

inoid rather than specifically hominid. Thus, although, as the authors state, this specimen may differ from *H. erectus* lower last premolars in being double- rather than single-rooted, double-rootedness is the rule among species of *Homo*, *Paranthropus* and *Australopithecus*, with exceptions restricted to *Ardipithecus* (single-rooted P₄)⁷ (if it is indeed a member of the hominid clade), in the new australopithecine from Chad (three-rooted P₄)⁸, *H. neanderthalensis* (but the roots can be bifid at their tips and bear interradicular grooves along their broad flanks; see ref. 4) and *H. sapiens* (see ref. 5). Since fossil and extant large-bodied apes also develop double-rooted P₄s (see ref. 9), the double-rootedness of the Longgupo P₄ could be interpreted as a primitive retention rather than indicative of its phylogenetic relationships or taxonomic identity. Similarly, a relatively large and simple talonid behind the metaconid and protoconid cusps is a feature common to hominoid lower last premolars and is not specific to hominids.

On the basis of the stone tools alone, one can make a case for the presence of hominids in China at whichever date (1 million or 2 million years ago) is eventually confirmed. Morphologically, however, two different hominoids are represented at this site. We eagerly await further evidence that will help resolve their identities.

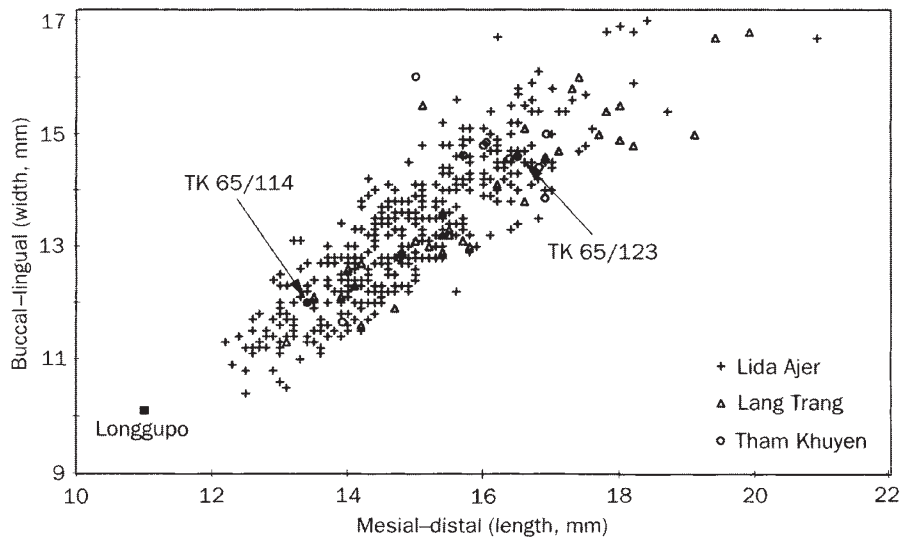
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HUANG ET AL. REPLY — The Longgupo incisor, an unworn permanent tooth from an individual 7 or 8 years of age¹⁰, is remarkable for its shovelling and crown proportions. Hominid incisors can appear shovelled from enlargement of either the marginal ridges or the basal tubercle; mesial-distal curvature; or a combination of these developments¹¹. Therefore, incisor shovelling in extant and extinct hominids is not homologous¹¹. The Longgupo incisor, with heavy marginal ridges, moderate tubercle and light curvature, recalls the condition for Early Pleistocene specimens such as WT 15000 (*Homo ergaster*) and ER 1813 (*H. habilis*). Crown



Lower molar dental metrics for Longgupo¹ and South-East Asian cave sites. The Longgupo M₁ is significantly smaller than the lower molars of *Pongo* from Lida Ajer¹³, Lang Trang¹⁵ and Tham Khuyen⁶ caves, which represent nearly all such teeth from South-East Asia. Data for Lang Trang and Tham Khuyen samples and for TK 65/114 and TK 65/123 were provided by V. T. Long, Institute of Archaeology, Hanoi; data for Lida Ajer and other Sumatran caves were from D. A. Hooijer¹³ and from J. de V.

proportions for the Longgupo incisor fall within the range for OH 6, OH 16, OH 39 and ER 1813 (*H. habilis*)², and just below the two specimens known from Zhoukoudian (*H. erectus*)¹². Finally, the crown axis parallels the root, a pattern observed in *H. erectus*^{12,13}.

For the Longgupo mandible, our discussion of dental apomorphies follows Schwartz and Tattersall's lead in relating the Longgupo molar to their "orang-utan-related species," which they define on the basis of two isolated molars but do not name. We have recently shown that the Tham Khuyen pongid dental assemblages compare morphologically and chronologically to those of Lang Trang, Vietnam, and Lida Ajer, Indonesia^{14,15}. The Longgupo molar is, nevertheless, significantly smaller than any other within this undifferentiated Middle Pleistocene population (see figure). As a consequence, although a five-cusped lower molar and double-rooted last premolar may be hominoid primitive retentions, these features do not align Longgupo with a pongid alternative.

Moreover, the Longgupo cheek teeth show two levels of hominid apomorphy. First, they have thick enamel and vertical buccal surfaces, both undeniably derived hominid features of primary order. Second, the Longgupo molar cusps are

placed peripherally and the fifth cusp is inclined buccally. As the double-rooted premolar is also considerably smaller than similar teeth from all Asian "large-bodied apes," the comparison is again spurious.

Finally, while the premolar's expanded talonid basin may be another hominoid primitive retention, the relationship between the basin, the cusps and the general plan of the premolar is distinctly hominid and compares directly to OH 13 and ER 992. In particular, the two principal cusps are disposed mesially, and the talonid itself has a deep fovea.

Given the fragmentary state and occlusal wear of the mandible and the limited value of an isolated incisor, the full taxonomic status of the Longgupo dental fossils awaits corroborative evidence. However, Longgupo's mandibular features do not recall Middle Pleistocene pongids, and the shovelling of its incisor does recall other Plio-Pleistocene hominids, not *H. sapiens*. With their combination of primitive and derived hominid features and the Plio-Pleistocene age of their cave context, the Longgupo specimens continue to suggest the earliest members of the human clade outside Africa.

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