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Middle Paleolithic Assemblages from the Indian Subcontinent Before and After the Toba Super-Eruption

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The Youngest Toba Tuff (YTT) eruption, which occurred in Indonesia 74,000 years ago, is one of Earth's largest known volcanic events. The effect of the YTT eruption on existing populations of humans, and accordingly on the course of human evolution, is debated. Here we associate the YTT with archaeological assemblages at Jwalapuram, in the Jurreru River valley of southern India. Broad continuity of Middle Paleolithic technology across the YTT event suggests that hominins persisted regionally across this major eruptive event.

The Youngest Toba Tuff (YTT) eruption of 74,000 years ago (74 ka) was Earth's largest volcanic event in the past two million years (1–3). It was two orders of magnitude larger (in erupted mass) than the largest known historic eruption, that of Tambora, also in Indonesia (4). The YTT involved the eruption of a minimum of 2800 km³ (7 × 10¹⁵ kg) of magma, of which at least ~800 km³ was transported in atmospheric ash plumes that blanketed an area from the South China Sea to the Arabian Sea (2, 3). Its impact on Earth's atmosphere and climate (5–7) and on local animal and plant populations remains a matter of contention (5, 7–12).

The Indian subcontinent contains extensive YTT deposits (13–15). Here we describe an archaeological sequence from south India that includes a substantial YTT layer and sheds light on the eruption's impact on climate, environments, and hominin populations. In the Kurnool District

of Andhra Pradesh in southern India, stratified archaeological sites in the Jurreru River valley contain stone artifacts in association with faunal remains in caves, rockshelters, and open-air localities (16, 17) (Fig. 1). The archaeological record spans all periods of the Paleolithic. In addition, current mining activities have exposed tephra deposits over an area of 64 ha. Ash is, however, certainly buried over a wider area within the valley (fig. S1), and we estimate its total volume at $7 \pm 0.7 \times 10^5$ m³, based on the interpolation of 225 depth observations made at mining exposures.

We conducted electron probe microanalysis (EPMA) of volcanic glass shards from the Jwalapuram tephra to compare their geochemical signatures with those of the Older Toba Tuff (OTT, dated to ~840 ka) and the Middle Toba Tuff (MTT, dated to ~500 ka) (4). The results show that the Jwalapuram ash is a distal deposit of the YTT (figs. S3 and S4), based on its close similarities with proximal deposits of YTT in Sumatra and with previously characterized distal occurrences in India (13, 14, 18).

Jwalapuram locality 3 preserves more than 7.5 m of sedimentary deposits, including a 2.55-m-thick deposit of ash, and a sequence of lithic artifacts that straddle the ash layer (fig. S2). Soft sediment deformation structures suggest that the tephra initially accumulated on a wet clay substrate, probably in a lacustrine environment. The abrupt transition from light gray ash to an orange (but still ash-rich) silt horizon immediately above the ash sequence represents a major change in depositional regime. We interpret this as evidence that the lake dried up soon after the ash fall, possibly during the onset of glacial conditions in oxygen isotope stage 4.

The stone tool assemblages were found in trenches placed across the landscape (that is, at Jwalapuram localities 3, 17, and 21). At Jwalapuram locality 3, we used optical dating to obtain burial ages for sediment samples from archaeological layers above (JLP-380) and below (JLP3A-200) the ash. Ages of 77 ± 6 and 74 ±

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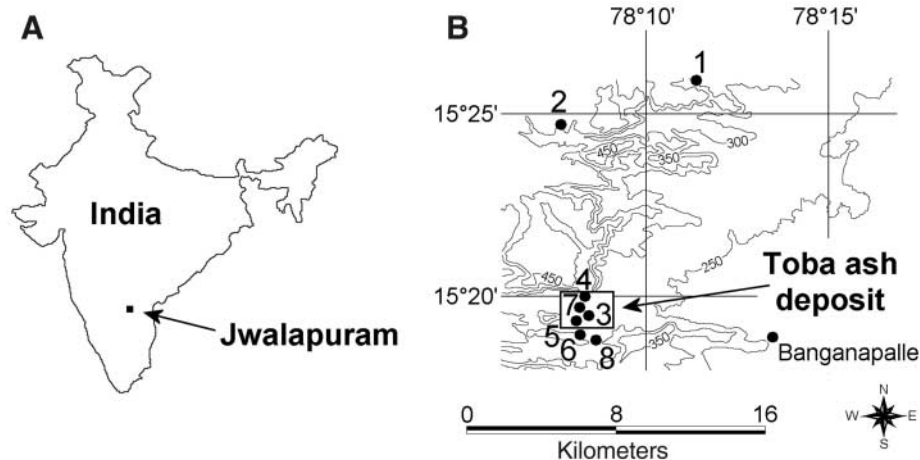
Fig. 1. Location of Jwalapuram, archaeological sites, and tephra deposits. (**A**) Location of the Jwalapuram study area. (**B**) Key archaeological localities in the Kurnool District include the Upper Paleolithic caves of Billasurgum (1) (17) and Muchchatla Chintamanu Gavi (2) (16). Jwalapuram localities include 17 (3, Middle Paleolithic), 9 (4, Microlithic), 3 (5, Middle Paleolithic), 20 (6, Middle Paleolithic), 21 (7, Middle Paleolithic), and Tank (8, Acheulean).

