

**Figure 1.** Scatter plot for fruit weight (g) and *B. dorsalis* oviposition punctures (#) in three mango varieties.

Theoretically, for a female fruit fly with multiple ovipositions on a single fruit, it is biologically advantageous to oviposit in a fruit with more pulp as more eggs can be laid for a unit of food resource (pulp) available to the maggots, spending lesser amount of time and energy. But this assumption was not true.

The objective of this study was to see whether fruit exploitation for oviposition varied with quantum (weight of fruit pulp). The results of the study indicate that in all the three varieties, oviposition by fruit flies was not influenced by the quantum (= weight) of the fruit pulp of mango. This does not exclude the role of other visual or olfactory cues. The plausible issue for a gravid polyphagous female seemed to be selecting a suitable host tree (mango) first and then to randomly oviposit within a host on an unlimited resource – fruits in this case, which on an average is 200–1000/mango tree, depending on the age of the orchard. So, we infer that fruit flies have a random selection of mango fruits for oviposition irrespective of fruit weight, either due to the incapability of discriminating a higher volume of visual or olfactory cues, expected in heavier fruits, or the fact that two ‘small’ fruits are as good as one ‘big’ fruit in a resource-unlimited situation, as in a typical mango orchard. So, for *B. dorsalis* to adapt a non-random ovipositional strategy once a host is selected does not confer any additional advantage. Thus, every fruit on a tree has equal probability of being selected by the fruit fly for oviposition. This was true for all three varieties chosen for the study and commercially speaking, every fruit is equally vulnerable to attack by fruit flies.

1. Jayanthi, P. D. K., Verghese, A. and Sreedevi, K., Effect of ovipositional duration on pupal recovery, adult emergence and sex ratio of mango fruit fly, *Bactrocera dorsalis* (Hendel). *Insect Environ.*, 2001, 6(4), 147–148.
2. White, I. M. and Harries, E. M. M., *Fruit Flies of Economic Significance: Their Identification and Bionomics*, CAB International, Wallingford, UK, and The Australian Center for Agricultural Research, Canberra, Australia, 1992, p. 601.
3. Kapoor, V. C., *Indian Fruit Flies*, International Science Publisher, New York, 1993, p. 228.

4. Price, P. W., Strategies for egg production. *Evolution*, 1974, 28, 76–84.
5. Jayanthi, P. D. K. and Verghese, A., A simple and cost-effective mass rearing technique for the tephritid fruit fly, *Bactrocera dorsalis* (Hendel). *Curr. Sci.*, 2002, 82(3), 266–268.
6. Verghese, A., Tandon, P. L. and Stonehouse, J. M., Economic evaluation of the integrated management of the Oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae) in mango in India. *Crop Prot.*, 2004, 23, 61–63.
7. Little, T. M. and Hills, F. J., *Agricultural Experimentation: Design and Analysis*, Wiley, New York, 1978.
8. Verghese, A., Madhura, H. S., Jayanthi, P. D. K. and Stonehouse, J. M., Fruit flies of economic significance in India with special reference to *Bactrocera dorsalis* (Hendel). In Proceedings of the 6th International Symposium on Fruit Flies of Economic Importance, Stellenbosch, South Africa, 6–10 May 2002, pp. 317–324.
9. Greenberg, S. M., Sappington, T. W., Setamou, M. and Coleman, R. J., Influence of different cotton fruit sizes on boll weevil (Coleoptera: Curculionidae) oviposition and survival to adulthood. *Environ. Entomol.*, 2004, 33, 443–449.
10. Prokopy, R. J., Green, T., Wong, T. T. Y. and McInnis, D. O., Influence of experience on acceptance of artificial oviposition substrates in *Ceratitidis capitata*. *Hawaii. Entomol. Soc.*, 1990, 30, 91–95.

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## The longest tusk of cf. *Anancus sivalensis* (Proboscidea, Mammalia) from the Tatrot Formation of the Siwaliks, Pakistan

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**This communication reports the first discovery of a well-preserved tusk in the Siwaliks, which is assigned to species cf. *Anancus sivalensis*. The tusk, with a length of 271.8 cm (8 ft 11 in), was excavated from Late Pliocene sediments of Tatrot village (northern Pakistan), which are part of the Tatrot Formation of the Upper Siwaliks and range in age from 3.4 to 2.6 Ma. Such a long tusk is hitherto unknown from the**

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**Siwalik sediments, and also is the longest tusk found to date in South Asia.**

**Keywords:** *Anancus sivalensis*, Proboscidean fossil, Tatrot Formation, tusk.

THE mid-Pliocene Tatrot Formation in northern Pakistan has produced substantial proboscideans with other taxa (Table 1). Other areas of Pakistan have also yielded proboscidean fossils, including Azad Kashmir, Murree Hills, Kohat, the hilly areas of the Dehra Ghazi Khan division, Bugti Hills in Baluchistan, Muslim Bagh in the southern part of the Bolan, and the district Dadu of Sind<sup>1</sup>. In addition, a piece of tusk has also been recovered from the Karimabad in Hunza Valley (Gilgit), northern Pakistan<sup>1</sup>.

