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Is there a genus *Archidiskodon* Pohlig, 1885, of the family Elephantidae Gray, 1821?

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SUMMARY

In 1885 Pohlig established the elephant genus *Archidiskodon*. The earliest representatives of the genus appeared at the beginning of the Pliocene in Africa. Representatives of the genus migrated to Eurasia and North America where they gave rise to several new species. Substantial climatic change in the Holarctic in the Pleistocene led to the emergence of the genera *Mammuthus* Brookes, 1828, and *Parelephas* Osborn, 1924, in Eurasia and North America, respectively. Some paleontologists consider *Archidiskodon* a junior synonym of *Mammuthus*, others regard it as valid. In an attempt to put an end to the disagreement, I here undertake a detailed comparison of the skeleton and teeth identified as *Archidiskodon* and *Mammuthus*. There are 23 different features and only 10 shared ones, which confirms the validity of the genus *Archidiskodon*.

SAMENVATTING

Pohlig beschreef in 1885 het olifantengeslacht *Archidiskodon*. De oudste vertegenwoordigers van dit genus verschijnen aan het begin van het Plioceen in Afrika. Vanuit Afrika migreerde *Archidiskodon* naar Eurazië en Noord Amerika, waar verscheidene nieuwe soorten ontstonden. De grootschalige Pleistocene klimaatsveranderingen op het noordelijk halfrond waren de oorzaak van het ontstaan van de geslachten *Mammuthus* Brookes, 1828 en *Parelephas* Osborn, 1924 in respectievelijk Eurazië en Noord Amerika. Volgens sommige paleontologen is *Archidiskodon* een junior synoniem van *Mammuthus*, anderen beschouwen het als een goed genus. In een poging om het pleit te beslechten geeft dit artikel een gedetailleerde vergelijking tussen skeletten en kiezen die als *Archidiskodon* en *Mammuthus* gedetermineerd zijn. Er zijn 23 verschillen en 10 overeenkomsten gevonden, hetgeen de geldigheid van het geslacht *Archidiskodon* bevestigt.

Introduction

Initially all the extant and extinct elephants (Family Elephantidae Gray, 1821) were placed in the genus *Elephas* Linnaeus, 1758. As early as 1828 Brookes distinguished *Mammuthus* as a separate genus, including the woolly mammoth, *M. primigenius* (Blumenbach), 1799. In 1885 Pohlig established the genus *Archidiskodon*. The latter included (FALCONER & CAUTLEY), 1845, described on the basis of fossils from the northern Himalayas, and *A. meridionalis* (Nesti, 1825) from Eurasia. Dispite similarity in molar structure, these two species differ sharply in craniological features. GARUTT (1957a) referred *A. planifrons* to the new genus *Protelephas*, but left *A. meridionalis* in *Archidiskodon*.

The elephants of the genus *Archidiskodon* appeared for the first time in Africa in the early Pliocene. They lived in savanna environments and fed mainly on twigs and leaves, as indicated by their dental morphology (GARUTT, 1977). In the second half of the Pliocene archidiskodont elephants dispersed to Eurasia and to North America, where they gave rise to a number of new species (GARUTT, 1986). The latest and most advanced representative of the genus was *A. tamanensis* Dubrovo, 1964, considered by its author a subspecies of *A. meridionalis*. Probably at this stage *Archidiskodon* penetrated into North America.

The cooling and aridization of the climate in the Pleistocene led to a decrease of the forest and to broad expansion of open landscapes, i.e. arctic steppe, forest-steppe, forest-tundra and tundra. Following this climatic and vegetational change, the Pleistocene mammalian fauna became a more "steppic" one and the species composing the specific biocenosis of the periglacial landscape dispersed over several continents.

Environmental change forced the archidiskodonts to adapt to a vegetation of shrubs and grasses. During this period *Archidiskodon* evolved into the genera *Mammuthus* and *Parelephas*, morphologically different from their ancestor of a more temperate environment (GARUTT, 1986). The earliest representative of the genus *Mammuthus* in Eurasia is the steppe mammoth, *M. trogontherii* Pohlig, 1885, known from Middle Pleistocene deposits of Europe, Central Asia, the Ural Mountains, Siberia and the Far East.

