



Figure 1 Relation between the relative dispersion of cloud droplet size distribution, ϵ , and the number concentration of cloud droplets, N . Symbols indicate programs and/or references from which the data points were derived. Connected points represent cases previously identified as evidence for an indirect aerosol effect. The parameter β is defined by equation (2). Green symbols (from ref. 8): triangle, FIRE, northeastern Pacific; crossed circles, SOCEX, Southern Ocean; filled circle, ACE1, Southern Ocean. Blue symbols: filled circles, ASTEX⁶, northeastern Atlantic; diamonds, SCMS⁹, Florida coast; filled triangles, Sounding⁹, ASTEX; filled squares, horizontal⁹, ASTEX; open inverted triangles, level 1; open upright triangles, level 2; open circles, level 3 — all from southwest of San Diego¹⁰; open diamonds, SCMS¹¹; stars, vertical, ASTEX¹²; plus signs, horizontal, ASTEX¹²; multiplication signs, ASTEX¹³; squares, INDOEX, Indian Ocean (G. M. McFarquhar, personal communication). Red circles, MAST^{6,14,15}, California coast.

polluted cloud compete for water vapour and broaden the droplet size distribution compared with clean clouds that have fewer droplets and less competition.

According to equations (1) and (2), an increase in ϵ acts to negate the effect of increased N on effective radius and cloud reflectivity. Because this effect has been largely neglected in estimates of the indirect aerosol effect, cooling by an indirect aerosol effect is likely to have been overestimated. From the data presented in Fig. 1, we estimate that a 15% increase in N at $N=100 \text{ cm}^{-3}$ causes a total forcing that ranges between -0.19 and -0.93 W m^{-2} , which corresponds to a factor that is 10–80% lower than the -1.03 W m^{-2} calculated for the Twomey effect alone².

The effect of the enhancement in ϵ is evidently large enough to be considered in assessing the indirect aerosol effect, and understanding the relation between ϵ and N will help to reduce the large uncertainty inherent in this effect.

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COMMUNICATIONS ARISING

Palaeoanthropology

Sahelanthropus or 'Sahelpithecus'?

Beginning with *Ramapithecus*, there has been a continued search for an ape-like hominid ancestor in the Miocene Epoch. *Sahelanthropus tchadensis* is an enigmatic new Miocene species, whose characteristics are a mix of those of apes and *Homo erectus* and which has been proclaimed by Brunet *et al.* to be the earliest hominid¹. However, we believe that features of the dentition, face and cranial base that are said to define unique links between this Toumaï specimen and the hominid clade are either not diagnostic or are consequences of biomechanical adaptations. To represent a valid clade, hominids must share unique defining features², and *Sahelanthropus* does not appear to have been an obligate biped.

We consider the following features that are proposed by Brunet *et al.* to constitute links with the hominid clade. First, they note that the canine is small. The canine breadth (the length is not given) is similar to the chimpanzee mean, being within the range of both chimpanzee and gorilla females and of chimpanzee males. The crown is low and the root is narrow relative to the crown, suggesting that Toumaï might have been female (canine area is a more reliable sex indicator than brow ridges); however, the postcanine teeth are all large compared with chimpanzees — as in several Miocene ape females.

The canine shows apical wear and has a thin strip of wear along the distal edge of the crown, which reaches the crown base. Although Brunet *et al.* conclude that the tooth was not used in honing, we find this difficult to reconcile with the details that they provide. Decades ago, when Miocene primate jaws with small canines and enlarged postcanine teeth were found, they were given distinct names (*Kenyapithecus* and *Ramapithecus*, for example) and were described as the earliest hominids because (it was assumed) the canine honing function had, by then, been replaced by tools (it was also assumed that they were bipeds)³. These specimens turned out to be female apes.

Second, the specimen has a large, continuous supraorbital torus, and the authors

claim that there are other facial similarities to *Homo*. However, the facial similarities are mostly not with early hominids but with Pleistocene *Homo*, and therefore do not provide any phylogenetic information (no evidence hints that *Homo erectus* could be 6–7 million years old). There is little subnasal prognathism because the canines are small and the subnasal region is short, and the closely packed anterior dentition, crowded together because of the expanded postcanine teeth, explains the absence of diastemata. The vertical height of the impressive supraorbitals is greater than in any extant ape or australopithecine, and can only be matched in *Homo erectus* and in a few later humans.

The supraorbital size is attributed to strong sexual selection¹, which we consider unlikely. The size and form of the supraorbital structures are probably a mechanical response⁴ to strain from anterior tooth loading in the region above the orbits, concentrated by the flexed frontofacial angle. The biomechanical model of the supraorbital region⁵ would predict that an orthognathic face such as that of *Sahelanthropus*, combined with a low forehead, creates the potential for greater strain during anterior tooth loading than would a prognathic face with a higher forehead, as in African apes. Significant force during anterior tooth use is indicated by the expanded posterior temporalis musculature — this muscle forms a sagittal crest that meets the nuchal crest very high on the posterior vault, in a gorilla-like morphology that far exceeds the much weaker-muscled chimpanzee condition. The supraorbital torus is the bony response to strain.

Third, Brunet *et al.* infer that the intermediate thickness of the specimen's postcanine enamel is also an important link. However, thickened enamel relative to chimpanzees would be expected whatever the phylogenetic relations of *Sahelanthropus*, not only because of the other adaptations to a diet that requires powerful mastication, but also because thickened enamel is a plesiomorphic condition.

