

## Identification of proboscidean tusk from the Plio-Pleistocene transition of the Pekecik Section, Eastern Turkey

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**ABSTRACT.** A fragment of proboscidean tusk from Pekecik (Plio-Pleistocene transition), Turkey, was studied to ascertain its taxonomic identification and biostratigraphic signal. Characteristic properties of the dentine (Schreger structures) were measured along the transversal and longitudinal sections. Schreger angles showed an increasing range from the tusk axis to the cement-dentine junction (CDJ) with values ranging from 61–109°. The variability of the qualitative Schreger pattern from the “X” type near the tusk axis to the “V” type at the cement-dentine junction (CDJ), were recorded. The wavelength of dentinal tubules showed a decreasing trend from 1.67 mm near the axis to 1.0 mm near the CDJ. Based on these properties, the specimen was compared with already published data and is tentatively assigned to a meridionaloid elephant cf. *Archidiskodon* sp. In our research, we conclude that the tusk microstructure features are a practical means of taxonomic study.

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## Идентификация бивня хоботного с плио-плейстоценовой границы в разрезе Пекеджик, Восточная Турция

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Я.И. Трихунков, Х. Челик

**РЕЗЮМЕ.** Фрагмент бивня хоботного из Пекеджика (переход от плиоцена к плейстоцену), Турция, был изучен для определения его таксономического статуса и биостратиграфического сигнала. Характерные свойства дентина (структуры Шрегера) измеряли на поперечном и продольном сечениях. Значения углов Шрегера увеличиваются от полости бивня до соединения цемент-дентин (CDJ) со значениями в пределах 61–109°. Отмечена изменчивость узора Шрегера от “V” типа в районе оси бивня до “X” типа в месте перехода цемента к дентину (CDJ). Длина волны дентиновых канальцев показывает тенденцию к уменьшению от 1,67 мм около оси до 1,0 мм около CDJ. На основании этих свойств образец был сопоставлен с уже опубликованными данными и предварительно отнесен к меридионалоидному слону cf. *Archidiskodon* sp. В своем исследовании мы пришли к выводу, что изучение особенностей микроструктуры бивня является перспективным методом таксономического определения хоботных.

**КЛЮЧЕВЫЕ СЛОВА:** четвертичный период, плиоцен, хоботное, бивень, структуры Шрегера, *Mammuthus*, *Archidiskodon*, CDJ.

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## Introduction

The mammalian order Proboscidea has shown a continuous evolutionary pattern since the Paleogene period (Osborn, 1936, 1942; Gheerbrant, 2009; Cantalapiedra *et al.*, 2021). From major physical features to minor internal structures, all have gone under a systematic nature of evolution. Although proboscideans have been studied since the early 17<sup>th</sup> century, tusks in the Proboscidea remain relatively less used for taxonomic identification. Tusks are an enlarged pair of incisors that keep growing throughout the lifetime of the individual (Espinoza & Mann, 1991; Ábelová, 2008).

The most distinguishing features of the proboscidean tusk's internal structure are the Schreger lines, which are seen in both the cheek teeth and tusks but are better developed in the latter (Espinoza & Mann, 1991). German scientist Bernhard Schreger (1800) first described these features (see also Koenigswald & Sander, 1997 and Lynch *et al.*, 2010). The lines are visually evident through the naked eye in the transversal cross-section of the tusk. The Schreger pattern consists of sets of intersecting lines radiating in a spiral fashion from the tusk axis (Miles & White, 1960; Trapani & Fisher, 2003). Espinoza & Mann (1991) described this structure as the engine turnings or Schreger Pattern. These intersecting dextral and sinistral lines form an angle of intersection, which is referred to as the Schreger angle (Fig. 1).

During the Plio-Pleistocene period, two major groups of extinct proboscideans from Eastern Turkey are known, belonging to southern elephant *Archidiskodon meridionalis* ssp. and bunodont mastodon *Anancus arvernensis* ssp. (Bernor & Lipscomb, 1991; Albayrak & Lister, 2012; Mayda *et al.*, 2014).

Another fossil elephant from Eastern Turkey, a partial skeleton assigned to *Mammuthus trogontherii*, originating from much younger, late Early Pleistocene deposits near Pasinler, has also been recorded (Dayan, 1985; Vasilyan *et al.*, 2014). No remains of large mam-

mals have been previously known from the Pekecik sequence. Therefore, this study is of importance for the paleontological grounding of regional stratigraphy.