The earliest record of proboscidean fossils in the Siwaliks goes back to the 17th century. Nevertheless, true scientific study on proboscidean fossils started later, around the middle of the 19th century<sup>2,3</sup>. A number of European and American researchers have described proboscidean fossils from Pakistan. Of these, it is worth mentioning the works of Falconer<sup>3-23</sup>.

In 2004, a team of palaeontologists from Punjab University, Lahore, on a routine winter excavation field trip from Tatrot village to Kakrala village (Figure 1), came across a partially exposed tusk buried horizontally in brown-grey siltstone. The tusk (PUPC 04/15) is now housed in the Abu Bakr Fossil Display and Research Centre of the Zoology Department, Punjab University, Lahore, Pakistan.

The aim of this communication is to describe and identify this tusk, the longest recovered to date from the Siwaliks of Pakistan. It is also one of the best-preserved elephantoid specimens in Pakistan and should consequently be described in detail.

Tatrot village lies in the Tatrot Formation of the Upper Siwaliks and is situated at about 70 km west of Jhelum city in the Potwar Plateau of northern Pakistan (Figure 1). The type locality is along the road from Gali Jagir to Sihal, north of the Soan river (32°22'N, 72°47'E), District Chakwal, the Punjab Province, Pakistan. The average thickness of the sediments of the Formation in the type locality is 300 m. The Tatrot Formation is composed of pale pinkish-orange-brown, clays, brown-grey siltstone and shale, greenish-grey, fine to medium-grained sandstone, and interbedded dark grey conglomerates<sup>24</sup>.

As the Upper Siwalik sediments of the Indian subcontinent span from the Late Pliocene to the Middle Pleistocene, ca. 3.3–0.6 Ma (Figure 1), they are considered as one of the longest fluvial sequences of their age in the world<sup>23,25</sup>. Medlicott<sup>26</sup> was the first to refer to this rock sequence as 'Upper Siwaliks', while Pilgrim<sup>9</sup> used the name 'Tatrot and Pinjor Stage/Zone' for this Formation. Finally, Kravtchenko<sup>27</sup> used the term 'Soan Formation' (Figure 1), which was later officially formalized by the Stratigraphic Committee of Pakistan<sup>28</sup>. Hussain *et*

*al.*<sup>29</sup> suggested that the Tatrot Formation might be older than previously thought and could be in the lower part of the Gauss magnetic zone, between 3.2 and 3.4 My. Barry *et al.*<sup>16</sup> suggested an age for the Tatrot Formation between 3.5 and 3.3 My. More recently, biostratigraphically, Dennell *et al.*<sup>30</sup> and Nanda<sup>31</sup> placed the upper boundary of the Tatrot Formation between 2.4 and 2.6 My. Thus, the Tatrot Formation roughly corresponds to the latest Pliocene (Figure 1).

The order Proboscidea originated in Africa, but spread all over the world during the Neogene and represented a diverse group of mammals, especially in Europe<sup>32</sup>. Proboscideans are known in Europe since the Early Miocene; their invasion from Africa and subsequent expansion in Europe and Asia during the Early Miocene is called the 'Proboscidean Datum Event'<sup>33,34</sup>. In the course of the 'Proboscidean Datum Event', which actually contains multiple immigration events of proboscideans from Africa to Asia and Europe<sup>18</sup>, primitive gomphotheres and mammutids immigrated during the Early Miocene into Asia Minor and southern Asia. First records are documented in Pakistan, Kazakhstan, China and Japan<sup>35</sup> in sediments stratified as or slightly younger than MN4.

The Late Pliocene interval represented at Tatrot by deposits of the Tatrot Formation was a time of dynamic transformation of the Siwalik ecosystem<sup>30</sup> and for the Siwalik proboscideans<sup>1</sup>. Prior to this, a predominance of trilophodont forms, viz. *Protonancus chinjiensis*, *Zygodon metachinjiensis* and *Gomphotherium browni* in the Chinji Formation, and a predominance of choerolophodont and tetralophodont forms, viz. *Choerolophodon corrugatus*, *Paratetralophodon hasnotensis* and *Stegolophodon cautley* in the Dhok Pathan Formation went into precipitous decline, leaving anancine gomphotheres as remnants of a once highly speciose Miocene radiation<sup>1,17</sup>.

