

## New *Sivapithecus* humeri from Pakistan and the relationship of *Sivapithecus* and *Pongo*

David Pilbeam\*, Michael D. Rose†, John C. Barry\* & S. M. Ibrahim Shah‡

\* Department of Anthropology, Peabody Museum, Harvard University, Cambridge, Massachusetts 02138, USA

† Department of Anatomy, New Jersey Medical School, 185 South Orange Avenue, Newark, New Jersey 07103-2757, USA

‡ Geological Survey of Pakistan, Quetta, Pakistan

**NEW humeri of two species of the Miocene hominoid *Sivapithecus* are described from near Chinji in Pakistan from between ~9 and 11 Myr ago. *Sivapithecus*, a middle and late Miocene hominoid from Turkey and Indo-Pakistan, is overall unlike any living hominoid, although facial-palatal similarities to the extant orangoutan, *Pongo*, have been used to support a hypothesis of close relationship. Living hominoids have postcranial similarities assumed to be shared derived, among them features of the proximal humerus. However, the new *Sivapithecus* proximal humeri differ from those of living hominoids, supporting an alternative hypothesis in which *Sivapithecus* and *Pongo* are not closely related. It is not clear how to choose between these incompatible hypotheses.**

The material comes from ~18 to ~1 Myr old Siwalik Group sediments exposed on the Potwar Plateau near Rawalpindi in Pakistan. Collections have been made there since 1973. Some 40,000 specimens including about 160 hominoids are known from over 800 localities<sup>1-7</sup>. Age determinations are based mainly on an extensive palaeomagnetic sampling programme<sup>8-11</sup>. The hominoid material is assigned to species of *Sivapithecus*<sup>12</sup>, thought to be the sister taxon of *Pongo* on the basis of facial similarities hypothesized as shared derived<sup>6,13-15</sup>. In other features—occlusal<sup>6</sup>, mandibular<sup>16</sup>, postcranial<sup>17-19</sup>—*Sivapithecus* and *Pongo* are mostly dissimilar.

GSP 30754 (Figs 1 and 2) is a left humeral shaft lacking epiphyses from locality Y311 in the Nagri Formation, 9.3 Myr old. It is assigned to *S. parvada*<sup>20</sup>, a newly described species distinct from other *Sivapithecus* species. It is morphologically similar to non-hominoid catarrhines and earlier hominoids, and is clearly not from a large carnivore or other non-primate mammal. A previously described partial humeral distal epiphysis from Y311, GSP 12271 (ref. 6), is similar in preservation and size to, and probably conspecific with, GSP 30754. The proximal third of the specimen curves laterally and anteriorly to its junction with the rest of the shaft. There is a flat, well-defined deltoid plane and associated crests. The olecranon fossa is deep and wide, with articular surface extending onto the lateral wall. GSP 30730, from locality Y76 in the Chinji Formation, 10.8 Myr old, although crushed and somewhat distorted, is an almost complete left humerus, probably of *S. indicus*, lacking only the head (Figs 1 and 2). The proximal shaft is oriented as in GSP 30754. As in GSP 12271 the distal articular surfaces resemble those of modern large hominoids. There is a well-rounded capitulum separated from the lateral trochlear ridge by a well developed groove, the *zona conoidea*, the ridge extending to the lateral wall of the olecranon fossa. The trochlear surface is markedly spool-shaped. Among living primates the distal humeral functional features of GSP 30730 and GSP 12271 are shared only with large hominoids, although the particular combination of features differs from that of any individual hominoid.

