Late Quaternary megafaunal extinctions in India: how much do we know?

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Abstract: Understanding global patterns of late Quaternary megafaunal extinction is impeded by geographic variation in data quality and quantity. The magnitude, timing and drivers of megafaunal extinctions remain poorly understood for India, a region with a strong history of palaeontological research. We review available data for all putative extinct Indian megafaunal taxa with direct or indirect reported evidence of potential survival into the global "megafaunal extinction window" (from ~50,000 years onwards). Assessment of late Quaternary megafaunal species richness is confused by multiple levels of taxonomic uncertainty, including the relationship of named Late Pleistocene taxa to extant taxa, and nomenclatural confusion over correct species names. There is sufficient evidence to recognise up to four genuine global megafaunal species-level extinctions in India during the Late Pleistocene: two proboscideans (*Palaeoloxodon namadicus*, *Stegodon* sp.), a hippopotamus (*Hexaprotodon* sp.), and possibly a horse (*Equus namadicus*). A fifth extinct megafaunal species, the Indian aurochs *Bos* [*primigenius*] *namadicus*, definitely persisted into the Holocene. Other Indian late Quaternary megafaunal species (*Rhinoceros* spp., *Bubalus palaeindicus*, *Sus* "*palaeindicus*", *Crocodylus palaeindicus*) are likely to be synonyms of extant species. Reconstructing regional extinction dynamics is further impeded by chronological uncertainty; however, attempts to obtain new dates for vertebrate samples from six late Quaternary sites in five regions were unsuccessful. Accurate understanding of the dynamics of megafaunal extinctions in India will require robust taxonomic, chronological and palaeoecological data, and we encourage further investigation of the region's rich late Quaternary record.

Key words: aurochs, *Bos namadicus*, extinction chronology, *Hexaprotodon*, *Palaeoloxodon*, Pleistocene extinction, radiometric dating, *Stegodon*

1. Introduction

The end of the late Quaternary, from ~50,000 years onwards, witnessed the global extinction of around one hundred genera of large-bodied terrestrial vertebrates ('megafauna'; mean adult body mass ≥45 kg) across every continent except Antarctica (Koch and Barnosky, 2006; Stuart, 2015). Spatiotemporal patterns and causal mechanisms of extinctions during the Late Pleistocene and Pleistocene-Holocene transition have attracted scientific interest and debate since the nineteenth century (Martin, 1967, 1984; Grayson, 1984; Monjeau et al., 2017), as they represent the most substantial extinction event in the recent geological record and are unique for their size-bias towards larger species (Smith et al., 2018). Both climate-driven environmental change and prehistoric human activity (either direct or indirect) have been implicated as causal drivers, thus potentially providing unique baseline data and a historical analogue for addressing the current biodiversity crisis (Turvey and Crees, 2019). Although most of the world's largest-bodied terrestrial species were lost, many large vertebrates survived into the recent historical period or even to the present, so understanding the dynamics of this event can also provide insights into intrinsic biological traits that may influence species extinction vulnerability or resilience in the context of multiple extrinsic stressors (Johnson, 2002; Turvey and Fritz, 2011). Robust regional datasets are required to determine levels and taxonomic patterns of late Quaternary losses, reconstruct species last-occurrence dates, and compare relative patterns of extinction and survival in the context of regional environmental change and prehistoric expansion of modern humans (Stuart, 2015).

There is currently significant disparity in our understanding of the taxonomy, chronology, and palaeoecological context of late Quaternary extinctions across different biogeographic regions, principally due to variation in historical research interest and differential regional fossil preservation. Long-term research programmes in northern Eurasia, combined with excellent preservation conditions, have permitted detailed species-specific understanding of spatiotemporal extinction dynamics and drivers (Lorenzen et al., 2011; Stuart and Lister, 2011, 2012; Lister and Stuart, 2019). Extensive research into late Quaternary extinctions across North America, South America and Australia has also resulted in good taxonomic understanding of megafaunal biodiversity loss, but differing preservational conditions and less comprehensive direct dating programmes mean that chronological information on regional extinction timings and therefore drivers is less robust (Price et al., 2018). Single continent- and region-wide reviews for Africa (Faith, 2014), China (Turvey et al., 2013), and southeast Asia (Louys et al., 2007) have provided important initial insights into comparative patterns of megafaunal survival and loss, but basic data on patterns of late Quaternary species richness and extinction chronologies are more poorly known for these regions.

Conversely, late Quaternary megafaunal extinctions remain poorly understood for the vast and biologically complex Indian subcontinent, constituting a significant gap in our ability to reconstruct spatiotemporal dynamics of global megafaunal extinctions, or properly assess causal drivers and patterns of inter-regional similarity or difference in extinction trajectories. It is particularly important to understand the history of megafaunal extinction and faunal responses to environmental and anthropogenic change through time for tropical and subtropical Asia, as this region is currently a global hotspot for current-day species loss (Schipper et al., 2008). Regional species occurrence records from the past 250 years demonstrate historical range contractions and regional extirpations of numerous large mammal species in response to forest loss and increasing human population density (Karanth et al., 2010). However, unlike most other continental areas, India still retains several native megafaunal herbivores (Asian elephant *Elephas maximus*, greater one-horned rhinoceros *Rhinoceros unicornis*, large bovids) and top predators (multiple *Panthera* spp.). There is a strong history of palaeontological research in India, and many sub-regions have documented late Quaternary fossil records with the potential to provide insights into regional megafaunal loss and survival before the historical era. However, much of this existing information has not yet been synthesised, or critically reviewed with specific reference to the late Quaternary megafaunal extinction debate.

1.1. Background to the Indian Quaternary record

India has experienced significant regional late Quaternary environmental change, and has a long history of hominin occupation (Dennell, 2009; Petraglia et al., 2012; Boivin et al., 2013; Mellars et al., 2013; Blinkhorn and Petraglia, 2017; Roberts et al., 2018). A calvarium and postcranial material of *Homo* sp. (possibly *H. erectus* or *H. heidelbergensis*) are known from the Narmada Valley of peninsular India, the most secure age estimate for which is ~236 ka (Sonakia, 1984; Sonakia and Biswas, 1998; Sankhyan, 2005; Dennell, 2009; Patnaik et al., 2009). The Late Acheulean to Middle Palaeolithic transition in South Asia apparently occurs significantly later than elsewhere in Eurasia, with the end of the Late Acheulian dating to ~130 ka, or possibly up to ~100 ka based upon minimum age estimates. Middle Palaeolithic technology is recorded from 96 ka, with subsequent technological continuity suggestive of regional hominin population continuity, and featuring specific lithic technologies common in the African record but lacking those associated with Neanderthals in the Levant and central Asia (Groucutt et al., 2015; Blinkhorn and Petraglia, 2017). However, this transition has alternately been dated to 385±64 ka using luminescence dating, and with proposed evidence for the Middle Palaeolithic from 172±41 ka based on OSL dating at Attitampakkam, Tamil Nadu, thus consistent with an older timeframe for the Out Of Africa model of human dispersal (Akhilesh et al., 2016). The Late Palaeolithic occurs from ~45 ka onward, with an early phase dominated by blade and microblade production, and with microlithic technology becoming widespread from ~38 ka (Dennell, 2009; Groucutt et al., 2015; Blinkhorn and Petraglia, 2017). The earliest well-dated *Homo sapiens* material from South Asia is from Fa Hien and Batadomba-Lena in Sri Lanka (~36 to 28 ka), while the oldest *H. sapiens* specimens from mainland South Asia are from Jwalapuram 9 in Andhra Pradesh (20 to 12 ka) (Dennell, 2009; Clarkson et al., 2009; Groucutt et al., 2015; Blinkhorn and Petraglia, 2017).