Fourth, the authors assign an anterior position to the foramen magnum on the basis of its front edge meeting the bicarotid and biporion chords, claiming that in chimpanzees the foramen magnum is posterior to these chords and that this positioning reflects their posture. STS 5, an obligate biped, does not differ from some chimpanzees by these criteria, however. Neither does this apply to the biporion chord of some chimpanzees, according to the position of the foramen magnum determined from photographs of 70 adult chimpanzee cranial bases aligned with the Frankfurt horizontal (J. Ahern, personal communication). This alignment is important in the determination, but we have no information

on how the *Sahelanthropus* position was assessed. Moreover, the anterior edge of the foramen is far from the back of the *Sahelanthropus* third molar, in contrast to hominids and similar to chimpanzees and female gorillas.

There are many other features that link the specimen with chimpanzees, gorillas or both, to the exclusion of hominids. Most significantly, the nuchal plane is long, flat and angled at about 55° to the Frankfurt horizontal: “relatively longer than in *Pan* [and] *Gorilla* ... and with crests as marked as those of *Gorilla*”¹. This describes the posterior cranial vault of a small quadrupedal ape with a powerful masticatory complex.

Because the face is orthognathic rather than prognathic and the anterior teeth are small, posture is the only credible explanation of this nuchal anatomy. It is evident that *Sahelanthropus* did not habitually hold its head in an upright position over the spine and was not an obligate biped. This contrast with all known hominids is itself sufficient to exclude *Sahelanthropus* from the hominid clade as we currently understand it.

We believe that *Sahelanthropus* was an ape living in an environment that was later inhabited by australopithecines and, like them, it adapted with a powerful masticatory complex. A penecontemporary primate with a perfect and well-developed postcranial adaptation to obligate bipedalism⁶ is more likely to have been an early hominid.

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Brunet et al. reply — In 1925, when Dart described *Australopithecus africanus*¹ as a hominid, critics interpreted it as a juvenile gorilla^{2–4}. Last year, Wolpoff’s colleagues (B.S. and M.P.) claimed that their Kenyan fossil *Orrorin* was a direct ancestor of *Homo*⁵, and now Wolpoff *et al.* conclude that *Sahelanthropus* was an ape (specifically, a female gorilla ancestor⁶) — a belief that, to our knowledge, is not supported by published or unpublished data.

Overlooking their flippant taxonomic proposal (the genus name ‘*Sahelpithecus*’), which disregards the requirement for a new genus to have a type species and description⁷, we disagree with their (presumably more serious) opinions on the morphology and phylogeny of the Toumaï fossil.

Because the Toumaï fossil is the earliest known hominid ancestor⁸, it is not surprising that it bears primitive characters. Following modern systematic practice, we used newly evolved characters (rather than shared primitive characters) to establish phylogenetic relationships⁸. Those who ignore these derived characters and concentrate on primitive ones will reach the conclusion that early hominids, including *Orrorin*, are related to modern apes. This has not been in dispute since Huxley and Darwin. For Wolpoff *et al.* to revert to the use of primitive characters in an attempt to undermine a clear statement of affinity of Toumaï is curious.

Wolpoff *et al.* make several erroneous assertions about the cranial face and base. For example, they mischaracterize the configuration of the face in *S. tchadensis*, claiming that supraorbital size is directly related to postcanine tooth size and/or to masticatory forces. However, experimental and developmental investigations^{9,10} have shown that strains caused by mastication in the brow ridge of orthognathic and prognathic primates are always tiny, much too small to engender bone-growth responses to loading. Instead, large brow ridges grow because of facial projection relative to the cranial base¹¹.

Wolpoff *et al.* also obfuscate the facial similarities to *Homo*. We did not suggest that *Homo erectus* is 6–7 million years old — the point with *Homo* was comparative, rather than phylogenetic. Relying on measurements of our published photographs of the distorted original, Wolpoff *et al.* wrongly assert that the nuchal plane is angled at about 55° to the Frankfurt horizontal. Undistorted, the nuchal plane’s angulation is outside the range of chimpanzees and within the range of fossil hominids¹². This configuration is nothing like that of any quadrupedal ape, with or without a powerful masticatory complex (which *Sahelanthropus* lacks, contrary to the assertions of Wolpoff *et al.*).

These authors not only misrepresent the specimen’s morphology, but also fail to identify a single character to support their suggestion that Toumaï is a gorilla rather

than a hominid ancestor. They interpret our description of distal dentin exposure of the upper canine as evidence of honing wear (roughly equivalent to describing an African millet pestle as a Samurai sword). The Toumaï canine is not honing because it does not display the sharpened distal edge that is shared by all apes. Rather, this tooth is similar to those of later hominids in both size and proportion to the post-canine teeth.

In a modern example of how to miss the morphology between measuring points, Wolpoff *et al.* argue that the size of the Toumaï canine is ape-like. It is well known that early hominid and modern ape canine buccolingual diameters overlap in size. But, as Broom and Robinson¹³ noted in their assessment of Zuckerman’s failed attempt to sideline *Australopithecus* 50 years ago: “If ... the affinities of an animal are to be determined by the size and indices of its teeth, and not by their structure, a horse may have to be put in the same group as a cow.” In its relative size, morphology and wear, the Toumaï canine is derived in the hominid direction relative to any ape.

This phylogenetic signal is significant. Ignoring it in favour of a belief based on *Orrorin* and primitive characters is unjustified, particularly as the phylogenetic position of the *Orrorin* fossils remains uncertain. Wolpoff *et al.* have described no derived ape feature of *S. tchadensis*, nor have they disproved any derived features that this species shares with later hominids⁸. Any alternative phylogenetic hypothesis should be based on explicit, supporting derived characters of Toumaï.

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