Proximal humeral shaft morphology similar to that of the *Sivapithecus* specimens is also found in *Proconsul*<sup>21</sup>, *Kenya-pithecus*<sup>19</sup>, and most living quadrupedal non-hominoid primates (Table 1). In suspensory and/or climbing anthropoids, especially hominoids, the shaft is straight and bears a convex deltoid plane<sup>19,21,22</sup>. The elbow joint complex in living hominoids provides stabilization throughout extensive flexion-extension and pronation-supination excursions<sup>23</sup>. GSP 30730 is probably the oldest known hominoid with the distal humeral morphology found in modern large hominoids, yet it is unusual in combining this with a curved proximal shaft morphology. (The distal humeri of *Rudapithecus*<sup>24</sup> and *Oreopithecus*<sup>25,26</sup> also

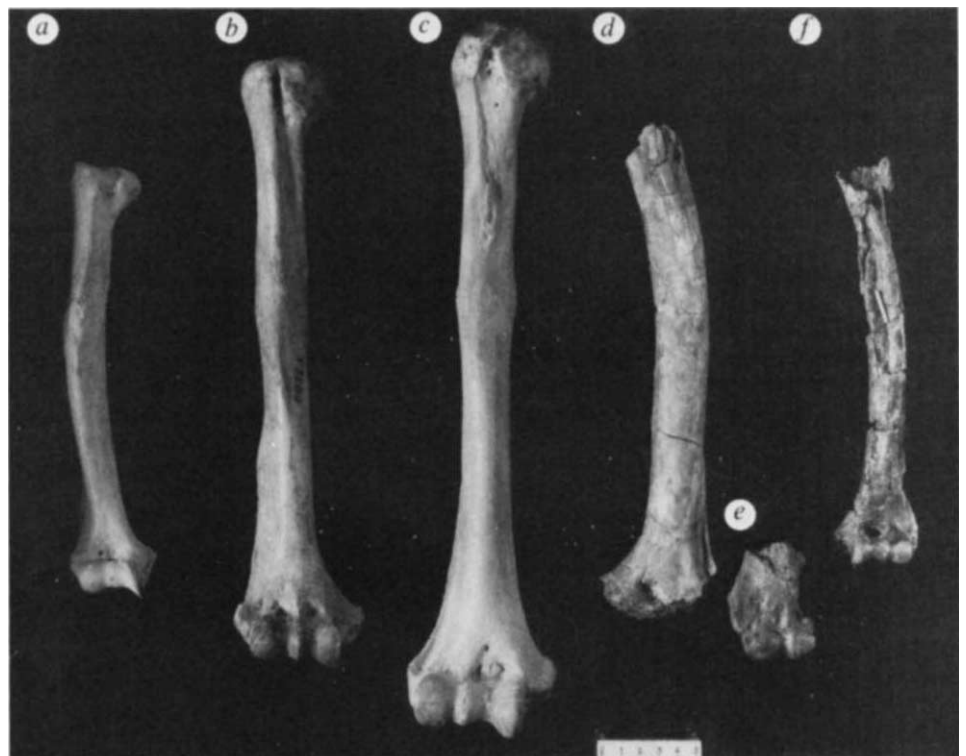


FIG. 1 Anterior views of humeri of a, *Papio hamadryas* (right). b, *Pan troglodytes* (right). c, *Pongo pygmaeus* (right). d, GSP 30754 (left). e, GSP 12271 (cast, right). f, GSP 30730 (left). Scale bar (cm).

TABLE 1 Distribution of some humeral features

	<i>Proconsul</i>	<i>Kenyapithecus</i>	<i>Sivapithecus</i>	<i>Rudapithecus</i>	<i>Cercopithecids</i>	African apes	<i>Pongo</i>
Medially inclined proximal shaft	?	?	+	?	+	-	-
Retroflexed proximal shaft	+	+	+	?	+	-	-
Flat deltoid plane	+	+	+	?	+	-	-
Mediolaterally broad trochlea	+	+	+	+	-	+	+
Markedly spool-shaped trochlea	-	-	+	+	-	+	+
Prominent lateral trochlear keel and deep, narrow <i>zona conoidea</i>	-	-	+	+	-	+	-

? = Not known; + = Feature present; - = Feature absent.