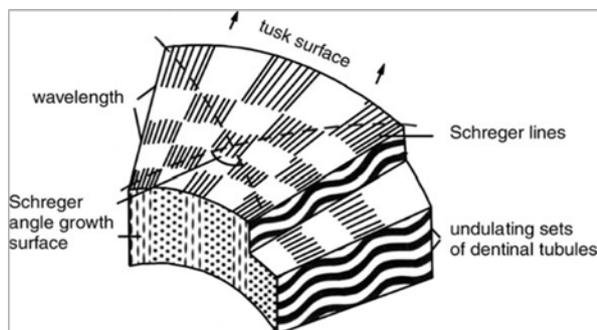
There are disagreements in the scientific community regarding the placement of species of meridionaloid elephants. Some researchers place it under the broad genus *Mammuthus* (Maglio, 1973; Lister, 1993, 1996; Palombo & Ferretti, 2005, and others). But in this paper, the authors have referred to the Late Pliocene and Early Pleistocene southern (meridionaloid) elephants under the genus *Archidiskodon*, a separate identity from the geologically subsequent Middle-Late Pleistocene genus *Mammuthus* based on distinct differences between the cranial, dental, and postcranial morphological attributes of the two genera of this family (Garutt *et al.*, 1977; Garutt, 1986, 1998; Titov, 2008; Baygusheva & Titov, 2012; Baigusheva *et al.*, 2016).

Concurrently, straight-tusked elephant *Palaeoloxodon* is also puzzled by different opinions about its nomenclature. Here, the authors restrict their comparisons to published tusk properties for European *Palaeoloxodon* and refer to the genus as stated (Aguirre, 1969; Palombo & Villa, 2001; Palombo *et al.*, 2017; Larramendi *et al.*, 2020).

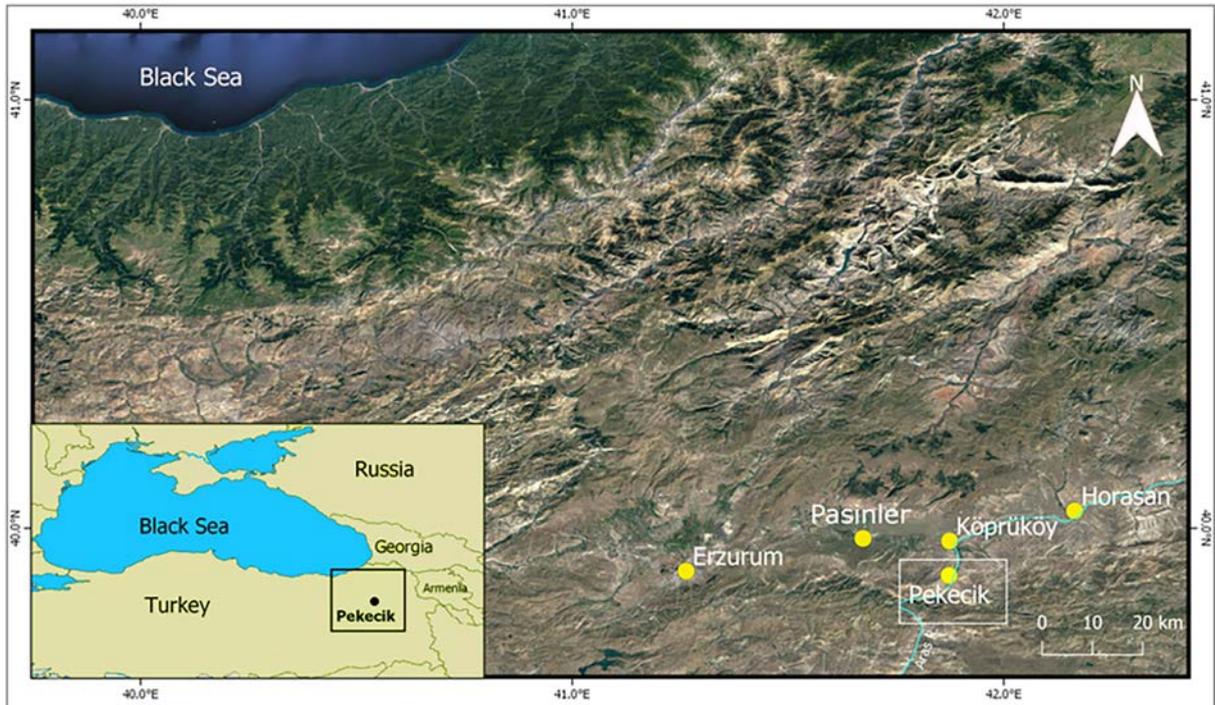
In this paper, we attempt to study features of the Schreger lines as observed on an isolated fragment of a fossil proboscidean tusk from Pekecik, Eastern Turkey, thereby deciphering its taxonomic identity. Taking into account the age of the locality, the specimen is a rare Plio-Pleistocene elephantid fossil which is important in understanding the void between the European and Central Asian occurrences of elephantids (Wei *et al.*, 2010). Meanwhile, we also appraise whether tusk characteristics are sufficient sources of information for a taxonomic and phylogenetic study amongst fossil proboscideans.