Abundant vertebrate fossil assemblages are present in the Siwalik Group exposed along the southern foothills of the Himalayas in India and Pakistan, which contains diverse assemblages of mammals in stratigraphic biozones dating from 18.3 Ma onwards (Patnaik, 2013; Flynn et al., 2016). However, even the youngest Siwalik fauna, from the Pinjor Formation, is 2.48 to 0.63 Ma based on magnetostratigraphy (Nanda, 2002; Siddiq et al. 2016), so is not directly informative about late Quaternary extinctions, and Late Pleistocene sediments in this region exist only as uplifted and incomplete fluvial terrace systems that have been affected by erosion and agriculture (Chauhan, 2008). Several Plio-Pleistocene megafaunal taxa originally described from the Siwaliks in the nineteenth century (Falconer and Cautley, 1845-1849; Falconer, 1859) have also been reported from palaeontological and Palaeolithic archaeological sites elsewhere in India, notably from Pleistocene alluvial deposits containing rich vertebrate fossils in the Manjra and Ghod Valleys, the Narmada Valley, and other river drainages across peninsular India (Khatri, 1966; Corvinus et al., 1972; Joshi et al., 1978; Badam, 2000, 2013; Chauhan, 2008; Nanda, 2008; Badam and Sankhyan, 2009; Sathe and Paddayya, 2013; Sathe, 2015a; Thakur et al., 2018). Numerous sites are interpreted as Late Pleistocene in age on the basis of characteristic megafaunal assemblages that have been used for regional biozonation (e.g. Badam, 1985; Ghosh, 1990; Chauhan 2008). Several representatives of the regional Late Pleistocene megafauna are sometimes stated to have persisted into the early Holocene (Khatri, 1966; Dassarma and Biswas, 1977; Sonakia and Biswas, 1998; Patnaik et al., 2009). However, few sites have been dated directly, with age inference based mainly on stratigraphic and faunal context. Mammalian fossils are also known from dated cave sites in peninsular India, but these sites generally lack representatives of the extinct regional megafauna (Prasad, 1996; Patnaik et al., 2008; Roberts et al., 2014).

The only recent regional summary of late Quaternary megafaunal spatiotemporal distributions was provided by Chauhan (2008), who reviewed records of Pleistocene mammal faunas from palaeontological and archaeological deposits on the Indian subcontinent on a site-by-site basis. However, Chauhan (2008) did not consider the late Quaternary record in the context of megafaunal extinction timings and dynamics, but instead focused on fossil taxa as stratigraphical and environmental indicators. Recent single-site assessment of faunal records from the Kurnool Cave deposits in Andhra Pradesh has been used to suggest widespread persistence of many living taxa from at least 200,000 years ago to the present across the Indian subcontinent, attributed to continued regional presence across the Pleistocene-Holocene boundary of a diversity of habitat types, including tropical forests, grassland savannahs and deserts, within wider landscape mosaics that could maintain high mammalian diversity (Roberts et al., 2014). Conversely, there is evidence from the same cave system of at least local extirpations of megafaunal taxa, including *Rhinoceros* sp. and *Equus* sp., possibly in response to increasing aridification during the Last Glacial Maximum (LGM) and/or prehistoric exploitation by humans (Patnaik et al., 2008). The only regionally extinct Indian megafaunal species that has been the subject of a comprehensive dating study is the ostrich *Struthio camelus*, which was present in India during the late Quaternary (Badam, 2005; Jain et al., 2017; Behera and Badam, 2019), with direct accelerator mass spectrometry (AMS) radiocarbon dating of ostrich eggshell across multiple sites indicating survival into the LGM (Blinkhorn et al., 2015). However, this extinct population is conspecific with ostriches that still occur in Africa, and direct dates remain largely unavailable for globally extinct Indian megafaunal taxa. Without a comprehensive assessment of well-dated fossil evidence for presence or extinction of individual taxa across multiple sites, it therefore remains difficult to understand the magnitude of species-level extinctions and faunal turnover in India within the context of the global megafaunal extinction debate.

To begin to resolve some of these issues, we held an international workshop at Deccan College Post Graduate and Research Institute (Pune, India) in February 2015 under the India-UK Scientific Seminar Scheme, which aimed to collate and assess available evidence for regional late Quaternary megafaunal extinction. Information from this workshop was subsequently synthesised with a comprehensive assessment of the existing literature and a targeted programme of radiometric AMS dating of fossil material, to establish a new baseline for understanding Indian late Quaternary megafaunal extinctions. Here we review available information about last-occurrence dates of all globally extinct megafaunal vertebrates in mainland India for which there is direct or indirect suggested evidence of survival into the global "megafaunal extinction window" (i.e. from ~50,000 years onwards, and following the regional expansion of modern humans). We also review the quality of these data for inferring extinction magnitude and timings, and for reconstructing wider faunal dynamics and response to change.

2. Possible victims of an Indian megafaunal extinction event

Numerous extinct megafaunal vertebrates and other extinct mammals have been reported from late Quaternary sediments across India (Table S1). However, few of these taxa are likely to be distinct from other extinct or extant taxa, or to have persisted into the Late Pleistocene-Holocene megafaunal extinction window. A series of late Quaternary sites in India that contain megafaunal fossils are also associated with Late Pleistocene radiometric dates, including AMS and non-AMS radiocarbon dates, infrared stimulated luminescence dates, and thermoluminescence dates (Figure 1). We provide details below about putatively extinct megafaunal taxa identified from these sites. Existing dates for sites with relevance for more than one extinct taxon are summarised in Table 1; further information on dating of other sites is provided under the species accounts below.

2.1. Proboscidea

2.1.1. ***Palaeoloxodon namadicus*** (Falconer and Cautley, 1846)

The genus *Palaeoloxodon* Matsumoto 1942, named originally for the Japanese species *P. naumanni* (Makiyama, 1924), encompasses a group of closely-related species including *P. namadicus* of the Indian subcontinent, the European straight-tusked elephant *P. antiquus* (Falconer and Cautley, 1847), the African *P. recki* (Dietrich, 1915), and the Chinese *P. huaihoensis* Liu, 1977. Many authors (Maglio, 1973; Sanders et al., 2010) have subsumed these species within the extant Asian elephant genus *Elephas*, including most Indian authors who have placed *P. namadicus* in *Elephas*, although *Palaeoloxodon* was retained by Rai (2004). However, Eurasian *Palaeoloxodon* species form a monophyletic clade (Ferretti, 2008; Larramendi et al., 2020), and the group is most usefully treated as a valid genus (Inuzuka and Takahashi, 2003; Lister, 2004; Shoshani et al., 2007). This is particularly the case since its relationship to *Elephas* and other genera is disputed, with morphology-based assumption of close relationship to *Elephas* (Maglio, 1973) recently challenged by molecular evidence suggesting an origin from *Loxodonta* (African elephants), or even as a hybrid between *Loxodonta* and *Elephas* (Meyer et al., 2017; Palkopoulou et al., 2018).