Some paleontologists, e.g. SIMPSON, 1945; AGUIRRE, 1968, 1969; MAGLIO, 1973; GUTH, 1982; COPPENS & BEDEN, 1982; HOOIJER, 1984; MOL & ESSEN, 1992; AGENBROAD, 1994, do not recognize the genus *Archidiskodon*, but consider it a junior synonym of *Mammuthus*. SIMPSON (1945) and BELYAEVA (1948), however retain *Archidiskodon* as a subgenus. Others acknowledge *Archidiskodon* as a valid genus, e.g. POHLIG, 1885, 1888; OSBORN, 1925, 1942; DUBININ & GARUTT, 1952; GARUTT, 1954, 1957a, 1957b, 1964a, 1964b, 1971, 1977, 1985, 1986; GARUTT & ALEKSEEVA, 1964; GARUTT & SAFRONOV, 1965; GARUTT, ALEKSEEVA & BAIGUSHEVA, 1975; GARUTT & FORONOVA 1976; GARUTT & BAIGUSHEVA, 1981; GARUTT & VANGENGEIM, 1982; GARUTT & URBANAS, 1986; GARUTT & NIKOLSKAYA, 1988; GARUTT *et al.*, 1990; DUBROVO, 1957, 1960, 1962, 1964, 1989; BAIGUSHEVA, 1959, 1964, 1984; BAIGUSHEVA & GARUTT, 1987; VANGENGEIM, 1961, 1977; GABUNYA, 1961; GABUNYA & VEKUA, 1963, 1967; GABUNYA & DUBROVO, 1990; DUBROVO & BAIGUSHEVA, 1964; APOSTOL,

1965, 1974; ALEKSEEVA & GARUTT, 1965; ALEKSEEVA, 1977, 1984; KONSTANTINOVA, 1965; MULLER, 1970; LEBEDEVA, 1972; VISLOBOKOVA, 1974a, 1974b; ZHYLKIBAEV, 1975; BOEF, 1976; GROMOV, 1977; AZZAROLI, 1977, 1983; VÖRÖS, 1979; DATUEV & LEBEDEVA, 1981; GUENTHER, 1986. Below a detailed comparison is given of the skeletons and teeth identified as *Archidiskodon* and *Mammuthus*.

Comparison

Skeletal and dental morphology shared by *Archidiskodon* and *Mammuthus*:

1. The top of the skull when viewed from the front or back is convex semi-circular in shape; incisura cranii is absent. In single cases the tribe Mammuthini may show a small depression on the top of the skull. This should be considered an atavism, as in the assumed ancestral tribe Phanagoroloxodontini Garutt, 1991, this feature is clearly marked (GARUTT, 1957c, 1958, 1986, 1991, 1992, 1995).

2. Facies frontalis is considerably narrowed from both sides and in the middle, it is concave in sagittal and slightly convex (seldom straight) in transversal direction. The tuber frontalis in its proximal part is more pronounced in the male than the female.

3. The nasal opening (orificum nasalis externus) is wide and crescent-shaped, its lateral rims are sharpened and directed down in the male, narrower with rounded rims in the female.

4. The processus nasalis is triangular with a pointed end. Its external surface is flat, while the inner surface is slightly concave with a weak longitudinal ridge near its base.

5. The fossae temporales have indistinct borders.

6. The intermaxillar bones (intermaxillaria) are bent and when viewed from the front or back form a figure resembling an X. They are wide at the level of the infraorbital foramina, gradually narrowing towards their middle part and then widening again towards their distal end, where the tusks emerge from the alveoli.

On the upper surface of the intermaxillar bones there is a longitudinal depression, which is narrow and deep in males, shallow with sloping rims in females. The relief of the depression depends on the degree of development of the tusks.

7. The tusks are characterized by pronounced twisting. On emerging from the alveoli they are directed down and out, then turn up and in towards one another. The twisting is more pronounced and the tusks more massive in males than females.

8. The thoracal vertebrae have pronounced spinous processes, longest and most massive in the anterior part of the column or between the third and seventh thoracal vertebrae, but gradually declining towards the lumbar section.

9. The ribs (costae) are oval in cross section, except the first and second pair which are flattened.

10. The wings of the iliac bones (ala ossis ilii) have straight rims.

Distinguishing skeletal and dental characters of *Archidiskodon* and *Mammuthus*:

1. The relative length of the skull. The skull of *Archidiskodon* is relatively low and elongated in sagittal direction: the length/height ratio ranges from 86.1 to 78.9%. As the Mammuthini evolved the skull became shorter. In *Mammuthus* the length/height ratio of the skull is 78.0-68.2%.

2. The occipital proportions. The relative height of the occiput gradually increased in the Mammuthini. In *Archidiskodon* the height/width ratio varies between 68.4-78.0%, in Mammuthus between 70.2-83.9%.

3. In *Archidiskodon* the surface of the occiput is flat, due to the development of the occipital tubercles, paired cone-shaped protuberances situated on both sides of the fossa nuchales. These protuberances are especially pronounced in the male. In *Mammuthus* the occipital tubercles are weak.