A gomphothere *Anancus* was widespread during the Pliocene and persisted until the Early Pleistocene<sup>32</sup>. In Eurasia, the genus was represented by three species: *Anancus arvernensis*, *A. alexeevae* and *A. kazakhstanensis*<sup>36-38</sup>. *A. arvernensis*, known from the Late Miocene–Pliocene of Europe, was large, and had a short and high skull with almost straight tusks about 2–3 m in length. *A. arvernensis* had the longest tusks which reached about 3 m in length in adult animals<sup>39</sup>. *A. alexeevae* was more advanced than *A. arvernensis* and better adapted for the increasing aridity. The species differs from *A. arvernensis* in being smaller sized<sup>36</sup>. *A. kazakhstanensis* (= *A. kazakhstanicus*) was known from Kazakhstan and differs from *A. arvernensis* in a weak development of accessory elements on molars and the lack of cement in the depressions<sup>38</sup>. *Anancus sinensis* is found in the Pliocene of China<sup>40</sup>.

From African deposits, three species of *Anancus* have been recognized according to the molar morphology during Mio–Pliocene: *A. kenyensis* from East and Central Africa; *A. petrocchii* from North and Central Africa<sup>41</sup>

**Table 1.** Various species of the Tatrot Formation in the Indo-Pakistan region<sup>1,20,31,60-64</sup> (M. Akhtar, unpublished)

Proboscidea	<i>Stegodon bombifrons</i> (Falconer & Cautley), 1847 <i>S. insignis</i> (Falconer & Cautley), 1846 <i>Paratetralophodon hasnotensis</i> (Lydekker), 1884 <i>Tetralophodon falconeri</i> Osborn, 1936 <i>Anancus sivalensis</i> (Cautley), 1836 <i>Elephas planifrons</i> Falconer & Cautley, 1845 <i>E. hysudricus</i> Falconer & Cautley, 1846 <i>Stegodon</i> sp.
Artiodactyla	<i>Cervus sivalensis</i> Lydekker, 1880 <i>C. punjabiensis</i> Brown, 1926 <i>C. triplidens</i> Lydekker, 1876 <i>Rucervus simplicidens</i> (Lydekker), 1876 <i>Kobus porrecticornis</i> (Lydekker), 1878 <i>Hydaspicobus auritus</i> Pilgrim, 1939 <i>Antilope cervicapra</i> Linnaeus, 1758 <i>A. subtorta</i> Pilgrim, 1937 <i>Proamphibos lachrymans</i> Pilgrim, 1939 <i>P. kashmiricus</i> Pilgrim, 1939 <i>Bison sivalensis</i> Lydekker, 1878 <i>Selenoportax vexillarius</i> Pilgrim, 1937 <i>Tetraconodon magnus</i> Falconer, 1868 <i>Hippohyus sivalensis</i> Falconer & Cautley, 1840 <i>Sus hysudricus</i> Martin, 1890 <i>S. giganteus</i> Falconer & Cautley, 1847 <i>Propotamochoerus</i> sp. <i>Hexaprotodon sivalensis</i> (Falconer & Cautley), 1880 <i>Camelus sivalensis</i> Falconer & Cautley, 1836
Perissodactyla	<i>Equus sivalensis</i> Falconer & Cautley, 1849 <i>Rhinoceros sivalensis</i> Falconer & Cautley, 1847 <i>R. palaeindicus</i> Falconer & Cautley, 1847
Primates	<i>Ramapithecus brevisrostris</i> Lewis, 1934
Rodentia	<i>Hystrix</i> sp.

(H. T. Mackaye, unpublished) and *A. osiris* from North Africa<sup>42</sup>. These species are mostly differentiated by the number of cone pairs on intermediate molars and the complexity of the third molar (H. T. Mackaye, unpublished).

In the Upper Siwalik deposits of the Indian subcontinent, two species of *Anancus* have been recognized based on the molar morphology: *A. perimensis* from the Indian Siwaliks, Peram Island<sup>43</sup> and *A. sivalensis* from the Pakistani Siwaliks, Tatrot<sup>1</sup>. *A. sivalensis* in Pliocene of the Siwaliks is relatively rare compared to one abundant elephant remains. The problem of poor material is present in the case of comparison with the endemic/Eurasian proboscidean faunas. *A. sivalensis* is the last representative of the Siwalik mastodonts in the Pliocene faunas of Tatrot and it is a typical advanced Late Pliocene Siwalik species<sup>1</sup>. *A. sivalensis* continued to evolve during the Pliocene until its disappearance from the region at the close of the Pliocene or probably early Pleistocene<sup>1</sup>.