Maglio (1973) considered *P. namadicus* and *P. antiquus* to be synonymous, with *namadicus* taking nomenclatural priority, but recent studies of cranial morphology and postcranial proportions (Larramendi et al., 2020) confirm their separate status. Nonetheless, especially with isolated bones and teeth, problems of identification exist between Indian Quaternary *Palaeoloxodon* and *Elephas* species, and the extant *E. maximus* co-occurs with *P. namadicus* at several Late Pleistocene sites in peninsular India and the Ganga Plain (Chakravarty 1931, 1935, 1938; Nanda, 2008; Ghosh et al., 2016).

Several *P. namadicus* specimens from peninsular and northern India are known from stratigraphic contexts suggestive of survival into the megafaunal extinction window, including from dated fossiliferous layers at Devakachar, Harwadi, Kalpi, Nandur Madhmeshwar, Rati Karar, Wangdari, and the Baghor coarse member at several sites in the Son Valley (Table 1). Proboscidean material from the Baneta Formation of the Narmada Valley was also assigned to "*Elephas* cf. *namadicus*" by Biswas (1997) and Sonakia and Biswas (1998), and was originally interpreted as early Upper Pleistocene in age (128,000-70,000 years old) based on magnetostratigraphy (Rao et al., 1997). However, a series of ^{14}C dates are available for the Baneta Formation from multiple sites in the Narmada Valley, showing that it falls within the age range of the megafaunal extinction window (Table 1).

Another indirectly dated specimen was recently described by Ghosh et al. (2016), who reported a fragmentary, worn skull identified as *Elephas* cf. *namadicus* from the eastern bank of the Dhasan River on the Ganga Plain. The authors excluded *E. maximus*, but could not exclude the possibility of the extinct Plio-Pleistocene ancestral form *E. hysudricus* Falconer and Cautley, 1846 (see

Lister et al., 2013). Sand from a thin lens in the fossil-bearing horizon yielded an OSL age of 56±5 ka, and Ghosh et al. (2016) considered that this also represents the age of the fossil, as its preservation suggests little or no water transport before deposition. *Palaeoloxodon* is also known from other Late Quaternary deposits in the southern Ganga Plain that are suggested to extend into the early Holocene but are not dated (Nanda et al., 2008; Ghosh et al., 2016).

2.1.2. *Stegodon* sp.

Three *Stegodon* species are reported from post-Siwalik late Quaternary faunas in India. Most specimens have been assigned to two species originally described from the Siwalik fauna, *S. insignis* (Falconer and Cautley, 1846) and *S. ganesa* (Falconer and Cautley, 1846). However, the validity and diagnostic characters of these species remain confused, due to uncertainty over which material Falconer originally intended the name *Stegodon ganesa* to be associated with, reassignment of some of the type series of *S. ganesa* to *S. bombifrons* by Lydekker (1885), and the subsequent suggestion by Osborn (1942) that the two taxa might represent males and females of the same species and should be synonymised under the invalid composite taxonomic combination "*Stegodon insignis-ganesa*". Late Quaternary *Stegodon* material from India is regularly referred to using this composite name, with the implication that *S. ganesa* represents a junior synonym of *S. insignis* (Khan, 1971; Joshi et al., 1978; Badam and Kumar, 1982; Sathe, 1989; Rai, 2004; Patnaik et al., 2005), although other authors maintain them as separate species (Deraniyagala, 1956; Saegusa, 1987; Saegusa et al., 2005). *Stegodon* material from the Late Pleistocene of the Narmada Valley has also been described as a third species, *S. namadicus* Biswas and Dassarma, 1981, which is cranially well-diagnosed and distinct from the Siwalik taxa (Biswas and Dassarma, 1981), and Late Pleistocene material from peninsular India may all be referable to this species.

Stegodon material referred to "*S. insignis-ganesa*" from Pleistocene sediments in Indian river valleys provides potential evidence for survival into the megafaunal extinction window. Material is known from dated fossiliferous horizons at Devakachar, Tadula and Wangdari (Table 1). An almost complete skeleton is also known from sandy silt at Amonda, Narmada Valley; this specimen was found in proximity to lithic artefacts although without confirmed association, and is associated with a reportedly recent but unpublished OSL date (Chauhan et al., 2013).

2.2. Perissodactyla

2.2.1. *Rhinoceros* spp.

India is known to have contained three rhinoceros species into the historical period (Rookmaaker, 1980). The greater one-horned rhinoceros *Rhinoceros unicornis* had a wide historical distribution across the terai grassland belt of the Himalayan foothills from Pakistan to eastern India and possibly also south of the Ganges, and persists as isolated populations in West Bengal, Uttar Pradesh, Assam, Nepal and Bhutan. The Javan rhinoceros *R. sondaicus* and Sumatran rhinoceros *Dicerorhinus sumatrensis*, both of which survive as critically endangered relict populations in insular southeast Asia, also occurred in northeastern India into the early twentieth century. All three species apparently co-occurred historically in northern Bengal, Assam, Sikkim, and regions adjoining northeastern Bangladesh, representing the world's most diverse postglacial rhinoceros fauna (Rookmaaker, 1980; Antoine, 2012). Rhinos, probably *R. unicornis*, had a much more extensive distribution in South Asia earlier in the Holocene, as evidenced by rock art, archaeological artefacts and faunal remains (Rookmaaker 1980; Chitalwala, 1990; Thomas et al., 1998; Sathe, 2010), and all three species known historically from India are recorded widely across tropical and subtropical Asia during the Pleistocene (Hooijer, 1946; Louys et al., 2007; Chauhan, 2008; Groves and Leslie, 2011; Antoine, 2012).

Several purportedly extinct rhinoceros species are reported from the Indian Pleistocene. Three species, *Rhinoceros deccanensis* Foote, 1874, *R. karnuliensis* Lydekker, 1886, and *R. palaeindicus* Falconer and Cautley, 1847, reportedly occur in Late Pleistocene contexts. A mandible assigned to *R. deccanensis* from a river terrace in the Ghataprabha Valley (Foote, 1876) has been estimated as 39,000-30,000 years old based on stratigraphical position (Badam and Jaykaran, 1993). Material assigned to *R. karnuliensis* from the Kurnool Caves has been estimated as 20,000-10,000 years old based on stratigraphical position (Murty, 1979). Three mandibles assigned to *R. palaeindicus* are reported from Harwadi (Table 1; material in Palaeontology Laboratory, Deccan College). In addition to major uncertainties surrounding these inferred dates, the taxonomic status of these putative species is also dubious. *Rhinoceros deccanensis* and *R. palaeindicus* have both been interpreted as junior synonyms of *R. unicornis* (Laurie et al., 1983; Tong, 2001; Antoine, 2012; Yan et al., 2014), and *R. deccanensis* is based on very incomplete material and should be considered a *nomen dubium*. *Rhinoceros karnuliensis* has been interpreted as a junior synonym of *R. sondaicus* (Hooijer, 1946); material from its type locality, the Kurnool Caves, was interpreted as representing *R. unicornis* by Prasad (1996) and Antoine (2012), and later assigned merely to *Rhinoceros* sp. by Roberts et al. (2014).