7 ka were obtained for the pre- and post-Toba samples, respectively (tables S2 and S3). These indicate that the dated quartz grains were last exposed to sunlight shortly before and after the Toba eruption, with no substantial hiatus in sediment deposition.

The pre-Toba archaeological layer at locality 3, chronologically bracketed by the ~74,000-year-old YTT and the underlying sediments dated to 77 ± 6 ka, contained 215 artifacts as well as a piece of red ochre that shows striations due to use. This stone tool assemblage consists of faceted unidirectional cores made from limestone (60%), quartzite (22%), and chert (11%), with elongate parallel flake scars indicating the production of blades. Frequent preparation of flake platforms is seen, suggesting that these flakes were struck from prepared cores similar to those found at the site. A small proportion of flakes were retouched into notches, informal scrapers, retouched blades, and a burin (Fig. 2). This pre-Toba assemblage falls within the Indian Middle Paleolithic (*19, 20*).

The post-Toba layer at locality 3, optically dated to 74 ± 7 ka, contains an assemblage of 108 stone artifacts that occur throughout the orange sandy stratum; a further 37 and 131 artifacts were recovered from the same matrix above the ash at localities 17 and 21, respectively. The technology and tool types at these three post-ash localities are similar to those found in the pre-ash assemblage, involving faceted unidirectional cores with some blade scars (Fig. 2). However, raw materials were used in different frequencies (limestone 31%, chert 28%, chalcedony 23%, and quartzite 12%). Most flakes are short and squat, although a few blades and bladelets (<2 cm in length) are also present (<5%), along with a bladelike core and a small bidirectional blade core with a faceted platform (Fig. 2). Retouched flakes above the ash include notches and side and end scrapers. Burins and bipolar reduction are also present, but rare. This combination of tool types is common in Late Pleistocene assemblages of India, usually identified as Middle Paleolithic (*19, 20*).

We provide here firm chronological evidence that hominins were present in the Jurreru River valley, south India, immediately before and after the YTT eruption. Analyses of the archaeological industries recovered from the site indicate a strong element of technological continuity between the pre- and post-Toba assemblages. Together with the presence of faceted unidirectional and bidirectional bladelike core technology, these pre- and post-Toba industries suggest closer affinities to African Middle Stone Age traditions (such as Howieson's Poort) than to contemporaneous Eurasian Middle Paleolithic ones that are typically based on discoidal and Levallois techniques (Fig. 3). The coincidence of (i) evidence of hominins flexible enough to exhibit continuity through a major eruptive event, (ii) technology more similar to the Middle Stone Age than the Middle Paleolithic, and (iii) overlap of the Jwalapuram artifact ages with the
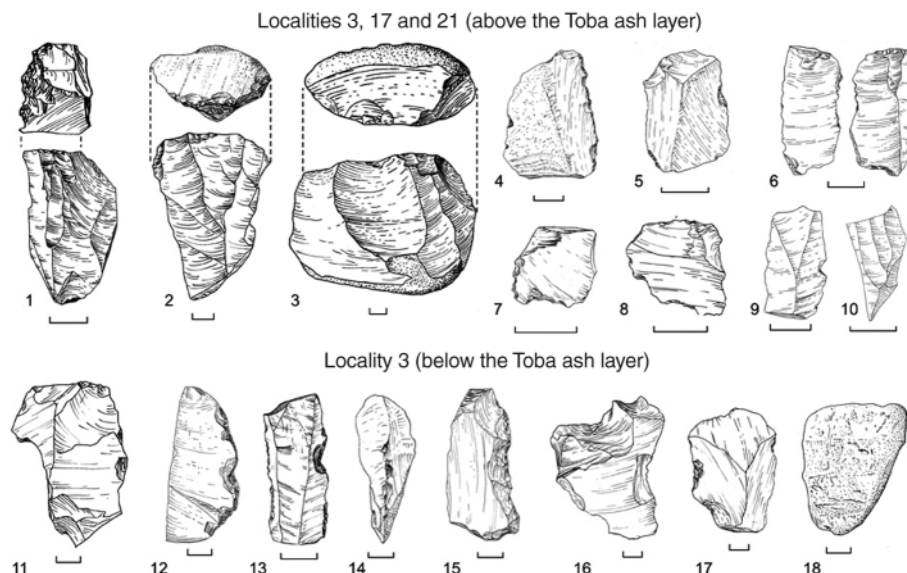