## Geological setting

The tusk sample was excavated from the Late Pliocene–Early Pleistocene transitional deposits (~2.6 Mya) near Pekecik, Erzurum Province, Eastern Anatolia, Turkey (Fig. 2) (Simakova *et al.*, 2021). The stratigraphy of the area was originally overviewed by Irritz (1972). He assigned the Pasinler basin fill to 500 m thick Pekecik beds that are uncomfortably lying on ultrabasic rocks, grading from coarse-grained conglomerates to fine-grained silts, as we move from the base to the upper part of the section. Later, Ünay & de Bruijn (1998) studied small mammal material from lignite-rich deposits near Pekecik brown-coal mine. They assigned the *Miomys–Borsodia* fauna to Late Villanyian, currently Early Pleistocene. The recent revision of the stratigraphy of the Pekecik sedimentary sequence, based on bio-magnetostratigraphic methods, showed its direct correlation to the maximum pulse of the Akchagylian transgression of the Caspian Sea and enabled its assignment to the terminal Late Pliocene close to ~2.6 Mya. The biostratigraphic age of the deposits is based on the small mammal association



**Fig. 1.** Schematic block representation of tusk properties (Schreger lines, dentinal tubules, etc.) in transverse and longitudinal sections. Features like Schreger pattern and Schreger angle are measured from the transverse section, while wavelength is measured along the longitudinal section (after Miles & White, 1960 and Ábelová, 2008).



**Fig. 2.** Location of Pekecik section and the surrounding area in Anatolia, Eastern Turkey.

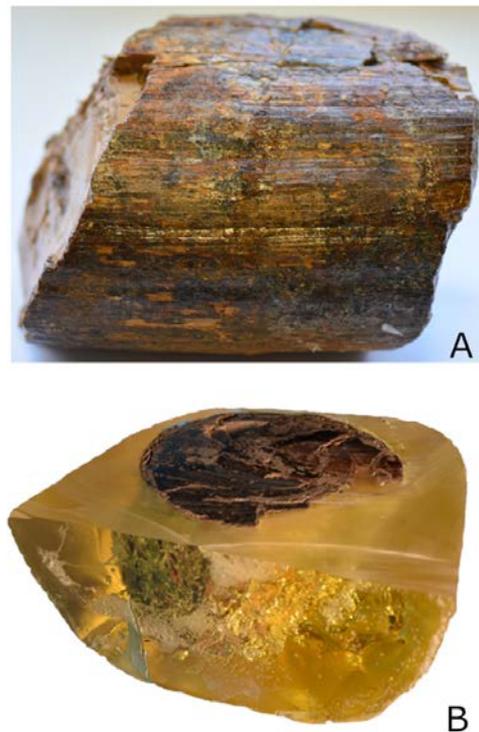
with *Mimomys praepliocaenicus*, *Pitymimomys stranzendorfensis*, *Clethrionomys primitivus*, and *Borsodia* ex gr. *praehungarica* (Simakova *et al.*, 2021), assignable to early MN17, at the Late Pliocene–Early Pleistocene transition (Tesakov, 2004).

### Material and methods

The studied specimen is a small, moderately preserved tusk fragment that required restoration in the laboratory. Despite its poor preservation, the fragment had its circular form almost preserved. The specimen was measured at 8.8 cm in length, and the diameter of the transversal section was recorded at 12 cm (Fig. 3A).

The larger part of the fossil tusk from Pekecik is preserved in the laboratory of the Department of Geological Engineering, Engineering Faculty, Firat University, Elazig, Turkey. A smaller part, used in this study, is catalogued in the collection of the Quaternary Stratigraphy Laboratory of the Geological Institute of Sciences (GIN), Russian Academy of Sciences, under the inventory number GIN 1176/500.

In this study, we analyzed features of the Schreger lines for the analysis of the tusk specimen. These features include the qualitative pattern (C, V, X patterns), the Schreger angle, and the wavelength of the channelled sets of dentinal tubules. These features were studied with respect to the distance from the tusk axis (Ábelová, 2008). The specimen was cut into transversal and longitudinal sections. To obtain the highest quality of sections, the tusk was initially embedded into a solution of epoxy resin and mixed hardener (Artline Crystal Epoxy) of 3:1 ratio,



**Fig. 3.** Tusk specimen GIN 1176/500 from Pekecik, Turkey. A — worked tusk sample; B — tusk embedded in epoxy resin showing transverse cut.

and then the specimen was cut for microscopic study (Fig. 3B). The transverse section was cut perpendicular to the tusk axis and was used to measure the Schreger angles and the qualitative Schreger pattern (Fig. 4). The longitudinal section was cut parallel to the axis, running along the entire length of the specimen showing undulating sets of dentinal tubules, to calculate the wavelength (Fig. 5). The longitudinal cuts were made near CDJ, near the axis, and equidistant from the CDJ and axis. We used a standard light microscope and a petrographic microscope with multiple magnification lenses to measure the different morphological attributes of the tusk structure (Fox, 2000; Trapani & Fisher, 2003). The best results were assessed at  $1.5\times$  magnification. Microphotographic images were taken using the microscope and a PC-connected digital camera.