2.2.2. ***Equus namadicus*** Falconer and Cautley, 1849

Equus namadicus is a stenonine horse that is widely reported from late Quaternary deposits in the Manjra, Ghod, Karha and Narmada Valleys and elsewhere across India (Khatri, 1966; Corvinus et al., 1972; Joshi et al., 1978; Badam, 1977a, 1979, 1985; Salahuddin, 1988; Chauhan, 2008; Sathe, 2008, 2015a; Patnaik et al., 2009; Sathe and Paddayya, 2013; Bernor et al., 2019; Rook et al., 2019). It is sometimes interpreted as an index fossil of the Middle Pleistocene (Thakur et al., 2018), and also as the ancestor of the extant Asiatic wild ass *E. hemionus*, which appears in India during the last glaciation (Dassarma and Biswas, 1976, 1977; Biswas, 1987), and reportedly replaces it in Late Pleistocene-Holocene deposits (Gromova, 1949; Hooijer, 1963; Patnaik et al., 2009; Badam, 2013). However, many authors record the occurrence of *E. namadicus* into the Late Pleistocene (Joshi et al., 1978; Badam, 1979, 1985; Chauhan, 2008; Badam and Sankhyan 2009; Sathe and Paddayya, 2013). Co-occurrence of *E. namadicus*, *E. hemionus*, and sometimes also the extant wild horse *E. caballus* is also reported from late Quaternary deposits in the Ghod, Mahanadi, Purna and Son valleys (Badam, 1985, 2000, 2002; Chauhan 2008; Thakur et al., 2018).

Species diversity, taxonomy and evolutionary history of Late Pleistocene-Recent equids is complicated, and the validity of other putative extinct late Quaternary species is unclear (MacPhee et al., 2002; Orlando et al., 2009; Bennett et al., 2017; Gaunitz et al., 2018). A variety of names have been applied to Middle-

Late Pleistocene Indian *Equus* material in recent decades (e.g. *namadicus, caballus, hemionus, hemionus khur, onager khur, asinus*; Badam, 1977a; Salahuddin, 1988; Chauhan, 2008), partly reflecting the complex taxonomy of extant hemiones (Groves and Grubb, 2011), although usually without any accompanying morphological information to justify taxonomic identification of equid fossils. There is no conclusive evidence for occurrence of *E. caballus* in India before the Holocene, and some Indian material originally assigned to *E. caballus* has subsequently been reassigned to *E. namadicus* (Badam, 1979; Badam and Sankhyan, 2009); recent research has aimed to investigate whether *E caballus* is indigenous or arrived in the early Holocene in association with Indo-European or Rgvedic peoples (Bökönyi, 1997; Meadow, 1997; Sathe, 2016; Sathe et al., 2019). The validity of extinct Indian *Equus* species described from the Siwaliks and younger deposits is also debated (Bernor et al., 2019), notably whether *E. namadicus* is distinct from *E. sivalensis* from the Early Pleistocene of the Siwaliks, as material assigned to both taxa shows considerable variability (Badam, 1977a; Gaur and Chopra, 1984). Falconer and Cautley (1849) also recognised a second *Equus* species, *E. palaeonus*, from the Late Pleistocene of the Narmada Valley, but Lydekker (1882, 1883), Matthew (1929) and Colbert (1934) reinterpreted this taxon as a young individual of *E. namadicus*.

Material identified as *E. namadicus* from Late Pleistocene contexts with associated dates is reported from the Baghor Coarse Member in the Son Valley, Devakachar, Harwadi, Inamgaon, Kalpi, Nandur Madhmeshwar, and Wangdari (Table 1). Equid material from most other Indian Late Pleistocene sites has been classified more generally as just hemionine, caballine or *Equus* sp., and we cannot confirm the species-level identity of this material with any confidence.

2.3. Artiodactyla

2.3.1. *Hexaprotodon* sp.

There has been confusion over whether South and Southeast Asian Neogene-Quaternary hippopotamus taxa should be referred to *Hippopotamus* or *Hexaprotodon*, but the cladistic review by Boisserie (2005) assigned all Asian material to *Hexaprotodon*. Five taxa have been recognised from the Quaternary of India and Pakistan: *Hexaprotodon dhokwazirensis* Akhtar and Bakr, 1995; *H. namadicus* Falconer and Cautley, 1847; *H. palaeindicus* Falconer and Cautley, 1847; *H. sivalensis* Falconer and Cautley, 1836; and *Hippopotamus deccanensis* Anantharaman et al., 2005. These taxa are sometimes considered separate species, synonyms (de Visser, 2008), or subspecies or chronotaxa within an evolving lineage (Badam, 2013; Sathe, 2015b). *Hexaprotodon namadicus* has been interpreted as a Middle Pleistocene index fossil (Badam, 1977b, 1988, 2002; Joshi et al., 1978; Thakur et al., 2018). *Hexaprotodon palaeindicus* and *H. namadicus* have also been regarded as sexual dimorphs, referred to using the misleading name combination "*Hexaprotodon palaeindicus namadicus*" (Salahuddin, 1999; Chauhan, 2008). Further research is required to assess the validity of all proposed species, since species-level identification has been based upon relative size of incisors, which cannot be determined in incomplete material and might represent intraspecific variation.

Hexaprotodon has sometimes been interpreted as having become extinct in India during the Middle Pleistocene, ~250,000 years ago (Deraniyagala, 1952; Weerawardhena et al., 2003). *Hexaprotodon sivalensis* is present in the youngest

Plio-Pleistocene faunas of the Siwaliks (Khan, 2018), but these deposits are older than the megafaunal extinction window. However, material referred to *Hexaprotodon palaeindicus* or *H. namadicus* is reported from numerous Indian Late Pleistocene sites, and *Hippopotamus deccanensis* is also reported from the Late Pleistocene of southern Deccan (Sathe and Paddaya, 2013).

Jukar et al. (2019) recently provided a direct AMS date of 13,344 ± 135 BP (16,467-15,660 cal BP) (lab number: NTUAMS-4285) for a right upper canine identified only as *Hexaprotodon* sp. (BNF2-1) from the Baneta Formation at Baneta in the Narmada Valley (Table 1). However, the authors noted that the sample contained no visible collagen, and dating was instead carried out on phosphates leached from the sample. *Hexaprotodon* material is also reported from the Baneta Formation at Khidiaghat in the Narmada Valley (Patnaik et al., 2009), and from Late Pleistocene contexts with associated dates from the Baghor Coarse Member in the Son Valley, Devakachar, Harwadi, Inamgaon, Kalpi, Nandur Madhmeshwar, Tadula, and Wangdari (Table 1). It is also recorded from the Mahagara gravels in the Belan Valley, with associated ^{14}C dates on freshwater mollusc shell of 19,175 ± 340 BP (lab number: TF-1245) and 25,790 ± 830 BP (lab number: PRL-86) (Agrawal and Kusumgar, 1975b; Thapar, 1979). Material referred to *Hexaprotodon palaeindicus* is present in the Upper Zone of the Narmada Valley mammalian sequence, which is interpreted as Late Pleistocene to Early Holocene in age (Biswas, 1997). Further material is known from other Pleistocene river valley sediments (e.g. a mandibular ramus with m2-3 from Rangna, Wardha Valley; Archaeological Survey of India, 2002), although these are not associated with radiometric dates or stratigraphic correlation.