#### SYSTEMATICS

Order PROBOSCIDEA Illiger, 1811

Suborder ELEPHANTIFORMES Tassy, 1988

Superfamily ELEPHANTOIDEA Gray, 1821

Family GOMPHOTHERIIDAE Hay, 1922

Subfamily ANANCINAE Hay, 1922

Genus *Anancus* Aymard, 1855

Type species: *Anancus arvernensis* (Croizet and Jobert, 1828).

cf. *Anancus sivalensis* (Cautley), 1836

#### Synonymy

*Mastodon sivalensis* ref. Falconer, 1868

*Pentalophodon sivalensis* (Cautley) Osborn, 1936

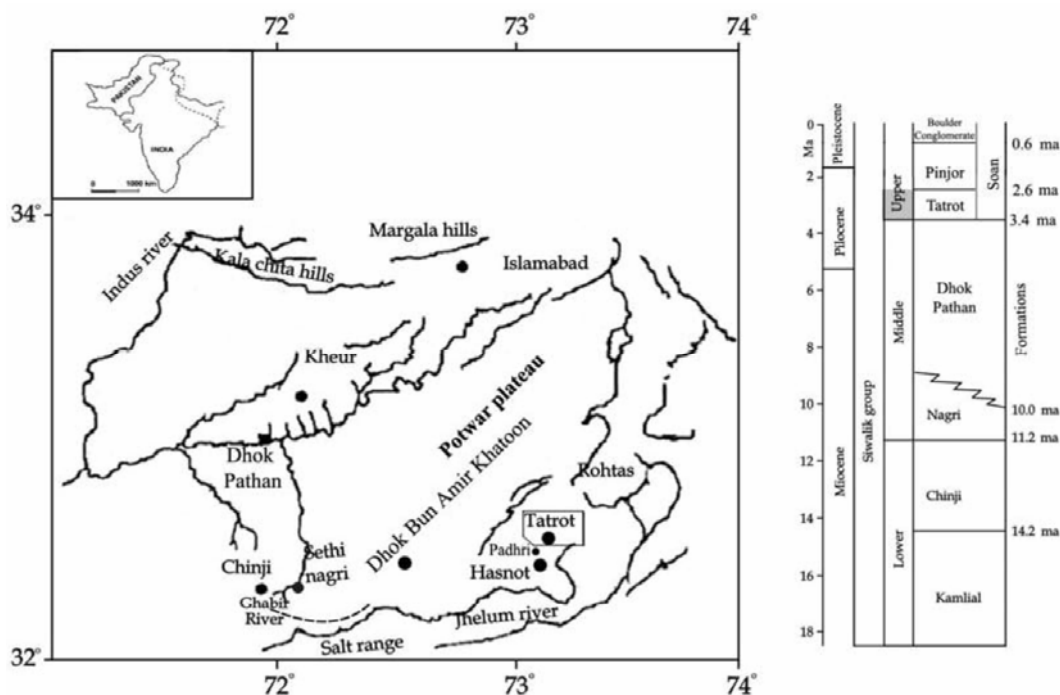
*Pentalophodon falconeri* Osborn, 1936

*Anancus sivalensis* (Cautley) Chakravarti, 1957

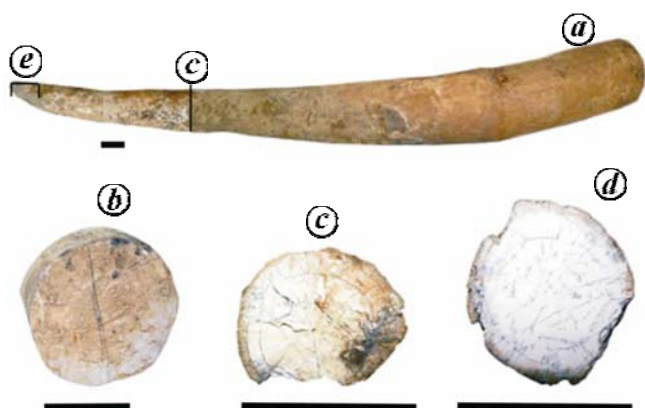
Type specimen: BMNH 2877 (figured by Falconer and Cautley, 1846, pls. xxxii and xxxiii, Figures 1 and 2).

Material: PUPC 2004/15, right tusk (Figure 2).

Locality: The referred specimen comes from the sediments of Tatrot village in the Upper Siwaliks (Tatrot Formation) of Pakistan (Figure 1).



**Figure 1.** Map of the Potwar Plateau encircling the study area and a generalized stratigraphic section of the major Siwalik formations.



**Figure 2.** PUPC 2004/15 tusk: *a*, Complete tusk; *b*, Posterior view; *c*, Cross-section in original condition (marked from where the cross-section is taken); *d*, Cross-section and *e*, Reconstructed part. Scale bar = 10 cm.

Diagnosis: Incisive tusks are very long, almost straight and slender, and distinguish *Anancus* from other proboscideans. The radius of curvature of the Schreger lines is constant and the angle is acute. There are no lower tusks, and the symphyseal region is brevirostrine. Crown height of tetralophodont intermediate molar (M2) progressively increases from anterior to posterior. Enamel in deciduous teeth is grooved, ptychoid or plicated externally. True molar cusps are simple and smooth, with anteroposterior compression. Cusps are straight but forwardly inclined and alternating progressively. Posterior central pretrite conule reduced on upper molars. Reduction of the anterior central pretrite conule on the lower molars and fusion

with the mesoconelet. Alternation of the pretrite and posttrite half-loph(id)s (anancyoidy), which allows the establishment of an alternative contact of successive loph(id)s<sup>1,43-46</sup>.