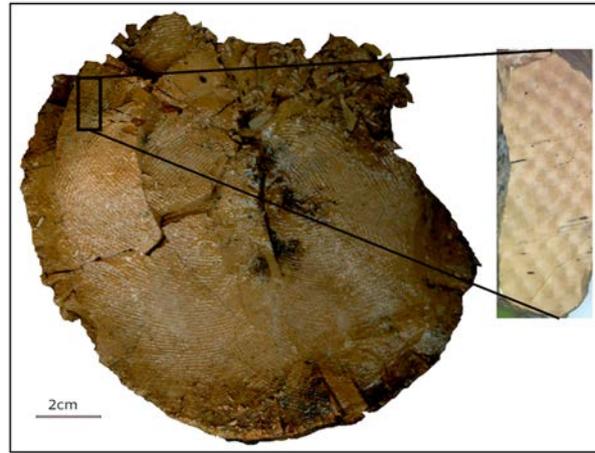
The Schreger patterns, namely “C”, “V”, and “X”, are the visible designs seen on the transverse section through the naked eye, within which patterns “V” and “X” are named as such because the corresponding patterns resemble these letters, and pattern “C” represents a checkerboard image (alternate dark-light pattern). Taxonomic identification of the tusk specimen can be made depending on the type and the location of these patterns (near the axis or CDJ) (Trapani & Fisher, 2003). We reported the qualitative appearance of the pattern based on this method using transversally cut sections. The presence or absence of these patterns was registered, moving from the tusk axis towards the CDJ.

Schreger angles were measured directly from the sample under the microscope and then were remeasured from the photographs of the transverse section. Specimen GIN 1176/500 was oriented with respect to the surface, and then the angles were calculated. The angles were measured with respect to the tusk axis, moving away from the axis towards the CDJ. Multiple measurements (min. 3) were carried out to reduce measurement errors, and then an average was calculated to obtain the results. The average range measured for the same area was approximately  $5^\circ$ . The angles varied depending on the location of the measured Schreger line intersections of the tusk because the dentine tubule density varies from the tusk axis to the CDJ (Espinoza & Mann, 1993).

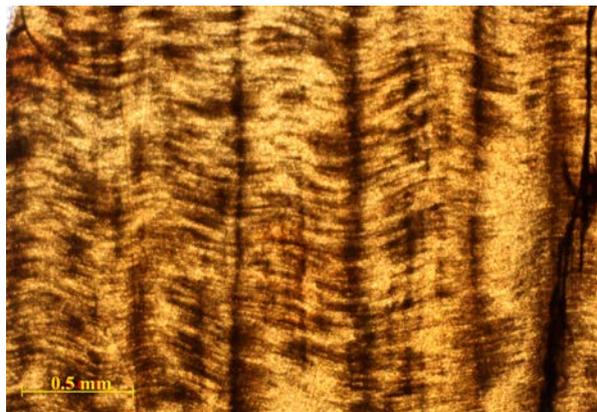
Wavelength was calculated by measuring the distance over which the dentine tubules move through one complete undulation. The wavelength was measured multiple times in longitudinal sections, and an average value was recorded (Trapani & Fisher, 2003; Ábelová, 2008).

## Results

Based on the aforementioned analytical procedures, the Schreger angles, Schreger patterns, and the wavelength of dentinal tubules were recorded. Table 1 shows the values of different attributes. The exact location of the specimen on the entire tusk is unknown, therefore the distance from the tusk axis plays a vital role in the discriminate analysis of the different measurements. Additionally, the specimen represents the first discovery



**Fig. 4.** Transverse section of the tusk specimen GIN 1176/500 (magnified picture showing intersecting Schreger lines with “X” pattern near CDJ).



**Fig. 5.** Section of the tusk specimen GIN 1176/500 cut across the longitudinal section, showing the undulating set of dentinal tubules near the CDJ.

of a large mammal fossil from the Pekecik section and therefore, is of great interest.

The Schreger angles in specimen GIN 1176/500 show a wide range of values from the axis to CDJ, with maximum readings coming between  $61\text{--}109^\circ$ . Near the axis, the specimen reached about  $\sim 61^\circ$ . The angle increased as we moved away from the axis. The transition area showed an angle of  $83^\circ$ , and the specimen reached a maximum angle of  $109^\circ$  near the CDJ. Depending on the Schreger angles measured on the transverse section, the quantitative Schreger pattern showed a similar attribute, as both features are interrelated. Specimen GIN 1176/500 showed a “V” pattern near the tusk axis area, corresponding to low angle values. Near CDJ at maximum angle values of  $\sim 109^\circ$ , the “X” pattern was visible. The transition area at high magnification showed a transition pattern phase between “V” and “X”. Wavelength measured at 1.67 mm near low angle values (tusk axis) and reduced in length to about 1.0 mm towards the high angle CDJ (Tab. 1).

## Comparison and discussion

### Schreger angle

For this study, multiple measurements of the Schreger angle were taken along the transverse section of the tusk from the axis to the CDJ, which colloquially are termed as inner (axis) and outer (CDJ).

As per the results of Trapani & Fisher (2003), the near CDJ angles for *Mammuthus* spp. are in the range of 100°, and Palombo & Villa (2001) concluded their near CDJ values in-between 65–90°, whereas Ábelová (2008) showed maximum measured angle values for *Mammuthus primigenius* between 40–110° with near CDJ values in the range of 85–110° (Tab. 2, 3). Our findings show a slight overlap in measurements with values reported from previously published studies (Palombo & Villa, 2001). This discrepancy may be because most of the published works were done on geologically much younger specimens, for example, *M. primigenius* (Late Pleistocene). Whereas specimen GIN 1176/500 is geologically older, presumably belonging to an Early Quaternary meridionaloid elephant,

judging from its context. Also, it needs to be kept in mind that the above-mentioned researches take into account multiple samples from a wide range of localities and hence show a higher variability, whereas our work deals with a single sample from one locality.