Early Holocene survival of *Hexaprotodon* in India has been suggested on the basis of possible hippopotamid remains reported from Sarai Nahar Rai and Mahadaha, two Mesolithic oxbow lake sites in the Ganga Plain (Alur, 1980; Joglekar et al., 2003). However, these records are disputed as potential misidentification of *Rhinoceros* (Pandey, 1989; Jukar et al., 2019).

2.3.2. *Bos* [*primigenius*] *namadicus* Falconer, 1859

The Indian aurochs *Bos namadicus* differs from other Indian late Quaternary megafaunal species in that, much as in Europe, it is now extinct but known to have survived well into the Holocene. Originally described as a distinct species by Falconer (1859), this taxon is sometimes considered to represent a subspecies of the Eurasian aurochs *B. primigenius* that diverged 200,000-100,000 years ago (Verkaar et al., 2004), and aurochsen had an approximately continuous distribution from Europe to India. The Indian aurochs is interpreted as the direct ancestor of zebu cattle *B. indicus*, from a mid-Holocene domestication event in northern India that was independent from the domestication of aurochs in Europe (Fuller, 2006; Chen et al., 2009). Two other Late Pleistocene Indian bovids, *Bibos palaeogaurus* (Rütimeyer, 1878) and *Leptobos frazeri* (Rütimeyer, 1878), are now considered junior synonyms of *Bos namadicus* (Pilgrim, 1939; Bibi, 2009).

Late Pleistocene material of *B. namadicus* is widespread across the Indian subcontinent (Sathe et al., 1986; Badam and Jain, 1998; Basak et al., 1998; Chauhan, 2008; Kshirsagar et al., 2016), and along with *Equus namadicus* it is one of the most abundant species in vertebrate fossil sites (Kshirsagar et al., 2016). There is direct evidence of Late Pleistocene anthropogenic exploitation, from remains in Acheulian layers at Yediapur 1A in southern Deccan that bear cut marks (Sathe and Paddayya, 2013). It is also reported from numerous Indian Holocene sites, including several sites in West Bengal: Bharatpur (Chalcolithic, ~1000 BC), Chandraketugarh (Early Historic, 200 BC–200 AD), Mochpal (Early Historic, 200 BC–200 AD), and Boral (Medieval, 200 BC–1100 AD) (Banerjee, 1976, 1981; Banerjee and Saha, 1976; Saha et al., 1999). However, there is uncertainty around identification and dating of many purported Holocene records. Late Pleistocene aurochs specimens from India are typically far more robust than Holocene specimens identified as *B. namadicus*, which also display greater variability in cranial and skeletal size and shape, implying possible confusion with domestic cattle (Grigson, 1985; Joglekar and Thomas, 1992). From the mid-Holocene, wild-type *B. namadicus* remains are typically reported alongside domesticated morphs and/or misidentified as domestic cattle. For example, according to Kshirsagar et al. (2016), *B. namadicus* was present at Mohenjodaro, Pakistan (2500 BC; Sewell and Guha, 1931) and at the hunter-gatherer site of Langhnaj, northern Gujarat (2000 BC; Clutton-Brock, 1965), but these sites postdate the known timing of domestication of *B. indicus*, so these remains may represent domesticated rather than wild individuals. Material of *B. namadicus* is also reported from Mehrgarh, Pakistan, which contains some of the earliest evidence of animal domestication in south Asia and is dated to ~6000 BC (Meadow, 1981). This record might constitute the only dated and reliably identified evidence for postglacial survival of *B. namadicus*, and morphological reassessment of material assigned to this taxon from Holocene sites across India is required.

2.3.3. ***Bubalus* [*arnee/bubalis*] *palaeindicus*** (Falconer, 1859)

This taxon was originally described as a species of *Bos* from the Early Pleistocene of the Siwaliks by Falconer (1859), but was reinterpreted as an extinct subspecies of the extant water buffalo *Bubalus bubalis* by Pilgrim (1939), and is considered very similar to modern *B. bubalis* but apparently larger in size (Akhtar, 2002). Some authors refer to this taxon as *Bubalus bubalis* var. *palaeindicus* (Pilgrim, 1939; Akhtar, 1992; Nanda et al., 2016), or have even assigned Indian Late Pleistocene buffalo material simply to *B. bubalis* (Corvinus et al., 1972). However, the distinct species name *Bubalus palaeindicus* has been used widely to refer to Late Pleistocene buffalo material from peninsular India (Khatri, 1966; Khan, 1971; Badam et al., 1996; Nanda, 2002, 2008; Chauhan, 2008; Patnaik et al., 2009; Sonakia and Biswas, 2011; Sathe and Paddayya, 2013; Badam, 2013; Sathe, 2015a; Thakur et al., 2018), and is sometimes explicitly considered distinct from other Pleistocene material referred to *B. bubalis* (Joshi et al., 1978; Badam et al., 1984). It has also been interpreted as ancestral to *B. bubalis* by many authors (Badam, 1984, 1985, 2013; Ghosh, 1990; Badam et al., 1996).

Another extinct buffalo species, *B. maruvatturensis*, was established on the basis of a distal right humerus from possible Late Pleistocene deposits in Tamil Nadu (Ghose et al., 1972). We consider this taxon to be a *nomen dubium* as the type specimen is fragmentary and lacks key diagnostic features, and it has been interpreted as a possible junior synonym of *Bubalus palaeindicus* by Badam et al. (1996). A well-preserved buffalo fossil from the Bhima Valley has been suggested to represent a further extinct species, although this specimen has not been properly described (Badam et al., 1996). Other extinct *Bubalus* species have been named from the Early to Middle Pleistocene Siwalik succession (Pilgrim, 1939; Nanda, 2002; Patnaik, 2013). Taxonomy of Quaternary-Recent Indian buffalos is further complicated by differentiation of modern wild water buffalos under the separate species name *B. arnee* (Kerr, 1792), the name *B. bubalis* being restricted to the domestic animal (Groves, 1996; Groves and Grubb, 2011), and by recognition that river and swamp domestic water buffalo breed-groups show a deep divergence of up to 270,000 years based on genetic analysis, so should potentially be classified as separate taxa (Kumar et al., 2007). Possible confusion of *Bubalus* and *Bos* skeletal elements in Quaternary deposits constitutes an additional complicating factor for reconstructing spatiotemporal distributions of Indian fossil bovids.

Cranial material referred to *B. palaeindicus* has been reported from Harwadi and Tadula (Tables 1-2). Cut marks on bones identified as either *Bos* or *Bubalus* are reported from two undated Late Pleistocene Acheulian sites from the Hunsgi Valley (Sathe and Paddayya, 2013).