The tusk is very long, almost straight and slender, lightly curved upward distally. It is one of the best preserved tusks of the Siwaliks. The tusk is broken at the tip of the anterior end, which has been reconstructed with cementing material. The exact missing part of the tusk is not known, but by observing its anterior conical end it is possible that more than 11 cm might have been lost (Figure 2). There are at least 37 first-order increments in the tusk, implying that the minimum age of the animal was at least 37 years at death.

The length of the tusk is 271.8 cm and its diameter ranges from 4.3 cm distally to 17.2 cm proximally. The maximum circumference of the tusk is 54.1 cm and the minimum circumference is 13.51 cm. The maximum width of the tusk is 16.55 cm, at about 219.45 cm from its tip. A transverse section of the tusk with a diameter of 9.7 cm has been cut to observe the Schreger lines. The transverse section is approximately circular. It has been observed that the bending radius of the Schreger lines seems constant and acute displaying ‘C’ and ‘X’ patterns (Figure 2 *d*).

The large size of the studied tusk associates it with large-tusked proboscideans (*Elephas*, *Loxodonta*, *Anancus*, *Mammuthus*, *Stegotetralodon*) in distinction to small-tusked proboscideans (*Deinotherium*, *Platybelodon*, *Ambelodon*, *Serbelodon*)<sup>47,48</sup>. *Gomphotherium* tusks are different from the studied form in being flattened with

continuous bands of enamel along the lateral surfaces<sup>48,49</sup>. *Stegotrabelodon* tusks are also different in their flat section<sup>50</sup>, while the tusks are large, more massive and curved in mammoth showing a double curvature generally more accentuated than in *Elephas* and *Loxodonta*<sup>51</sup>. Nevertheless, *Loxodonta* and *Elephas* tusks differ from the studied tusk in having moderate bend and torsion<sup>52</sup>. The studied tusk shows similar morphological characters with that of *Anancus*, in which the tusks are straight and elongated<sup>39,43,44</sup>.

Comparison with Schreger lines also indicates differences in various proboscidean forms. The morphology of these lines differs among proboscidean taxa, offering a useful discriminating character. Schreger lines are visible in tusk cross-sections as intersecting spiral lines (Figure 2c and d). The angles formed by the intersecting lines near the periphery of the cross-section are most often used for identification<sup>46,53</sup>. *Loxodonta* and *Elephas* are distinguished by possessing larger Schreger angles. Unlike the studied form, mammoths have 'V' pattern of Schreger lines, whereas *Elephas* lack the 'V' pattern but the angle values are as high as 120°. In *Elephas* these angles are well obtuse; in *Mammut* they reach the maximum value of more than 100° about halfway between the pulp cavity and the dentinel cement junction; in *Anancus* the angles are acute<sup>46,53</sup> (Figure 2d). The 'C' and 'X' patterns of Schreger lines (Figure 2d) of the studied tusk are clearly different from those of the '*Loxodonta–Elephas*' group and similar to the pattern observed in the 'Mastodons' group<sup>46,53</sup>. The acute angles formed by the Schreger lines near the dentinel cement junction in the studied tusk suggest an attribution to *Anancus*. Nevertheless, considering the above morphological data, the proboscidean tusk from Tatrot certainly represents *Anancus*.

The Late Pliocene deposits of Tatrot represent only a single species of *Anancus*, *A. sivalensis*<sup>1</sup>. The large size, circular cross-section and acute Schreger lines with constant bending radius of the described specimen indicate that it probably can be assigned to *A. sivalensis*<sup>1,39,43,46</sup>. Tusks of *A. sivalensis* have not been recorded previously; so no further comparison with the studied form is possible. Lack of numerous specimens and some diagnostic features hamper closer identification than cf. *A. sivalensis*. The large diameter of the tusk also indicates that it probably belongs to a large male individual which ranged the mid-to-late Pliocene territories of the Siwaliks<sup>1,40</sup>.

A number of specimens from the late Pliocene of the Siwaliks have been referred to as *Anancus*. Originally, *A. sivalensis* was named *Pentalophodon sivalensis*<sup>43</sup> and later was placed in the genus *Anancus* by Chakravarti<sup>12</sup>. The determination of *A. sivalensis* was based upon a fragmentary right lower third molar formerly designated by Cautley<sup>4</sup> as *Mastodon sivalensis*. Later, Sarwar<sup>1</sup> described a small tooth fragment (PUPC 67/290, formerly as UZ 67/290, fig. 45) of *A. sivalensis* from Kakrala (Tatrot Formation).