Similarly, Agostini *et al.* (2012) published data for outer Schreger angle for a young representative of *Mammuthus* (= *Archidiskodon*) *meridionalis* from Campo di Pile, Italy, in the range of 85° to 95° with an average value of 89°. The age of the said locality is placed somewhere between 0.9–1.1 Mya, similar to other published data for tusk properties for relatively young representatives of meridionaloid elephants. Agiadi & Theodorou (2005) published tusk feature values for Early Quaternary representatives of *M. (=A.) meridionalis* from Vlachioti and Megalopolis localities in Greece. Their outer Schreger angle values were measured in the range of 83–128°, which conforms with our results.

The near tusk axis Schreger angle, according to Trapani & Fisher (2003) and Ábelová (2008), shows a decrease in the value from the CDJ, which is in agreement with our results.

**Table 1.** Measured values for the discriminant attributes of the tusk specimen GIN 1176/500 based on the distance from the tusk axis to CDJ, Pekecik, Turkey.

Distance from tusk axis	Schreger angle (°)		Wavelength (mm)		Schreger pattern
Near CDJ	109	Decreasing angle	1.0	Increasing length	X
Transition area	83				V/X variation with minor C
Near tusk axis	61		1.67		V

**Table 2.** Values of tusk properties near the axis compared between the studied specimen and published data.

Tusk properties near the axis	Studied and compared taxa		
	<i>cf. Archidiskodon</i> sp.	<i>M. primigenius</i>	<i>Mammuthus</i> spp.
	Studied sample GIN 1176/500	Ábelová (2008) (max. readings)	Trapani & Fisher (2003)
Schreger angle (°)	61–65	50–80	–
Schreger pattern	V	V	V
Wavelength (mm)	1.67	2.1	>1

**Table 3.** Values of tusk properties near the CDJ compared between the studied specimen and published data.

Tusk properties near CDJ	Studied and compared taxa		
	<i>cf. Archidiskodon</i> sp.	<i>M. primigenius</i>	<i>Mammuthus</i> spp.
	Studied sample GIN 1176/500	Ábelová (2008) (max. readings)	Trapani & Fisher (2003)
Schreger angle (°)	105–109	85–110	70–100
Schreger pattern	X	C	X
Wavelength (mm)	1.0	1.1	>1

As per Palombo & Villa (2001), the Schreger angle for genus *Anancus*, as observed near the CDJ and tusk axis, is almost the same and does not show a decreasing trend and therefore, rules out the possibility of specimen GIN 1176/500 belonging to *Anancus* sp., as our results indicate a wide difference in the angles between the CDJ and tusk axis.

### Schreger pattern

Trapani & Fisher (2003) showed that the genus *Mammuthus* exhibits an “X” pattern near CDJ and a “V” pattern near the axis. It rarely shows a “C” pattern. In contrast, Ábelová’s findings (2008) did agree with Trapani & Fisher’s (2003) results but also presented a “C” pattern visible in 65% of her studied tusks of *M. primigenius* (Tab. 3). The Schreger pattern shows an alteration relative to its distance from the tip of the tusk, and we infer that this might be the reason for this difference in their results (Figs. 6A, 6B).

Agostini *et al.* (2012) reported a “V” shaped Schreger pattern near low angles for a young *M. (=A.) meridionalis*, and Agiadi & Theodorou (2005) presented a uniform “X” pattern throughout their meridionaloid elephants with a few instances of “C” pattern while showing no presence of “V” pattern.

Our results, in totality, correspond to that of the *Archidiskodon–Mammuthus* lineage (Fig. 6C). In terms of the Schreger pattern as visible on the transverse section measured from the tusk axis to the CDJ, specimen GIN 1176/500 shows a transition from “V” pattern to “X” with no sign of “C” pattern.