2.3.4. *Sus* "*palaeindicus*"

The only wild species of *Sus* present in India today is the wild boar *Sus scrofa cristatus*, which is widespread across the region (Meijaard et al., 2011), but this species is rarely recorded in Indian late Quaternary mammal assemblages (Biswas and Dassarma, 1981; Salahuddin, 1988; Prasad, 1996; Chauhan, 2008; Patnaik et al., 2008). Instead, the extinct species *Sus namadicus* Pilgrim, 1926 is widely reported from late Quaternary sites, and is recognised in the Indian literature as a Middle Pleistocene index fossil, although the geological age of the type material is unknown (Badam, 1977b, 1988, 2002; Joshi et al., 1978;

Sankhyan, 1997; Sonakia and Biswas, 1998; Chauhan, 2008; Patnaik et al., 2009; Badam, 2013; Thakur et al., 2018). This taxon is reportedly replaced in Late Pleistocene assemblages by another extinct species referred to as *S.* "*palaeindicus*" (Badam, 2000; Badam and Sankhyan, 2009). This name is a *nomen nudum*, as it has apparently never been associated with a formal species diagnosis or description, and is clearly not intended to refer to the only formally described Indian fossil suid with this species name, *Potamochoerus palaeindicus* Pilgrim, 1926 from the Pliocene of the Siwaliks. A further extinct species, *S. karnuliensis*, is reported from the Late Pleistocene of the Kurnool Caves, and was interpreted by Badam (1979) as a valid species derived from the Siwalik taxon *S. falconeri* Lydekker, 1884. Frantz et al. (2015) considered that several *Sus* species formerly existed across continental Eurasia but disappeared following the spread of *S. scrofa* out of southeast Asia. However, the diagnostic characteristics and distinction of these putative late Quaternary Indian species from extant *S. scrofa* are unclear.

A complete mandible assigned to *S.* "*palaeindicus*" is known from Inamgaon (Table 1), although its m2 and m3 are unerupted, making species identification even more uncertain (Badam, 2002).

2.4. Other megafauna

2.4.1. ***Crocodylus palaeindicus*** Falconer, 1859

Crocodylus palaeindicus Falconer, 1859 and *C. sivalensis* Lydekker, 1886 were both originally described from the Plio-Pleistocene of the Siwaliks, but material assigned to these taxa is reported widely from India, Pakistan and Myanmar, and from the Late Miocene to Early-Middle Pleistocene of the Siwaliks succession, including the oldest fossils currently referable to *Crocodylus* (Brochu, 2000; Oaks, 2011). These two species are now interpreted as synonyms, with perceived variation interpreted as either preservational or ontogenetic (Brochu, 2000). Possible survival of *C. palaeindicus* into the megafaunal extinction window is suggested by crocodile maxillary fragments tentatively assigned to this species from Harwadi and Tadula (Table 1).

Crocodylus palaeindicus is considered very similar and closely related to the extant mugger crocodile *C. palustris*, with confusion over identification of some fossil skulls as either *C. palaeindicus* or *C. palustris* (Badam, 1973). Several authors have suggested *C. palaeindicus* is ancestral to *C. palustris* (Lydekker, 1886; Mook, 1933; Garg, 1988). However, this interpretation is complicated by description of material assigned to *C.* cf. *palustris* or *C.* aff. *palustris* from the Middle-Upper Siwalik succession (Pliocene-Pleistocene) of northern India and Nepal (Patnaik and Schleich, 1993; Corvinus and Schleich, 1994; Nanda et al., 2016). Both species are reported from the Late Pleistocene of Devakachar, Narmada Valley (Joshi et al., 1978; Patnaik, 1995), suggesting that, if indeed separate taxa, they were contemporaneous and sympatric. Brochu (2000) identified a small set of characters that apparently differed between examined specimens of *C. palaeindicus* and *C. palustris*, but material assigned to *Crocodylus* cf. *palustris* from the Middle-Upper Siwalik succession is also morphologically distinct from modern individuals of *C. palustris* (Patnaik and Schleich, 1993). Whilst sympatric crocodilian species pairs co-occur in other landscapes (Hekkala et al., 2011; Marioni et al., 2013), the taxonomic validity of *C. palaeindicus* requires further investigation to identify whether Late Pleistocene material from

India can definitely be assigned to the hypodigm of *C. palaeindicus* rather than *C. palustris*, or whether systematic morphological criteria exist to differentiate these two putatively distinct taxa.

3. AMS dating for Indian fossil sites

To try to establish a more robust radiometric framework for fossil sites and regions previously suggested to contain evidence of megafaunal persistence into the megafaunal extinction window, we submitted 25 vertebrate fossil samples from six late Quaternary sites in five regions (Inamgaon, Ghod Valley; Betamcherla-Muchchatla Chintamanu Gavi, Kurnool Caves; Harwadi and Tadula, Manjra Valley; Talayyaghat, Narmada Valley; Johla, Wardha Valley) from the collections of the Palaeontology Laboratory of Deccan College for AMS dating at the Oxford Radiocarbon Accelerator Unit (Table 2). Most samples were identified to species or genus, and included material from the Deccan College collections referred to four nominally extinct late Quaternary Indian megafaunal taxa (*Bos namadicus*, *Bubalus palaeindicus*, *Equus namadicus*, *Hexaprotodon* sp.). However, pre-screening at Oxford indicated that all samples contained <0.3% N (and in nearly all cases <0.1% N), so full collagen extraction for AMS dating was not attempted (Tom Higham, Oxford Radiocarbon Accelerator Unit, pers. comm.).

4. Discussion

Our review of existing information about the magnitude and timing of late Quaternary megafaunal extinctions in India highlights a series of limitations with current palaeontological baselines, such that accurate understanding of the magnitude, dynamics and drivers of regional extinctions will require more robust data (Table 3). Such data limitations are by no means restricted to India, and we recommend further investigation of the region's late Quaternary fauna using modern methods in taxonomy, chronology, and palaeoecology.

Accurate assessment of species richness in India's late Quaternary megafaunal communities is currently confused by multiple levels of taxonomic uncertainty. All extinct Late Pleistocene megafaunal taxa with extant congeners have been interpreted as "ancestral forms" of species occurring in India today, but have been considered taxonomically distinct at the species level (Badam, 2013). There has been little attempt to conduct morphological or morphometric analysis to assess the validity of putatively distinct Late Pleistocene taxa, either in relation to extant taxa or to other named extinct congeners, and few have been investigated within cladistic frameworks (Brochu, 2000; Boisserie, 2005; Chakraborty, 2010). Confirmation of reported taxonomic identifications is rarely possible because Late Pleistocene faunal lists often lack detailed descriptions or illustrations of relevant material (Nanda, 2008). Nomenclatural confusion also exists over the correct species names for many taxa. Names that have been applied to most Late Pleistocene megafaunal species were originally used in the nineteenth century for fossils from the older Siwalik succession, and were later assigned to animals from younger deposits that in many cases may not be conspecific. Several names used in the regional literature apparently represent *nomina dubia* and *nomina nuda*, and names have often been used to differentiate taxa primarily on the basis of locality, habitat or biozone rather than on well-diagnosed morphological differences.