4. The occipital condyli in *Archidiskodon* project slightly above the occipital surface; in *Mammuthus* they project still less.

5. During the evolution of the Mammuthini the concavity in sagittal direction of the facies frontalis decreased.

6. The relative width of the forehead increased during the evolution of the Mammuthini: in *Archidiskodon* the ratio minimum width of the frontal surface/width of the occiput varies from 29.0 to 47.1%, in *Mammuthus* from 31.8 to 54.3%.

7. In *Archidiskodon* the supraorbital processes are short and the width of the skull in the region of the processes is smaller than the width of the occiput. In the former width either exceeds that of the occiput (in males) or equals it (in females).

8. In *Archidiskodon* the orbits as a rule do not project relative to the skull profile, but in Mammuthus they sometimes do.

9. In *Archidiskodon* the lacrymal tubercles are poorly developed, whereas in *Mammuthus* they are more pronounced, especially in males.

10. In *Archidiskodon* the lower rim of the nasal opening is situated higher than or on a level with the upper rims of the orbits. In *Mammuthus* the nasal opening is shifted downward so that its lower rim is on a level with a line drawn horizontally through the orbits. Analogous down-

shifting of the nasal opening occurs also in other groups of elephants.

11. In *Archidiskodon* the processus nasalis projects to a marked degree in relation to the frontal surface (especially in males). In *Mammuthus* this projection is insignificant.

12. The zygomata of *Archidiskodon* are relatively higher than in *Mammuthus*.

13. During the evolution of the Mammuthini the relative length of the intermaxillar bones increased. Their length/width ratio, measured at the level of the infraorbital foramina, varies in *Archidiskodon* from 147.3 to 176.9%, in *Mammuthus* from 163.5 to 209.7%.

14. In *Archidiskodon* the tusks are less spirally twisted than in *Mammuthus*.

15. The mandible of *Archidiskodon* is lower, sagittally more elongated, and has lower ascending rami than that of *Mammuthus*.

16. The submental process (processus submentalis) in *Archidiskodon* is long and massive. In *Mammuthus*, particularly in the late forms, it is weakly developed, short and thin. Some atavistic individuals of *M. trogontherii* have a long and massive rostrum.

17. In *Archidiskodon* the width of the mandible, measured between the external edges of the angles, is smaller than the width measured at the condyli. In *Mammuthus* the inverse relationship is true.

18. Of the dental characters, those of M3 are most diagnostic. In *Archidiskodon* the tooth crowns are relatively low and wide, in contrast to *Mammuthus* (GARUTT & FORONOVA, 1976; GARUTT, 1977). The lamellar number in *Archidiskodon* varies from 11 to 23, in *Mammuthus* from 20 to 31. The average length of the lamellae in *Archidiskodon* is 26.3-17.1 mm, in *Mammuthus* 25.0-6.0 mm. The number of lamellae per 100 mm of crown length varies from 3.8 to 5.8 in Archidiskodon and from 4.0 to 12.6 in *Mammuthus*. The thickness of the enamel in *Archidiskodon* is 2.0-5.0 mm and in *Mammuthus* 0.9-3.5 mm.

19. In different forms of elephants the wear pattern of the teeth due to mastication is different. In *Mammuthus* the wear pattern of the teeth is more irregular than in *Archidiskodon* (GARUTT & FORONOVA, 1976, GARUTT, 1977).

20. The relative length of the neck vertebrae (vertebrae cervicales) in *Archidiskodon* exceeds that in *Mammuthus*. This reflects on the structure of the cervical part of the vertebral column, which is more elongated in *Archidiskodon* than in *Mammuthus*.

21. The relative length of the caudal vertebrae (vertebrae caudales) of *Archidiskodon* exceeds that in *Mammuthus*. The shortness of the tail in *Mammuthus* is due both to the shortness of the vertebrae themselves and to decrease in their numbers (to 20-21).

22. The manus of *Archidiskodon* is characterized by the serial arrangement of the carpal bones, i.e. each proximal carpal bone articulates directly with a corresponding bone in the distal row. In *Mammuthus* the carpal bones are aserially arranged as a result of the broadening of the lunar bone (GARUTT, 1951, 1954, 1964a, 1964b).

23. The relative size of the phalanges in *Mammuthus* is smaller than in *Archidiskodon*. In addition, in some cases a reduction of the number of phalanges can be seen in the former, i.e. the third phalanges disappear.

The comparison shows that the difference between the two genera is significant. There are only 10 shared features, but 23 distinctive ones. In my opinion this confirms the validity of *Archidiskodon*, but allows us to unite these genera, together with *Parelephas*, in the tribe Mammuthini.

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