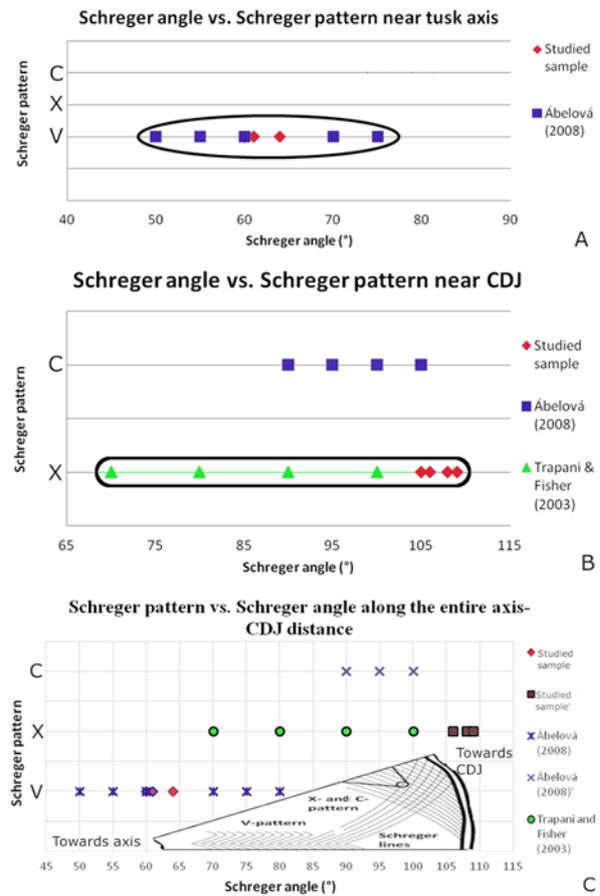
### Wavelength

As per the published results of Trapani & Fisher (2003) and Ábelová (2008), representatives of genus *Mammuthus* have a longer wavelength near the tusk axis and this value decreases towards CDJ. Our results show a 1.67 mm wavelength value near the tusk axis and are reduced to a length of 1.0 mm near the CDJ. When compared to the wavelength values of Ábelová (2008), her results exhibit 2.1 mm near the tusk axis and 1.1 mm near the CDJ. Our results are slightly lower in comparison.

### Conclusions

The results were sufficient to assign the specimen GIN 1176/500 to a particular genus of Proboscidea, using the properties of the tusk even without having the tusk location information.

Measurements were recorded at multiple locations across the entire axis-CDJ radius of the specimen GIN 1176/500 from Pekecik, Turkey. Specimen GIN 1176/500 shows a higher Schreger angle value near the CDJ and a smaller angle near the tusk axis. The wavelength is >1 mm throughout the specimen and decreases as we move from the tusk axis to CDJ. The Schreger lines on the transverse section show an “X” pattern near the high angle CDJ and a “V” pattern near the low angle tusk axis.



**Fig. 6.** Graphical representation of Schreger pattern plotted against Schreger angle along the entire axis-CDJ distance. 6A — the graph shows a higher concentration of “V” pattern near low angle areas; 6B — shows a higher concentration of “X” pattern near high angle areas. Some “C” patterns are also visible which are indicative of high angle areas; 6C — an amalgamation of near axis and near CDJ Schreger patterns plotted for different representatives of *Mammuthus* spp. and cf. *Archidiskodon* sp. Different signs for the studied sample and Ábelová (2008) indicate near the axis and near CDJ measurements (modified after Virág, 2012).

Since the area under study (Pekecik, Eastern Anatolia) is at the crossroads between Europe to the west, and the Asian heartlands to the east, it has a rich fossil assemblage in terms of mammalian fauna, therefore, it was of utmost importance to try and compare specimen GIN 1176/500 with all possible representatives of Elephantidae of different geological ages, whose fossils have either been excavated or could have traversed in the said locality. It is the first documented find of a large mammal remain in the locality. Hence, to put all doubts aside, specimen GIN 1176/500 was also compared with the now-extinct Middle–Late Pleistocene straight-tusked Eurasian elephant *Palaeoloxodon*. Palombo & Villa (2001) and

Agiadi & Theodorou (2005) reported measurements on *Palaeoloxodon antiquus* and *Palaeoloxodon falconeri*. *Palaeoloxodon* species have Schreger angles comparable to present-day *Elephas* and *Loxodonta*, i.e., their outer Schreger angle readings were much higher than seen in specimen GIN 1176/500. Therefore, it is safe to say that specimen GIN 1176/500 does not belong to representatives of *Palaeoloxodon*.

All the acquired results from the current study, when examined alongside the other specimens from different geographical areas corresponding to *Mammuthus* and *Archidiskodon* from different geological ages, gives a credible platform to distinguish and identify the studied sample. Taking into account the known geological age (Late Pliocene-Early Pleistocene) of the site (Pecekik, Turkey) from where the specimen GIN 1176/500 has been excavated and the measurements for different tusk features, tusk characteristics are similar to that of the extinct genus *Archidiskodon*. Specimen GIN 1176/500 differs from extinct mastodon *Anancus* spp. in terms of their outer and inner Schreger angles and it also differs from elephant *Palaeoloxodon* spp. as outer angle values of specimen GIN 1176/500 are much smaller than the registered values for *Palaeoloxodon*. Therefore, based on measured morphometric similarities and dissimilarities, we assign specimen GIN 1176/500 to a geologically older representative of meridionaloid elephant, preferably cf. *Archidiskodon* sp.

The study subsequently confirms that the tusk properties of a fragmented tusk specimen, even without the spatial knowledge of the fragment from the entire tusk, are useful for taxonomic identification. Similarly, the fact that specimen GIN 1176/500 belongs to cf. *Archidiskodon* sp. but has some of its characteristics overlapping with that of genus *Mammuthus*, raises the question of whether tusk specimens are a viable source for a phylogenetic study. As per Palombo & Villa (2001) and Ábelová (2008), tusk features are not phylogenetically informative, but we argue that the range of the geological age for their samples is too small and that a greater range is required to answer this question indubitably. Unfortunately, at the moment, with a single Early Pleistocene specimen, it was not sufficient information to comment on its viability for a phylogenetic study. More studied Early Quaternary specimens will check the usability of tusk properties in phylogenetic studies.