The genus *Anancus* arose in the late Miocene and was present all around Europe, including England<sup>43</sup>. It was also present throughout Africa<sup>45,54,55</sup>, but remained low in numbers. In Asia, it was abundant in Pakistan<sup>1,43</sup>, China<sup>40,56</sup> and Japan<sup>57</sup>. By the late Pliocene, the archaic forms had disappeared and the crown genus had undergone episodes of evolutionary change, evidenced by parallel acquisition of enhanced cranio-dental specializations for grazing<sup>58</sup>. The middle/late Pliocene transition is correlated with global cooling and a considerable increase in aridity (marked by the most ancient loess formations in Pakistan, Tajikistan, Uzbekistan, etc.). Along with other environmental changes, these events led to a wide occurrence of inhabitants (elephants, horses, rhinoceroses, ruminants) of open woodlands and grasslands in the temperate latitudes of Eurasia<sup>59</sup>.

*A. sivalensis* was coincident or nearly contemporaneous with the first appearance of the crown elephant genus *Elephas*<sup>1</sup>. During the late Pliocene, *A. sivalensis* coexisted with elephants in the Indo-Siwaliks. Other taxa, including rhinos, hypsodont equids, reduncines, antilopes and bovines<sup>60</sup> (M. Akhtar, unpublished), are suggestive of more open conditions at Tatrot during the time of deposition of the Tatrot Formation. Reduncines and *Antilope* inhabit savanna, woodland and grassland<sup>22</sup>. The abundance of antelopes indicates a mixture of woodland and grassland biomes. The presence of deer usually points towards a forested environment (Table 1). This observation suggests a more open habitat in Tatrot, and probably indicates a mixed or woodland environment for the Tatrot Formation of the Upper Siwaliks during the Pliocene–Pleistocene.

1. Sarwar, M., Taxonomy and distribution of the Siwalik Proboscidea. *Bull. Dep. Zool. Univ. Punjab, new series*, 1977, **10**, 1–172.
2. Hussain, S., Revision of *Hipparion* (Equidae, Mammalia) from the Siwalik Hills of Pakistan and India. *Veslag Bayer Akad. Swiss, new series*, 1971, **147**, 1–68.
3. Falconer, H., Palaeontological Memoirs and Notes of the Late Hugh Falconer, 1868, **1**, 1–590; 1868, **2**, 1–675.
4. Cautley, P., Note on the teeth of the *Mastodon* a dents étroites of the Siwalik Hills. *J. Asiat. Soc. Bengal*, 1836, **5**, 294–296.
5. Lydekker, R., Additional Siwalik Perissodactyla and Proboscidea. *Mem. Geol. Surv. India*, 1884, **10**(3), 1–34.
6. Lydekker, R., Indian Tertiary and Post-Tertiary vertebrate Siwaliks. Mammalia. *Palaeontol. Indica* (Suppl. I), 1886, **10**(4), 1–22.
7. Lydekker, R., The Fossil Vertebrata of India. *Rec. Geol. Surv. India*, 1887, **20**, 51–79.
8. Lydekker, R., Notes on Indian fossil Vertebrata. *Rec. Geol. Surv. India*, 1888, **21**, 145–146.
9. Pilgrim, G., Notices of new mammalian genera and species from the Tertiaries of India – Calcutta. *Rec. Geol. Surv. India*, 1910, **40**, 63–71.
10. Pilgrim, G., The vertebrate fauna of the Gaj Series in the Bugti Hills and the Punjab. *Palaeontol. Indica, New Series*, 1912, **4**, 1–83.
11. Pilgrim, G., Correlation of the Siwaliks with Mammal Horizons of Europe. *Rec. Geol. Surv. India*, 1913, **XLIII**, 264–326.