show a derived hominoid condition, but their shaft morphology is not known, or is unclear because of crushing.) The functional pattern of the hominoid distal humerus has generally been interpreted in terms of suspensory behaviour, with variations in the pattern in living hominoids being linked to particular mixtures of quadrupedalism, climbing and suspension in individual species<sup>27-29</sup>. Complete and partial *Sivapithecus* postcranial specimens are known from all parts of the limbs except the leg<sup>6,17-19</sup>. These, together with the new specimens, indicate that *Sivapithecus* was, like *Proconsul* and *Kenyapithecus*, and perhaps other more poorly known Miocene hominoids, basically quadrupedal and that climbing and suspension were probably less emphasized in the locomotor repertoire. This evidence suggests that features, including those of the distal humerus, now associated with specialized suspensory and climbing functions in hominoids had their origin in an already partly derived morphology that was first associated with more quadrupedal and less suspensory activities.

*Pongo* and *Sivapithecus* are similar in certain palatal and facial characteristics by which they differ from all other living and fossil hominoids, and which have been interpreted as shared derived characteristics<sup>13-15</sup>. There are no such features unequivocally present in the known parts of the *Sivapithecus* postcranium.

As mentioned above for the distal humerus, *Sivapithecus* postcranials do share several features with extant large hominoids, particularly African apes. Thus the calcaneo-cuboid joint includes features related to extensive, stabilized pronation-supination movements<sup>18</sup>, a stable semi-flexed and medially rotated position of the external pollex is indicated by proximal phalangeal features, and the hallux is robust, with a broad flat terminal phalanx<sup>6</sup>. These features have been interpreted as being primitive for large hominoids<sup>19</sup>. The above-mentioned humeral shaft features, together with features of the talus, medial calcaneus, distal cuboid, proximal capitate and the proximal manual phalangeal base are primitive with respect to the apparently shared derived state of these features in living large hominoids. Functionally, these primitive features are associated with generalized quadrupedalism and are shared by *Sivapithecus*, more primitive fossil hominoids, and many living non-hominoid anthropoids. This is not to be expected if *Sivapithecus* is the sister taxon of *Pongo*.

Two mutually exclusive hypotheses follow. First, that *Sivapithecus* and *Pongo* are sister taxa, in which case a number of postcranial features shared by living large hominoids must represent convergences. Second, that *Sivapithecus* and *Pongo* are not sister taxa, in which case their palatal and facial



FIG. 2 Lateral views of humeri of a, *Papio hamadryas* (right). b, *Pan troglodytes* (right). c, *Pongo pygmaeus* (right). d, GSP 30754 (left). e, GSP 12271 (cast, right). f, GSP 30730 (left). Scale bar (cm).

similarities are not shared derived features but either convergent derived or shared primitive features. (A variant of the first hypothesis, that *Sivapithecus* and *Pongo* are sister taxa, and the apparently primitive features of the *Sivapithecus* postcranium are reversals from a more derived condition, is unlikely in light of the close similarity of these features in *Sivapithecus* and the taxa mentioned above.) Distinguishing between the two hypotheses will require detailed studies of apparently shared derived postcranial features of living hominoids, and a re-examination of the apparently shared derived palatal and facial features of *Sivapithecus* and *Pongo*. There is some evidence that

marked torsion of the humeral head (not determinable for any currently available fossil hominoid) may have been acquired independently in at least some living hominoid lineages<sup>19,30,31</sup>. The hominoids are a group of low taxonomic diversity and high morphological variability. But even with a denser hominoid fossil record, problems will remain with the objective definition of characters, assessment of homology versus convergence as alternative explanations for similarity of character states<sup>32</sup>, and determination of whether character states are primitive or derived. We are not confident that biologically plausible procedures exist for unambiguously settling these issues. □

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## Activation of facilitation calcium channels in chromaffin cells by D<sub>1</sub> dopamine receptors through a cAMP/protein kinase A-dependent mechanism

Cristina R. Artalejo\*, Marjorie A. Ariano†, Robert L. Perlman\*‡ & Aaron P. Fox\*§

The University of Chicago \* Department of Pharmacological and Physiological Sciences, † Department of Pediatrics and the Joseph P. Kennedy Jr Mental Retardation Research Center, 947 E. 58th St, Chicago, Illinois 60637, USA