Nonetheless, it does open areas of interest as specimen GIN 1176/500, belonging to cf. *Archidiskodon* sp., is the first anatomical specimen of a large mammal excavated from the Pecekik area in Eastern Turkey, and it contributes to the understanding of the development of Late Pliocene-Early Pleistocene mammalian fauna from that area.

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## References

- Ábelová M. 2008. Schreger pattern analysis of *Mammuthus primigenius* tusk: Analytical approach and utility // Bulletin of Geosciences. Vol.83. P.225–232.
- Agiadi K. & Theodorou G. 2005. Tusk Paleohistology as a tool in the discrimination of fossil tusks from Greece // Alcover J.A. & Bover P. (eds.). Proceedings of the International Symposium “Insular Vertebrate Evolution: The Palaeontological Approach”. Mallorca, Spain: Monografies de la Societat d’Història Natural de les Balears. Vol.12. P.1–8.
- Agostini S., Palombo M.R., Di Canzio E. & Tallini M. 2012. *Mammuthus meridionalis* (Nesti, 1825) from Campo di Pile (L’Aquila, Abruzzo, Central Italy) // Quaternary International. Vol.276–277. P.42–52.
- Aguirre E. 1969. Revisión sistemática de los “Elephantidae” por su morfología y morfometría dentaria // Estudios Geológicos, (Madrid). Vol.24. P.1–25.
- Albayrak E. & Lister A.M. 2012. Dental remains of fossil elephants from Turkey // Quaternary International. Vol.276–277. P.198–211.
- Baigusheva V.S., Titov V.V. & Foronova I.V. 2016. Teeth of early generations of Early Pleistocene elephants (Mammalia, Elephantidae) from Sinyaya Balka/Bogatyri site (Sea of Azov Region, Russia) // Quaternary International. Vol.420. P.306–318.
- Baygusheva V. & Titov V. 2012. The evolution of Eastern European meridionaloid elephants’ dental characteristics // Quaternary International. Vol.255. P.206–216.
- Bernor R.L. & Lipscomb D. 1991. The systematic position of “*Plesiohipparion*” aff. *huangheense* (Equidae, Hipparionini) from Gülyazi, Turkey // Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie. Vol.31. P.107–123.
- Cantalapiedra J.L., Sanisidro Ó., Zhang H., Alberdi M.T., Prado J.L., Blanco F. & Saaninen J. 2021. The rise and fall of proboscidean ecological diversity // Nature Ecology & Evolution. Vol.5. P.1266–1272.
- Dayan E. 1989. Über pleistozäne Elefantenfunde im Umland von Erzurum in Ostanatolien. Ein Beitrag zur Fundgeschichte des *Elephas trogontherii* im Becken von Pasinler // Stuttgarter Beiträge Naturkunde, Serie B. Vol.147. P.1–21.
- Espinoza E.O. & Mann M.J. 1991. Identification Guide for Ivory and Ivory Substitutes. Second edition. Baltimore: World Wildlife Fund and Conservation Foundation. 38 p.
- Espinoza E.O. & Mann M.J. 1993. The history and significance of the Schreger pattern in proboscidean ivory characteriza-