12. Chakravarti, D., A geological, palaeontological and phylogenetic study of the Elephantoidea of India, Pakistan and Burma: Part 1, Gomphotheriidae. *J. Paleontol. Soc. India*, 1957, **2**, 83–94.
13. Pilbeam, D. *et al.*, Geology and palaeontology of Neogene strata of Pakistan. *Nature*, 1977, **270**, 684–689.
14. Pilbeam, D., Behrensmeyer, A., Barry, J. and Shah, S., Miocene sediments and faunas of Pakistan. *Postilla*, 1979, **179**, 1–45.
15. Pilbeam, D., Morgan, M., Barry, J. and Flynn, L., European MN units and the Siwalik faunal sequence of Pakistan. In *The Evolution of Western Eurasian Neogene Mammal Faunas* (eds Bernor, R. L., Fahlbusch, V. and Mittmann, H.-W.), Columbia University Press, New York, 1996, pp. 96–105.
16. Barry, J. *et al.*, Faunal and environmental change in the Late Miocene Siwaliks of northern Pakistan. *Paleobiology*, 2002, **28**, 1–72.
17. Tassy, P., Les Elephantoidea Miocènes du Plateau du Potwar, Groupe de Siwalik, Pakistan. *Ann. Paléontol.*, 1983, **69**(4), 317–354.
18. Tassy, P., The 'Proboscidean Datum Event'. How many proboscideans and how many events? In *European Neogene Mammal Chronology* (eds Lindsay, E. H., Fahlbusch, V. and Mein, P.), Plenum Press, New York, 1990, pp. 237–252.
19. Shoshani, J. and Tassy, P., *The Proboscidea: Evolution and Palaeoecology of Elephants and their Relatives*, Oxford University Press, Oxford, 1996.
20. Nanda, A. C., Upper Siwalik mammalian faunas of India and associated events. *J. Asian Earth Sci.*, 2002, **21**, 47–58.
21. Antoine, P. O., Welcomme, J. L., Marivaux, L., Baloch, I., Benammi, M. and Tassy, P., First record of Paleogene Elephantoidea (Mammalia, Proboscidea) from the Bugti Hills of Pakistan. *J. Vertebr. Palaeontol.*, 2003, **23**(4), 978–981.
22. Basu, P. K., Siwalik mammals of the Jammu Sub-Himalaya, India: an appraisal of their diversity and habitats. *Quat. Int.*, 2004, **117**, 105–118.
23. Dennell, R., Coard, R. and Turner, A., The biostratigraphy and magnetic polarity zonation of the Pabbi Hills, northern Pakistan: an Upper Siwalik (Pinjor Stage) Upper Pliocene–Lower Pleistocene fluvial sequence. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 2006, **234**, 168–185.
24. Shah, S., Stratigraphy and economic geology of Central Salt Range. *Rec. Geol. Surv. Pakistan*, 1980, **52**, 1–104.
25. Behrensmeyer, A. and Barry, J., Biostratigraphic surveys in the Siwaliks of Pakistan. A method for standardized surface sampling of the vertebrate fossil record. *Palaeontol. Electron.*, 2005, **8**(1), 1–24.
26. Medlicott, H., On the geological structure and relations of the southern portion of the Himalayan range between the Rivers Ganges and Ravee. *Mem. Geol. Surv. India*, 1864, **3**, 1–67.
27. Kravtchenko, K., Soan Formation upper unit of Siwalik group in Potwar. *Sci. Ind.*, 1964, **2**(3), 230–233.
28. Shah, S. M. I., Stratigraphy of Pakistan. *Mem. Geol. Surv. Pak.*, 1977, **12**, 1–138.
29. Hussain, S. *et al.*, Biostratigraphy of the Plio–Pleistocene continental sediments (Upper Siwaliks) of the Mangla–Samwal anticline, Azad Kashmir, Pakistan. *Proc. K. Ned. Akad. Wet., Ser. B*, 1992, **95**, 65–80.
30. Dennell, R. W., Coard, R. and Turner, A., Predators and scavengers in Early Pleistocene southern Asia. *Quat. Int.*, 2008, **192**, 78–88.
31. Nanda, A. C., Comments on the Pinjor mammalian fauna of the Siwalik Group in relation to the Post-Siwalik faunas of Peninsular India and Indo-Gangetic Plain. *Quat. Int.*, 2008, **192**, 6–13.
32. Göhlich, U. B., Order Proboscidea. In *The Miocene Land Mammals of Europe* (eds Rössner, G. and Heissig, K.), Friedrich Pfeil Verlag, Munich, 1999, pp. 157–168.
33. Berggren, W. A. and Van Couvering, J. A., The late Neogene: Biostratigraphy, geochronology and paleoclimatology of the last 15 million years in the marine and continental sequences. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 1974, **16**, 1–216.
34. Madden, C. T. and Van Couvering, J. A., The Proboscidean datum event: Early Miocene migration from Africa. *Geol. Soc. Am., Abstr. Programs*, 1976, **8**, 992–993.
35. Tassy, P., The earliest gomphotheres. In *The Proboscidea. Evolution and Palaeoecology of Elephants and their Relatives* (eds Shoshani, J. and Tassy, P.), Oxford University Press, New York, 1996, pp. 89–91.
36. Bajgusheva, V. S., Fossil Theriofauna of the Liventzovka sandpit. *Trans. Zool. Inst.*, 1971, **49**, 5–29.
37. Alekseeva, L. I., Early Anthropogene Theriofauna of eastern Europe. *Science*, Moscow, 1977, vol. 42, pp. 117–134.
38. Tleuberina, P. A., Late Neogene fauna of south-eastern Kazakhstan. *Science*, Alma-Ata, 1982, vol. 47, pp. 86–90.
39. Theodorou, G., Spjeldnaes, N., Hanken, N., Lauritzen, S., Velitzelos, E., Athanassiou, A. and Roussiakis, S., Description and taphonomic investigations of Neogene Proboscidea from Rhodes, Greece. *Ann. Geol. Pays Helleniques*, 2000, **38**, 133–156.
40. Hsieh, H., Notes on two new brevirostrine mastodonts from Shansi. *Vertebr. Palasiat.*, 1962, **6**, 88–108.
41. Tassy, P., Les Proboscidiens (Mammalia) Fossiles du Rift occidental, Ouganda. In: *Geology of the Albertine Rift Valley, Uganda–Zaire*, *Palaeobiology*. CIFEG Occasionally Publication, Orléans, 1994(II), pp. 217–257.
42. Geraads, D. and Metz-Muller, F., Proboscidea (Mammalia) du Pliocène final d'Ahl al Oughlam (Casablanca, Maroc). *Neues Jahrb. Geol. Paläontol.*, 1999, **1**, 52–64.
43. Osborn, H., *Proboscidea, Vol. I*. The American Museum of Natural History Press, New York, 1936, pp. 1–802.
44. Hautier, L., Mackaye, H. T., Lihoreau, F., Tassy, P., Vignaud, P. and Brunet, M., New material of *Anancus kenyensis* (Proboscidea, Mammalia) from toros-menalla (Late Miocene, Chad): Contribution to the systematics of African anancines. *Afr. Earth Sci.*, 2009, **53**(2–5), 171–176.
45. Tassy, P., Nouveaux Elephantoidea (Mammalia) dans le Miocène du Kenya. *Cahiers de Paleontologie*, Éditions du Centre de la Recherche Scientifique, Paris, 1986, pp. 1–135.
46. Palombo, M. and Villa, P., Schreger lines as support in the Elephantinae identification. In *The World of Elephants – International Congress, Rome, 2001*, vol. 2, pp. 656–660.
47. Göhlich, U. B., Oligocene–Miocene vertebrates from the valley of lakes (Central Mongolia): Morphology, phylogenetic and stratigraphic implications. *Ann. Naturhist. Mus. Wien A*, 2007, **108**, 271–289.
48. Göhlich, U. B., The Proboscidea (Mammalia) from the Miocene of Sandelzhausen (southern Germany). *Palaeontology (Zurich)*, 2010, **84**, 163–204.
49. Fox, D. L., Growth increments in *Gomphotherium* tusks and implications for late Miocene climate change in North America. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 2000, **156**, 327–348.
50. Ferretti, M. P., Torre, D. and Rook, L., The *Stegotrabelodon* remains from Cessaniti (Calabria, Southern Italy) and their bearing on late Miocene biogeography of the genus. In *Proceedings of the First International Congress of La Terra degli Elefanti, The World of Elephants* (eds Cavarretta, G. *et al.*), Consiglio Nazionale delle Ricerche, Roma, 2001, pp. 633–636.
51. Palombo, M. and Ferretti, M. P., Elephant fossil record from Italy: knowledge, problems, and perspectives. *Quat. Int.*, 2005, **126–128**, 107–136.
52. Doukas, C. S. and Athanassiou, A., Review of the Pliocene and Pleistocene Proboscidea (Mammalia) from Greece. *Deinsea*, 2003, **9**, 97–110.
53. Trapani, J. and Fisher, D. C., Discriminating proboscidean taxa using features of the Schreger pattern in tusk dentin. *J. Archaeol. Sci.*, 2003, **30**, 429–438.