Fig. 2. Selected Jwalapuram artifacts that pre-date (locality 3) and post-date (localities 3, 17, and 21) the YTT. Above the ash: 1, bladelet core with faceted platform; 2 and 3, flake cores with faceted platforms; 4, side scraper; 5, utilized flake; 6, atypical end scraper on blade; 7, side and end scraper; 8, utilized flake; 9, broken blade; 10, broken blade. Below the ash: 11, notch and burin; 12, ventrally retouched side scraper; 13, side scraper on broken blade; 14, side scraper on ridge straightening flake; 15, ventrally retouched side and end scraper; 16, ventrally retouched scraper; 17, notch; 18, ground ochre. Scale bar, 1 cm.
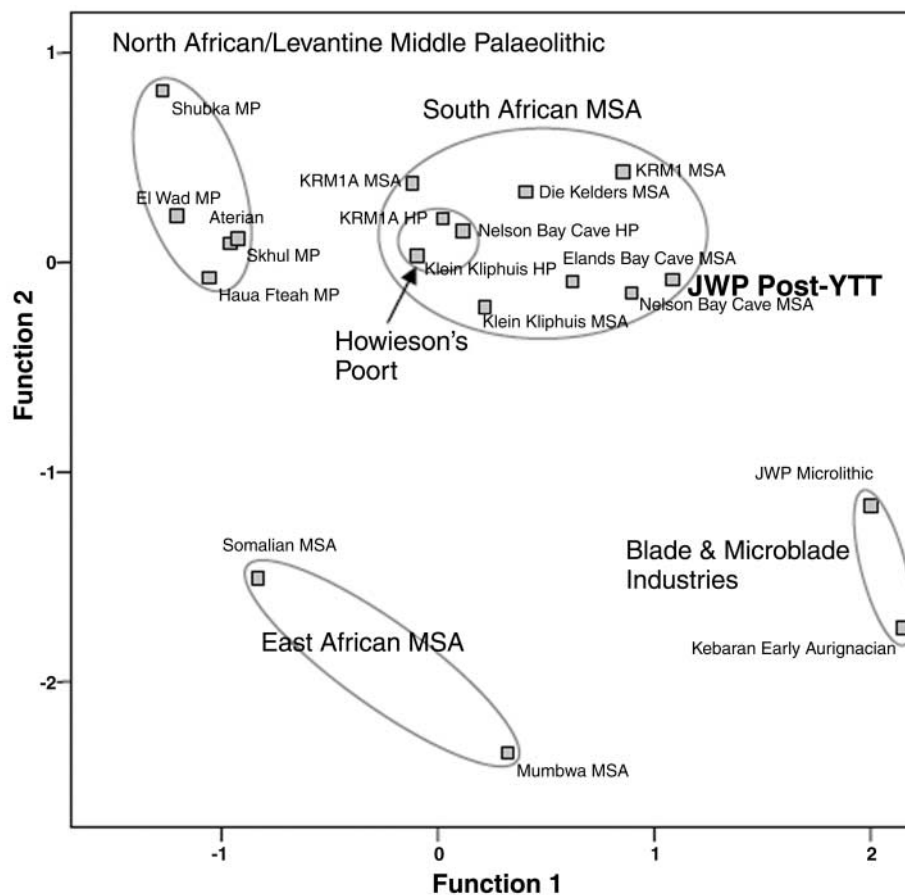

Fig. 3. Discriminant analysis of 670 cores from Middle Stone Age (MSA), Middle Paleolithic (MP), and early Upper Paleolithic (UP) contexts in Africa, the Levant, and India. Functions 1 and 2 account for 70.1% of the variation. Functions 1 to 3 are all significant at the $P = <0.0005$ level. JWP, Jwalapuram; KRM, Klasies River Mouth.

earlier end of the most commonly cited genetic coalescence dates (21–23) may suggest the presence of modern humans in India at the time of the YTT event. This interpretation would be consistent with a southern route of dispersal of modern humans from the Horn of Africa (24); the latter, however, will remain speculative until other Middle Paleolithic sites in the Indian subcontinent and Arabian Peninsula (25) are excavated and dated.