‡ Department of Anatomy and Neurobiology, University of Vermont, Burlington, Vermont 05405, USA

**FACILITATION calcium channels<sup>1–4</sup> in unstimulated bovine chromaffin cells are normally quiescent<sup>3</sup> but are activated by large pre-depolarizations or by repetitive depolarization in the physiological range. The activation of these 27-pS dihydropyridine-sensitive channels by repetitive stimulation<sup>4,5</sup>, such as by increased splanchnic nerve activity, can lead to an almost twofold increase in Ca<sup>2+</sup> current in these cells<sup>3</sup>. This increase in Ca<sup>2+</sup> current is of probable physiological importance in stimulating rapid catecholamine secretion in response to danger or stress. We have identified D<sub>1</sub> dopaminergic receptors on bovine chromaffin cells by fluorescence microscopy<sup>6</sup>. Here we show that stimulation of the D<sub>1</sub> receptors activates the facilitation Ca<sup>2+</sup> currents in the absence of pre-depolarizations or repetitive activity, and that activation by D<sub>1</sub> agonists is mediated by cyclic AMP and protein kinase A. The recruitment of facilitation Ca<sup>2+</sup> channels by dopamine may form**

**the basis of a positive feedback loop mechanism for catecholamine secretion.**

Figure 1a, a plot of peak current as a function of test pulse potential, shows that the dopamine agonist apomorphine (0.1 μM) greatly increases the Ca<sup>2+</sup> current. Nisoldipine (1 μM), a dihydropyridine antagonist, completely inhibited the Ca<sup>2+</sup> current recruited by apomorphine (Fig. 1a). It has been shown previously that dihydropyridine antagonists such as nisoldipine specifically suppress the facilitation Ca<sup>2+</sup> current but do not affect other currents in bovine chromaffin cells<sup>3</sup>; thus, apomorphine seems to activate only the facilitation Ca<sup>2+</sup> current. Figure 1b, a plot of peak current versus time, illustrates that dopamine (10 μM) could also recruit the facilitation Ca<sup>2+</sup> current. The effects of dopaminergic agonists were apparently mediated by D<sub>1</sub> dopamine receptors as the specific D<sub>1</sub> dopamine agonist SKF-38393 (1 μM) activated the facilitation Ca<sup>2+</sup> current (Fig. 1c). In 11 experiments the D<sub>1</sub> agonist increased chromaffin cell Ca<sup>2+</sup> current to 182 ± 6% of control. The D<sub>1</sub> response could be prevented by the specific D<sub>1</sub> antagonist SCH 23390 (1 μM; Fig. 1c) but not by the serotonergic antagonist ketanserin (10 μM, N = 4; not shown). The D<sub>2</sub> agonist quinpirole did not activate facilitation, nor did it have any other effects on Ca<sup>2+</sup> currents<sup>7–9</sup>, even at concentrations up to 100 μM (not shown). Large pre-pulses, which activated facilitation Ca<sup>2+</sup> channels in untreated cells, did not increase Ca<sup>2+</sup> currents in cells that had been treated with SKF-38393 (Fig. 1d), indicating that pre-pulses and dopamine activated the same group of Ca<sup>2+</sup> channels. Taken together, these results suggest that the activation of D<sub>1</sub> dopamine receptors specifically recruited facilitation Ca<sup>2+</sup> channels in chromaffin cells.

Chromaffin cells have been reported to have D<sub>2</sub> but not D<sub>1</sub> dopamine receptors<sup>7–9</sup>. Figure 2 confirms the presence of D<sub>1</sub> dopamine receptors in bovine chromaffin cells. Fluorescence microscopy using the rhodamine conjugate of the 4'-amino derivative of the D<sub>1</sub> antagonist SCH 23390 (ref. 6) demonstrated binding to almost all the cells (Fig. 2a). Binding of the fluorescent ligand was not affected by ketanserin (10 μM, Fig. 2b)

§ To whom correspondence should be addressed.