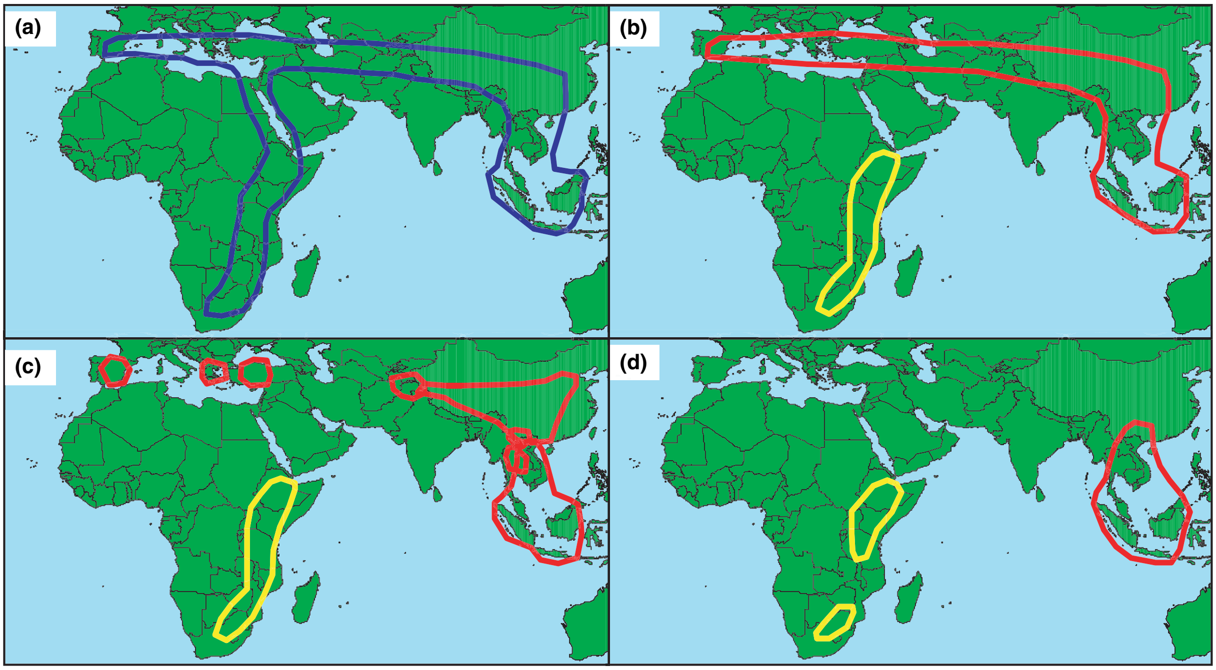

Figure 4 Vicariant differentiation model for the dental-hominoid clade. (a) Generalized ancestral range established at least 13 Ma based on the minimum fossil age of *Sivapithecus* and *Khoratpithecus*. (b) Vicariant differentiation of hominids (yellow), orangutans and their fossil relatives (red) by at least 13 Ma, assuming hominids are sister group to the other dental hominoid taxa. (c) Hominid range (yellow) and vicariant differentiation of non-hominid taxa (red) by at least 13 Ma. (d) Disjunction of *Pongo* and Asian *Gigantopithecus* (red) from australopiths (yellow) *c.* 2.5 Ma resulting from extinction of Central Asian and European relatives by *c.* 7 Ma.

dating back to at least 6–7 Ma. The TOC formerly comprised a series of islands and inland seas (Meulenkamp & Sissingh, 2003; Golonka, 2004; Zhu *et al.*, 2005) until they were obliterated by the collision of India with southern Asia *c.* 35 Ma (Aitchison *et al.*, 2007; Ali & Aitchison, 2008). Uplift of the Tibetan Plateau also began about that time, although the rate and extent of uplift remains unresolved, with some models predicting that the present elevations date from the late Eocene (*c.* 40 Ma) and others suggesting moderate uplift and relatively low relief until the Miocene *c.* 15 Ma (Shackleton & Chengfa, 1988; Garzione *et al.*, 2000; Spicer *et al.*, 2003; Wang *et al.*, 2003; Sun *et al.*, 2005; Harris, 2006; Sobel *et al.*, 2006). Major uplift of the Himalayas may not, however, have begun until the early Miocene, *c.* 20 Ma (Wang *et al.*, 2008).