- tion // Journal of the American Institute for Conservation. Vol.32. P.241–248.
- Fisher D.C., Trapani J., Shoshani J. & Woodward M. 1998. The Schreger pattern in mastodon and mammoth tusk dentin // Current Research in the Pleistocene. Vol.15. P.105–107.
- Fox D.L. 2000. Growth increments in *Gomphotherium* tusk and implications for late Miocene climate change in North America // Palaeogeography, Palaeoclimatology, Palaeoecology. Vol.156. P.327–348.
- Garutt V.E. 1986. [Origins of elephants Elephantidae and their phylogeny] // Proceedings of the Zoological Institute of the Academy of Sciences of the USSR. Vol.149. P.15–32. [in Russian]
- Garutt V.E., Alexejeva L.I. & Baigusheva V.S. 1977. On the oldest *Archidiskodon* elephants from the Anthropogene of the USSR // Journal of the Paleontological Society of India. Vol.20. P.4–9.
- Garutt W.E. 1998. Is there a genus *Archidiskodon* Pohlig, 1885, of the family Elephantidae Gray, 1821? // Cranium. Vol.15. No.1. P.15–20.
- Gheerbrant E. 2009. Paleocene emergence of elephant relatives and the rapid radiation of African ungulates // Proceedings of the National Academy of Sciences of the USA. Vol.106. No.26. P.10717–10721.
- Irritz W. 1972. Lithostratigraphie und tektonische Entwicklung des Neogens in Nordostanatolien (Kanäozoikum und Braunkohlen der Türkei // Beihefte zum Geologischen Jahrbuch. Vol.120. P.3–111.
- Koenigswald W.v. & Sander P.M. 1997. Glossary of terms used for enamel microstructures // Koenigswald W.v. & Sander P.M. (eds.). Tooth Enamel Microstructure. Rotterdam: Press Balkema. P.267–280.
- Lambert W.D. 2005. The microstructure of proboscidean ivory and its application to the subordinal identification of isolated ivory specimens // Bulletin of the Florida Museum of Natural History. Vol.45. No.4. P.521–530.
- Larramendi A., Zhang H., Palombo M.R. & Ferretti M.P. 2020. The evolution of *Palaeoloxodon* skull structure: disentangling phylogenetic, sexually dimorphic, ontogenetic, and allometric morphological signals // Quaternary Science Reviews. Vol.229. P.e10690.
- Lister A.M. 1993. “Gradualistic” evolution: its interpretation in Quaternary large mammal species // Quaternary International. Vol.19. P.77–84.
- Lister A.M. 1996. Evolution and taxonomy of Eurasian mammoths // Shoshani J. & Tassy P. (eds.). The Proboscidea: Evolution and Palaeontology of Elephants and Their Relatives. Oxford: Oxford University Press. P.204–213.
- Lynch C.D., McGillicuddy C.T., O’Sullivan V.R. & Sloan A.J. 2010. Gabriel-Philippe de la Hire and the discovery of Hunter-Schreger bands // British Dental Journal. P.461–465.
- Maglio V.J. 1973. Origin and evolution of the Elephantidae // Transactions of the American Philosophical Society. Vol.63. No.3. P.1–149.
- Mayda S., Titov V.V., Kaya T., Tesakov A.S., Halaçlar K., Tan A., Alççek M.C., Syromyatnikova E.V. & Karakütük S. 2014. *Anancus* in Turkey // Proceedings of the VI International Conference on Mammoths and their Relatives. Thessaloniki, Greece: Scientific Annals, School of Geology, Aristotle University. Special Vol.10. P.127–128.
- Miles A.E. & White J.W. 1960. Ivory // Proceedings of the Royal Society of Medicine. P.775–780.
- Osborn H.F. 1936. Proboscidea. Vol.1. New York: American Museum of Natural History. 1675 p.
- Osborn H.F. 1942. Proboscidea. Vol.2. New York: American Museum of Natural History. 802 p.
- Palombo M.R. & Villa P. 2001. Schreger lines as support in the Elephantinae identification // Cavarretta G., Giolia F., Mussi M. & Palombo M.R. (eds.). La Terra degli Elefanti/ The World of Elephants. Attideli 1 Congresso Internazionale/Proceedings of the 1<sup>st</sup> International Congress. Rome: Consiglio Nazionale delle Ricerche. P.656–660.
- Palombo M.R. & Ferretti M.P. 2005. Elephant fossil record from Italy: knowledge, problems, and perspectives // Quaternary International. Vol.126–128. P.107–136.
- Palombo M.R., Ferretti M.P., Larramendi A. & Zhang H. 2017. How many *Palaeoloxodon* species in Eurasia? Disentangling phylogenetic, dimorphic, ontogenetic, allometric and environmentally-driven characters // VII International Conference of Mammoths and Their Relatives. Taichung, Taiwan: ICMR. P.2–5.
- Schreger B. 1800. Beitrag zur Geschichte der Zähne // Beiträge für die Zergliederungskunst. Vol.1. P.1–7.
- Simakova A.N., Tesakov A., Çelik H., Frolov P.D., Shalaeva E.A., Sokolov S.A., Trikhunkov Y.I., Trifonov V.G., Bachmanov D.M., Latyshev A.V., Ranjan P.B., Gaydalenok O.V., Syromyatnikova E.V., Kovaleva G.V. & Vasilieva M.A. 2021. Caspian-type dinocysts in NE Turkey mark deep inland invasion of the Akchagylia brackish-water basin during the terminal Late Pliocene // Quaternary International. Vol.605–606. P.329–348.
- Tesakov A.S. 2004. [Biostratigraphy of Middle Pliocene — Eopleistocene of Eastern Europe (based on small mammals)]. Moskva: Nauka. 247 p. [in Russian]
- Titov V.V. 2008. [Late Pliocene Large Mammals from North-eastern Sea of Azov Region]. Rostov-on-Don: SSC Russian Academy of Sciences Publishing. 262 p. [in Russian, with English summary]
- Trapani J. & Fisher D.C. 2003. Discriminating proboscidean taxa using features of the Schreger pattern in tusk dentin // Journal of Archaeological Science. Vol.30. P.429–438.
- Ünay E. & Bruijn H. 1998. Plio-Pleistocene rodents and lagomorphs from Anatolia // Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen. No.60. P.431–466.
- Vasilyan D., Schneider S., Bayraktutan M.S. & Şen Ş. 2014. Early Pleistocene freshwater communities and rodents from the Pasinler Basin (Erzurum province, north-eastern Turkey) // Turkish Journal of Earth Sciences. Vol.23. P.293–307.
- Virág A. 2012. Histogenesis of the unique morphology of proboscidean ivory // Journal of Morphology. P.1406–1423.
- Wei G., Hu S., Yu K., Hou Y., Li X., Jin C., Wang Y., Zhao J. & Wang W. 2010. New materials of the steppe mammoth, *Mammuthus trogontherii*, with discussion on the origin and evolutionary patterns of mammoths // Science China: Earth Sciences. Vol.53. P.956–963.