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Buddenbrockia Is a Cnidarian Worm

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A major evolutionary divide occurs in the animal kingdom between the so-called radially symmetric animals, which includes the cnidarians, and the bilaterally symmetric animals, which includes all worm phyla. *Buddenbrockia plumatellae* is an active, muscular, parasitic worm that belongs to the phylum Myxozoa, a group of morphologically simplified microscopic endoparasites that has proved difficult to place phylogenetically. Phylogenetic analyses of multiple protein-coding genes demonstrate that *Buddenbrockia* is a cnidarian. This active muscular worm increases the known diversity in cnidarian body plans and demonstrates that a muscular, wormlike form can evolve in the absence of overt bilateral symmetry.

Most metazoans (true animals), including arthropods, annelids, mollusks, chordates, and all worm phyla, belong to the Bilateria. This clade excludes cnidarians, ctenophores, sponges, and placozoans. Myxozoans were originally placed outside the Metazoa, despite the presence of characters such as multicellularity of spores, septate junctions, and putative nematocysts (1–3). Sequencing of 18*S* ribosomal DNA (rDNA) confirmed that they are highly modified metazoans (4). However, precisely placing them in the animal kingdom has proven difficult. Most myxozoans are microscopic aquatic endoparasites with either plasmodial or sac-shaped bodies, with no gross similarity to other animals. There are two classes of myxozoans, the clades Myxosporea, with over 2000 species, and the Malacosporea, with two

described species and two others recently identified by rDNA comparisons (5). Myxozoans parasitize a wide range of hosts, including fish, annelids, and (for malacosporeans) bryozoans. Myxozoans form complex spores containing polar capsules similar to the stinging organelles (nematocysts) of cnidarians, which they use to attach to a new host. Polar capsules differ from typical nematocysts of cnidarians in lacking chemo- and/or mechanosensory structures and neural connections that modulate discharge (6).

If polar capsules and nematocysts are homologous, then myxozoans could be cnidarians or the sister group to cnidarians. Alternatively, nematocyst-like structures may have evolved before the divergence of cnidarians and bilaterians, or they could have arisen independently. Some analyses of myxozoan 18*S* rDNA sequences have also suggested that myxozoans are related to cnidarians, most notably, when the highly divergent rDNA sequence of the endoparasitic cnidarian *Polypodium hydriforme* is included (3). In contrast, other rDNA analyses suggest myxozoans are bilaterians (7, 8). These contradictory phylogenetic results may be a consequence of the highly divergent (long-branch) rDNA sequences of myxozoans (9), making placement difficult.

The report of bilaterian-like Hox genes in two myxozoan species (10) and the surprising finding

that a rare endoparasitic worm that infects freshwater bryozoans, *Buddenbrockia plumatellae* (11) (Fig. 1), is actually a myxozoan (7, 12) have further confounded the placement of the myxozoans. *Buddenbrockia* worms are highly active, with continuous and vigorous sinuous writhing within the body cavity of bryozoan hosts (12, 13). The worms escape from their bryozoan hosts, probably through the vestibular pore, and undergo repeated coiling and straightening (13). The vermiform (wormlike) body plan of *Buddenbrockia* is reminiscent of bilaterian taxa, although *Buddenbrockia* lacks a recognizable nervous system, gut, and external
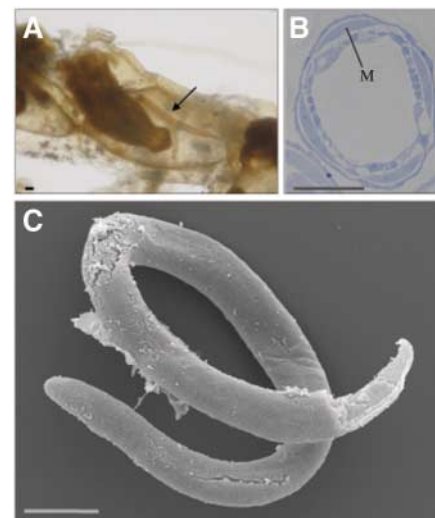

Fig. 1. (**A**) A zooid of the bryozoan *Plumatella* with *Buddenbrockia* worms (arrow) in the body cavity. Scale bar, 40 μm. (**B**) Cross section of an immature *Buddenbrockia plumatellae* worm. Note the presence of four longitudinal muscle blocks (M) and absence of gut. Scale bar, 20 μm. (**C**) Scanning electron microscopy image of a *Buddenbrockia plumatellae* worm. Scale bar, 100 μm.

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