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54. Macinnes, D., Miocene and Post-Miocene Proboscidea from East Africa. *Trans. Zool. Soc., London*, 1942, **25**, 33–106.
55. Sanders, W. J., Taxonomic review of fossil Proboscidea (Mammalia) from Langebaanweg, South Africa. *Trans. R. Soc. South Afr.*, 2007, **62**, 1–16.
56. Hopwood, A., Fossil Proboscidea from China. *Palaeontol. Sin.*, 1935, **3**, 1–108.
57. Shikama, T., The first discovery of *Pentalophodon* from Japan. *Proc. Imp. Acad., Tokyo*, 1936, **12**, 292–295.
58. Cerling, T. E., Harris, J. M., MacFadden, B. J., Leakey, M. G., Quade, J., Eisenmann, V. and Ehleringer, J. R., Global vegetation change through the Miocene/Pliocene boundary. *Nature*, 1997, **389**, 153–158.
59. Vislobokova, I., On Pliocene faunas with Proboscideans in the territory of the former Soviet Union. *Quat. Int.*, 2005, **126–128**, 93–105.
60. Pilgrim, G. E., The fossil Bovidae of India. *Palaeontol. Indica*, 1939, **26**, 1–356.
61. Colbert, E. H., Siwalik mammals in the American Museum of Natural History. *Trans. Am. Philos. Soc., New Series*, 1935, **26**, 1–401.
62. Pilgrim, G. E., Siwalik antelopes and oxen in the American Museum of Natural History. *Bull. Am. Mus. Nat. Hist.*, 1937, **72**, 729–874.
63. Khan, M. A., Iliopoulos, G. and Akhtar, M., Boselaphines (Artiodactyla, Ruminantia, Bovidae) from the Middle Siwaliks of the Hasnot, Pakistan. *Geobios*, 2009, **42**, 739–753.
64. Khan, M. A., Kostopoulos, D. S., Akhtar, M. and Nazir, M., *Bison* remains from the Upper Siwaliks of Pakistan. *Neues Jahrb. Geol. Paläontol.*, 2010, **258**(1), 121–128.

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