Absence of a fossil record for the dental hominoid clade south of the Himalayan orogeny may suggest that the ancestral range extended through central Asia rather than through the Indian subcontinent. Uncertainties about the rate of tectonic uplift do not permit confident reconstruction of topography within that region during the early to middle Miocene. Palaeobotanical records do, however, provide evidence that much of the Tibetan region supported forested habitats until at least the middle Miocene (Dewey *et al.*, 1988; Fortelius *et al.*, 2002; Spicer *et al.*, 2003; Sun *et al.*, 2005), and suggest that warm and wet subtropical forests ranged between southern Europe and China during the early and middle Miocene (Andrews & Bernor, 1999) with warm temperate forests in Central Eurasia to early Miocene times (Bruch & Zhilin, 2007). We therefore conclude that the ancestral range of the dental-hominoid clade was established during a time of ecological and tectonic continuity between these continents along the TOC and EARS and preceding differentiation of dental-hominoid taxa by at least 12–13 Ma.

In our biogeographical reconstruction, the origin of the dental-hominoid clade lies not specifically within Europe, Africa or Asia, but within all three regions together, whereby the TOC–EARS was the common historical denominator of the ancestral range. Subsequent tectonic and climatic developments promoted differentiation (Agustí *et al.*, 1996) of the hominids in East Africa (Fig. 4b), and the dental-hominoid genera *Hispanopithecus* in Spain, *Ouranopithecus* in Greece, *Ankarapithecus* in Turkey, *Sivapithecus* in Central Asia, *Gigantopithecus* in Central and eastern Asia, and *Lufengpithecus*, *Khoratpithecus* and *Pongo* in Southeast Asia (Fig. 4c). In this historical and biogeographical context the apparent geographical disjunction between a presumed African origin for humans and the Asian distribution of orangutans is an artefact of extinction of intervening populations (Fig. 4d).

The vicariant form-making model does not preclude the possibility that the range of ancestral hominids also extended beyond the boundaries of Africa (as potentially indicated by the australopith affinities of the enigmatic *Homo floresiensis* of Indonesia; Schwartz, 2007). Given the uncertainties of defining Hominidae (Schwartz, 2004b, 2007), as well as the lack of character state representation in several fossil taxa, new fossil material may lead to greater resolution of relationships within this clade. The vicariant-differentiation model proposed here implies that large-bodied Miocene apes did not disappear from Africa, but are represented in the Plio-Pleistocene by specimens that have been misidentified as hominid (see also Schwartz, 2004a). The presence of as yet unrecognized orangutan-related taxa in Africa may be indicated by isolated fossil teeth from the Pliocene of East Africa allocated to *Australopithecus* that display an orangutan-like configuration of having peripherally placed and crest-connected cusps that subtend broad basins (Schwartz & Tattersall, 2003; Schwartz, 2004a,b), as well as by the worn molars of *Chororapithecus abyssinicus* (Suwa *et al.*, 2007) and *Nakalipithecus nakayamai* (Kunimatsu *et al.*, 2007), both *c.* 10 Ma from Africa, that are characterised by 'thick enamel' as well as in the latter by peripherally positioned cusps (Kunimatsu *et al.*, 2007).

Ancestral divergence

We suggest that a widespread distribution of the dental hominoid clade ancestor was already established in central and eastern Asia by 12–13 Ma because the relevant fossil record demonstrates that taxic differentiation had already occurred by that time. This divergence estimate, of course, pre-dates the fossil record of the more distantly related *Dryopithecus* (10–12 Ma) and *Oreopithecus* (7 Ma) of Europe and, with respect to other large-bodied hominoid fossils, is only *c.* 4 Myr younger than the earliest European *Griphopithecus* (16.5 Ma) and the earliest African taxa such as *Nacholapithecus* (15 Ma), *Afropithecus* (17.5 Ma) and *Morotopithecus* (17–20 Ma; Begun, 2007). Because fossils represent only the minimum age of a taxon, they cannot empirically constrain its maximum age (Croizat, 1964). Thus the currently known large-bodied hominoid fossil record can only be cited in support of the dental hominoid clade ancestor establishing its distribution range some time prior to *c.* 13 Ma. Even though fossils can only represent minimal estimates of phylogenetic age, molecular clocks often transform minimal fossil calibrations into actual or maximal molecular divergence estimates – whether expressed as a single value or as an upper and lower range (Grauer & Martin, 2004; Heads, 2005).