In terms of taxonomic uncertainty, we consider that there is sufficient evidence to recognise up to four genuine global megafaunal species-level extinctions in India during the Late Pleistocene: two proboscideans (*Palaeoloxodon namadicus*, *Stegodon* sp.), a hippopotamus (*Hexaprotodon* sp.), and possibly a horse (*Equus namadicus*). However, although now-extinct species of *Hexaprotodon* and *Stegodon* may have persisted into the LGM in India, the species-level identity (and, indeed, possible species diversity) of both taxa during the Indian Late Pleistocene is uncertain. Although *E. namadicus* is a stenonine and extant Eurasian equids are caballines or hemiones, the identity of Late Pleistocene equid material referred to *E. namadicus* needs to be confirmed. Late Quaternary Eurasian horse taxa have also been extremely oversplit (Boulbes and van Asperen, 2019), so that Indian fossil equids require further investigation to confirm their distinctiveness and relationships to other proposed extinct and extant taxa. A fifth megafaunal species, the Indian aurochs *Bos* [*primigenius*] *namadicus*, definitely persisted into the Holocene, but arguably represents a pseudo-extinction since this taxon survives in domesticated form as zebu cattle. Other putative extinct Late Pleistocene Indian megafauna require further assessment to determine whether they can be morphologically differentiated from extant taxa, and it is likely that some or all of them simply represent fossil material of modern species.

In addition to taxonomic uncertainty, understanding late Quaternary megafaunal extinctions in India is also impeded by chronological uncertainty, associated with a general lack of direct or recent radiometric dates and the reduced reliability of secondary stratigraphic contexts. Most inferred Indian Late Pleistocene megafaunal assemblages are either undated or were dated several decades ago, using methods that are now recognised as potentially prone to error (e.g. less control for potential contaminants; much wider temporal error bars; Lister and Stuart, 2013). Whereas direct AMS dates are available on eggshell across multiple sites for the regionally extinct ostrich (Blinkhorn et al., 2015), and direct electron spin resonance dates are available for unidentified ungulate teeth from other Indian late Quaternary deposits (Patnaik et al., 2009), only one direct date of any kind is currently available for any identified representative of India's globally extinct late Quaternary megafauna, from a *Hexaprotodon* specimen unidentifiable to species level (Jukar et al., 2019). However, dating was conducted on the specimen's mineral carbon fraction, which is more susceptible to diagenesis than collagen, raising potential concerns even with this date (Lister and Stuart, 2013). All other available Late Pleistocene dates associated with extinct Indian megafauna constitute indirect dates on freshwater mollusc shell or associated sediments (Table 1). Although past dating of Indian late Quaternary sites targeted samples from contexts that showed no apparent taphonomic signs of transportation or secondary deposition, it is known that many Late Pleistocene faunal assemblages from key regions such as the Narmada Valley have undergone hydrodynamic sorting resulting in transportation of fossils and delayed burial of bones (Badam et al., 1986), raising inevitable concerns over the relationship between available site dates and the ages of specific fossils. Dates on freshwater mollusc shell might also be affected by a "hard water" reservoir effect, which could affect age estimates by several hundred years, as well as by contamination from secondary carbonates and/or recrystallized calcite (Yates, 2016).

Late Quaternary faunal turnover in India has generally been considered in terms of biozonation and biostratigraphy rather than extinction dynamics and drivers (Chauhan, 2008). In the absence of robust date series for different taxa, it is currently impossible to determine whether taxonomically valid extinct Indian megafaunal species disappeared in a synchronous or staggered event, or whether different species or populations experienced more spatiotemporally complex extinction dynamics across differing landscapes (cf. Lister and Stuart, 2019). The available direct last-occurrence date for *Hexaprotodon* falls within Heinrich event 1, an interval of severe drought in South Asia during the LGM (Zhou et al., 2016; Jukar et al., 2019). However, confirmation of this date and further direct dates are necessary to understand the timing and dynamics of *Hexaprotodon* extinction in India. Extant hippopotamid species vary substantially in their water-dependency, making it difficult to infer the likely vulnerability of Indian *Hexaprotodon* to drought events without a better understanding of its specific ecology (Robinson et al., 2017). Carbon isotope analysis has shown that whole-tooth ∂^{13}C values for late Quaternary hippopotamids from the Narmada and Manjra valleys have values indicative of C4 plant grazing (Sathe et al., 2018), and further study of dental histology and trace elements in hippopotamids and other late Quaternary mammals and reptiles from peninsular India suggests that dietary shifts occurred during this period (Sathe, 2018). Sathe (2004) also found evidence for a correlation between drought events and patterns of taphonomic representation in the fossil record of the Manjra Valley, and wider-scale investigations can potentially help to identify climatic and environmental events that regulated regional late Quaternary megafaunal population dynamics. These palaeoecological insights highlight the need for species-specific extinction chronologies to identify temporally correlated environmental changes (climatic and/or anthropogenic) that might have caused extinctions across other taxa, to assess individualistic species responses to external drivers, and ultimately to make meaningful fauna-wide comparisons with late Quaternary extinction dynamics across other well-sampled continental regions.

Ultimately, new taxonomic assessments and direct date series are needed to answer all of these questions, and we strongly encourage further investigation of India's rich late Quaternary record to improve our understanding of the region's megafaunal extinctions. We recommend that future authors explain their reasoning and provide evidence for species identifications when reporting Late Pleistocene faunal remains, and conduct critical taxonomic revision of putative extinct taxa based upon both morphometrics and ancient biomolecules (ancient DNA and/or collagen) to establish accurate parameters for taxonomic identification; however, we recognise that the high thermal age of Late Pleistocene samples from this region may preclude molecular taxonomy. We also encourage new dating projects, targeting multiple species and sites across different Indian ecoregions to minimise taxonomic, taphonomic and spatial sampling bias, and ideally based upon new *in situ* material with well-constrained stratigraphic contexts. Our own efforts demonstrate that AMS dating of late Quaternary samples may be hindered by low collagen preservation. However, alternative methods such as uranium-series dating or enamel amino acid racemization dating might prove effective, as these methods have yielded new direct dates for megafaunal samples from other tropical environments (Price at al., 2013; Louys et al., 2016; Turvey et al., 2017; Dickinson et al., 2019). Such approaches should also investigate sites pre-dating our defined Late Pleistocene-Holocene megafaunal extinction window, to assess possible longer-term regional faunal turnover in response to earlier Quaternary climatic change or pre-*sapiens* hominin dispersals (Smith et al. 2018, 2019). New data should be interpreted within the context of palaeoclimatic and palaeovegetation reconstruction and modelling, and should also be assessed within a wider faunal context to understand patterns and correlates of vulnerability or resilience shown by different extinct and extant megafaunal species in India, from the Pleistocene to the present. Together, this series of complementary approaches can hopefully strengthen understanding about India's megafaunal extinction event, and also provide predictive insights into extinction dynamics that can contribute toward conservation of the region's surviving but threatened megafauna.

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Figure legends

Figure 1. Map of India showing locations of main late Quaternary sites mentioned in text.

Table 1. Indian late Quaternary sites with associated Late Pleistocene dates, and that contain fossil material of >1 extinct megafaunal vertebrate species. Note that only one of these dates represents a direct date from a taxonomically identified specimen of an extinct megafaunal taxon.