It was because of the assumption of maximum divergence that Sarich (1971) could assert that no fossil pre-dating the molecular estimate of a presumed human–chimpanzee divergence could be hominid – no matter what it looked like. Nevertheless, despite its claimed scientific objectivity, the molecular-clock based theory of African ape–human origins has yielded divergence estimates that range from post-dating the earliest australopiths to pre-dating the earliest known dental hominoids (Arnason *et al.*, 1996, 1998, 2000; Janke & Arnason, 2001; Stauffer *et al.*, 2001; Schrago & Russo, 2003; Steiper & Young, 2006; Hobolth *et al.*, 2007). Such dates indicate that there is no necessary reason why the origin of the hominid lineage should be limited to the commonly cited molecular-clock estimates of *c.* 6–8 Ma, especially in light of the widespread acceptance (even among molecular systematists) of the hypothesis that the common ancestor of *Pongo* and *Sivapithecus* diverged well before the oldest known fossil member of *Pongo* (*c.* 1 Ma). In addition, our finding that the African apes are related as the sister group of a diversity of dental-hominoid clade taxa (including hominids) suggests that the divergence of African apes is also older than the oldest fossil members of the dental-hominoid clade – that is, *c.* 13 Ma.

Ancestral origins revisited

Lack of phylogenetic resolution of relationships for all taxa within the dental hominoid clade precludes a precise temporal sequencing of geographical divergences. A key question for future research is whether hominids represent the sister group of all other dental hominoids (and therefore diverged by at least 13 Ma) as suggested in our restricted comparison (Analysis D), or whether they are more closely related to some other members of the dental-hominoid clade and therefore of more recent origin. Interestingly, there are conceptual similarities between the dental-hominoid theory of human origins and the *Ramapithecus* theory that was supported in the 1960s and 1970s by prominent palaeoanthropologists such as Richard Kay, David Pilbeam, Elwyn Simons and Ian Tattersall.

Initially known only from partial upper and lower jaws with teeth, *Ramapithecus* was first identified as a hominid because it possessed low-cusped cheek teeth and thick-enamelled molars. Unexpectedly, however, subsequently discovered partial crania of *Sivapithecus* (within which *Ramapithecus* soon thereafter became subsumed as the female of the taxon) were found to share with the orangutan derived cranial features. Since by this time (the 1980s) all molecular anthropologists and most palaeoanthropologists believed that hominids were most closely related to the African apes, the obvious affinity between *Sivapithecus* and the orangutan was interpreted as precluding a close relationship between these latter taxa and hominids (Lewin, 1987; Schwartz, 1987, 2005; Lewin & Foley, 2004). If the same argument were applied to the australopiths, they, too, would have to be regarded as non-hominid, yet bipedal, apes. If orangutan-like australopiths are hominids, the original predictions of the affinities to hominids of *Sivapithecus* (when various specimens were still referred to *Ramapithecus*) by Kay, Pilbeam, Simons, Tattersall and others may be more correct than not, because the morphological evidence presented here corroborates the inclusion of *Sivapithecus* as a member of the same clade that includes the orangutan relatives that were once believed to be ancestral to hominids (Schwartz, 2004a).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Character states for extant large bodied hominoids comprising the great ape genera (*Gorilla*, *Pan*, *Pongo*) and humans (*Homo*) with lesser apes (*Hylobates*) and monkeys (Catarrhini and Platyrrhini) as the outgroup.

Appendix S2 Character states for extant (as in Appendix S1) and fossil large bodied hominoids with extant lesser apes and monkeys as the outgroup.

Appendix S3 Problematic nature of hominid characters proposed for *Sahelanthropus* by Brunet *et al.* (2002).

Appendix S4 Problematic aspects of characters proposed in support of hominid–African ape monophyly by Strait & Grine, 2004.

Appendix S5 Comments on the validity or relevance of characters used by Begun *et al.* (1997) to support the monophyly of *Australopithecus* (represented only by *Australopithecus afarensis* from Hadar) and *Pan*.

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