Site name	Region	Date type	Dated sample	Reported date (BP)	Lab number	Associated extinct megafauna	Reference
Kalpi	Ganga Plain	infrared stimulated luminescence		45,000±9,000		*Palaeoloxodon namadicus*, *Equus namadicus*, *Hexaprotodon* sp.	Singh et al., 1999; Tewari et al., 2002
		infrared stimulated luminescence		43,000±7,000			
Baghor Coarse Member (several sites)	Son Valley	^{14}C	freshwater mollusc shell	20,135±220	Beta 4791	*Palaeoloxodon namadicus*, *Equus namadicus*, *Hexaprotodon* sp.	Williams et al., 2006; Jones et al., 2009
		^{14}C	freshwater mollusc shell	26,250±420	Beta 4793		
		thermoluminescence	dark brown sandy clay at 5m depth (Nakjhar Khurd, section G8)	26,100±5,400	Alpha 898		
		infrared stimulated luminescence		24,000±3,000	BN2		
		infrared stimulated luminescence		39,000±9,000	BN3		
Baneta Formation (Baneta and Hathnora	Narmada Valley	^{14}C	carbonaceous clay (Baneta 1)	8,740±540	BS 2278	*Palaeoloxodon* cf. *namadicus*, *Hexaprotodon* sp.	Patnaik et al., 2009; Jukar et al., 2019
		AMS	*Hexaprotodon* sp. canine (Baneta)	13,344±135	NTUAMS-4285		
		^{14}C	bovid tooth dentine (Hathnora 1)	13,150±340	BS 2240		

		^{14}C	carbonaceous clay (Hathnora 2)	24,280±390	BS 2264		
		^{14}C	freshwater mollusc shell	35,660±2,540	BS 2216		
Rati Karar and Devakachar	Narmada Valley	^{14}C from Rati Karar; sediments at Devakachar interpreted as of comparable age	freshwater mollusc shell	31,750±1,820	TF–967	*Palaeoloxodon namadicus*, *Stegodon* sp., *Equus namadicus*, *Hexaprotodon* sp.	Agrawal and Kusumgar, 1975a; Badam, 1986
Nandur Madhmeshwar	Godavari Valley	^{14}C	freshwater mollusc shell	27,410±425	BS 163	*Palaeoloxodon namadicus*, *Equus namadicus*, *Hexaprotodon* sp.	Pilgrim, 1905; Rajagopalan et al., 1982; Mishra, 1995
Inamgaon	Ghod Valley	^{14}C	freshwater mollusc shell	21,725+630/-585	TF–1003	*Equus namadicus*, *Hexaprotodon* sp., *Sus* "*palaeindicus*"	Corvinus et al., 1972; Agrawal and Kusumgar, 1975a
		^{14}C	freshwater mollusc shell	19,290±360	TF–1177		
Tadula	Manjra Valley	^{14}C	freshwater mollusc shell	34,470±2070	BS 562	*Stegodon* sp., *Hexaprotodon* sp., *Bubalus palaeindicus*, *Crocodylus palaeindicus*	Sathe, 1989
Wangdari	Manjra Valley	^{14}C	freshwater mollusc shell	26,820±750	BS 561	*Palaeoloxodon namadicus*, *Stegodon* sp., *Equus namadicus*, *Hexaprotodon* sp.	Sathe, 1989
Harwadi	Manjra Valley	stratigraphic correlation with molluscs		26,820 to 34,470		*Palaeoloxodon namadicus*, *Rhinoceros palaeindicus*, *Equus namadicus*, *Hexaprotodon* sp.,	Sathe, 1989; Sathe and Paddayya, 2013; Sathe, 2015a

						Bubalus palaeindicus, Crocodylus palaeindicus	

Table 2. Vertebrate fossil samples submitted for AMS dating at the Oxford Radiocarbon Accelerator Unit, collected from Indian late Quaternary fossil sites or fossil-bearing landscapes that have previously been suggested to contain evidence of megafaunal persistence into the "megafaunal extinction window" but currently lacking direct dates on vertebrate material. Key: BTC-MCG, Betamcherla-Muchchatla Chintamanu Gavi.

Taxon	**Element**	**Catalogue number**	**Site**	**Locality**
Bos namadicus	Maxilla	INM/425/DC	Inamgaon	Ghod Valley
Sus sp.	Mandible	INM/601/DC	Inamgaon	Ghod Valley
Panthera sp. (*pardus*?)	First phalanx	KRL/52/DC	BTC-MCG	Kurnool Caves
Tetraceros quadricornis	Molar	KRL/147/DC	BTC-MCG	Kurnool Caves
Turtle	Plastron	KRL/22/DC	BTC-MCG	Kurnool Caves
Varanus sp.	Cervical vertebra	KRL/26/DC	BTC-MCG	Kurnool Caves
Bubalus palaeindicus	Cranium	MNJ/1119/DC	Harwadi	Manjra Valley
Bubalus palaeindicus	Cranium	MNJ/977/DC	Harwadi	Manjra Valley
Elephas sp.	Mandible	MNJ/969/DC	Harwadi	Manjra Valley
Elephas sp.	Mandible	MNJ/974/DC	Harwadi	Manjra Valley
Elephas sp.	Mandible	MNJ/809/DC	Harwadi	Manjra Valley
Elephas sp.	Radius	MNJ/980/DC	Harwadi	Manjra Valley
Equus namadicus	Cranium	MNJ/1000/DC	Harwadi	Manjra Valley
Hexaprotodon sp.	Canine	MNJ/957/DC	Harwadi	Manjra Valley
Hexaprotodon sp.	Incisor	MNJ/850/DC	Harwadi	Manjra Valley
Hexaprotodon sp.	Incisor	MNJ/1008/DC	Harwadi	Manjra Valley
Rhinoceros unicornis	Mandible	MNJ/983/DC	Harwadi	Manjra Valley
Rhinoceros unicornis	Molar	MNJ/967/DC	Harwadi	Manjra Valley
Crocodylus palustris	Maxilla	MNJ/15/DC	Tadula	Manjra Valley
Elephas sp.	Tusk	MNJ/807/DC	Tadula	Manjra Valley
Crocodylus palustris	Maxilla	NMD/23/DC	Talayyagha	Narmada Valley
Hexaprotodon sp.	Mandible	NMD/1341/DC	Talayyagha	Narmada Valley
Trionyx sp.	Carapace	NMD/490/DC	Talayyagha	Narmada Valley
Elephas sp.	Scapula	WDH/28/DC	Jhola	Wardha Valley
Elephas sp.	Tusk	WDH/25/DC	Jhola	Wardha Valley

Table 3. Different categories of taxonomic and chronological uncertainty associated with proposed representatives of the late Quaternary Indian megafaunal extinction event.

Taxon	**Potential confusion with other (putative/valid) extinct Late Pleistocene species?**	**Potential confusion of material with extant species?**	**Possible "ancestral form" (chronospecies) of extant species?**	**Direct terminal Pleistocene dates available?**
Palaeoloxodon namadicus	Yes	Yes	—	—
Stegodon sp.	Yes	Yes	—	—
Rhinoceros spp.	Yes	Yes	Yes	—
Equus namadicus	Yes	Yes	Yes?	—
Hexaprotodon sp.	Yes	—	—	Yes? (questionable)
Bos [*primigenius*] *namadicus*	Yes	Yes	Yes	—
Bubalus [*arnee*/*bubalis*] *palaeindicus*	Yes	Yes	Yes	—
Sus "palaeindicus"	Yes	Yes	Yes	—
Crocodylus palaeindicus	—	Yes	Yes	—