

古北区 *Saiga* 属(偶蹄目,牛科)在更新世时期的地理分布和进化历史

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关键词 古北区 更新世 *Saiga* 分布 进化

Saiga 是一种小型牛类,站立时肩高 80 厘米。它的主要特征是鼻子形似象鼻:灵活,向下延伸超过下颌;角弯曲,具横脊,长达 35 厘米。在更新世晚期,它与披毛犀—猛犸象动物群的分布范围大致相同。

人们还不能确定谁是 *Saiga* 的直接祖先。但它与西藏 *Pantholops* 的现生种 *Pantholops hodgsoni* 和化石种 *P. hundesiensis* 有亲密关系。Gentry(1968) 把中国青海晚中新世的 *Qurlignoria* 也归入到 Simpson(1945) 建立的 Saigini 族中。由此推测,至少从晚中新世以来, *Saiga* 族已自成一支独立的演化线。

最早的 *Saiga* 发现于西伯利亚东北下 Kolyma 河 Olyorian 期的地层中。Sher(1967) 把它归入到阿拉斯加晚更新世 *Saiga ricei* 种中。然而,在种的归属上,这可能还有问题。

有关中更新世 *Saiga* 的报道极少。但这些报道已表明在这一时期 *Saiga* 已从亚洲中部向西扩散,远至西欧。

在最后间冰期时, *Saiga* 在接近 Baku (Apsheiron) 岛的 Binagadi 出现。Aleksperova(1955) 为该地大量的 *Saiga* 标本建立一新种: *Saiga binagadensis*。比较表明,它应该是 *Saiga tatarica* 一亚种: *Saiga tatarica binagadensis* Aleksperova, 1955。

在最后冰期时, *Saiga* 已在古北区达到它最大的分布范围(图 1)。已知含 *Saiga* 的化石地点超过 180 个。在乌拉尔山区,它向北分布到达北纬 62 度;在鄂博河流域,它延伸进入北极区;向东它到达白令陆桥。*Saiga* 还在阿拉斯加存在。然而,由于比利牛斯山和阿尔卑斯山成为迁移的障碍, *Saiga* 未能进入亚平宁半岛;在中国东北、内蒙和山西等省也没有发现它的踪迹。

西伯利亚东北区晚更新世至早全新世的 *Saiga* 种是 *Saiga tatarica borealis*, 而在克里米亚和苏联西南部一些旧石器地点的 *Saiga* 化石标本应归入 *Saiga tatarica tatarica*。欧洲的 *S. prisca* 和阿拉斯加的 *S. ricei* 可能是 *S. tatarica borealis* 的同义词(Baryshnikov et Tikhonov, 1989)。

在 *Saiga* 的进化中,角心有逐渐变得粗壮,角心基部相互靠近和两角心向上分开程度变小的趋势。因此, R. D. Kahlke(1990) 提出 *Saiga* 可能含有两种类型: “Bottrop

类型”和“Pahren 类型”(图版 I, 1—2)。前者为原始的 *Saiga*, 包括欧亚大陆第二间冰期、最后间冰期和最后冰期的类型; 后者主要以欧洲 Weichselian 期的一些破碎头骨为代表。这种分类将来有可能与 Baryshnikov *et* Tikhonov(1989) 提出的分类合并。

现生的 *Saiga* 包括两个亚种: *S. tatarica tatarica* 和 *S. tatarica mongolica*。前者分布于苏联卡尔梅克和哈萨克斯坦的草原和半干燥地区; 后者出现在蒙古。

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PLEISTOCENE DISTRIBUTIONAL AND EVOLUTIONARY HISTORY OF THE GENUS SAIGA GRAY, 1843 (MAMMALIA, ARTIODACTYLA, BOVIDAE) IN THE PALAEARCTIC

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The saiga is a small bovid which was distributed over large parts of the range of the Late Pleistocene *Mammuthus-Coelodonta* faunal complex. It developed superb adaptations to the dry continental climate with frequent sand- and snow-storms. This animal, which reaches up to 80cm in shoulder-height, is particularly characterised by its very mobile, trunk-like nose which extends clearly beyond the lower jaw. The curved and ringed horns can reach 35cm in length.

A direct ancestor for the genus *Saiga* has not yet been demonstrated. Closely related to the saigas, but with a less specialized facial morphology of the skull, is the now rare chiru of the Tibetan mountain steppe, *Pantholops hodgsoni* (ABEL) (also known as the orongo or Tibetan antelope) (see Feng *et al.* 1986, p. 227—230). A fossil form of this genus, *P. hundesiensis* Lydekker, is recorded from Xizang (Tibet). In addition, Gentry (1968, p. 769) has suggested that *Qurlignoria*, a bovid related to *Pantholops* from ?Lower Pliocene sediments of the Qaidam Pendi (Tsaidam basin, Qinghai Province, China), belongs in Simpson's (1945, p. 161) Tribe Saigini. On the basis of specialized anatomical features, especially the strongly reduced nasals (see also Glitsch 1871), it is likely that the lineage of the saigas has undergone independent evolution since at least the Miocene, as suggested by Bannikov (1963, p. 25).

The possibly oldest fossils of saiga yet recorded are those assigned to the Olyor faunal complex of the lower Kolyma River (northeastern Siberia). These remains, which are also the most northeasterly record of the genus in Eurasia, were first referred by Sher (1967, p. 406, 1971a, p. 251, 1971b, p. 123) to *S. ricei*, a taxon founded on a fossil from Lilian Creek (Fairbanks, Alaska) (Frick 1937, p. 547), and

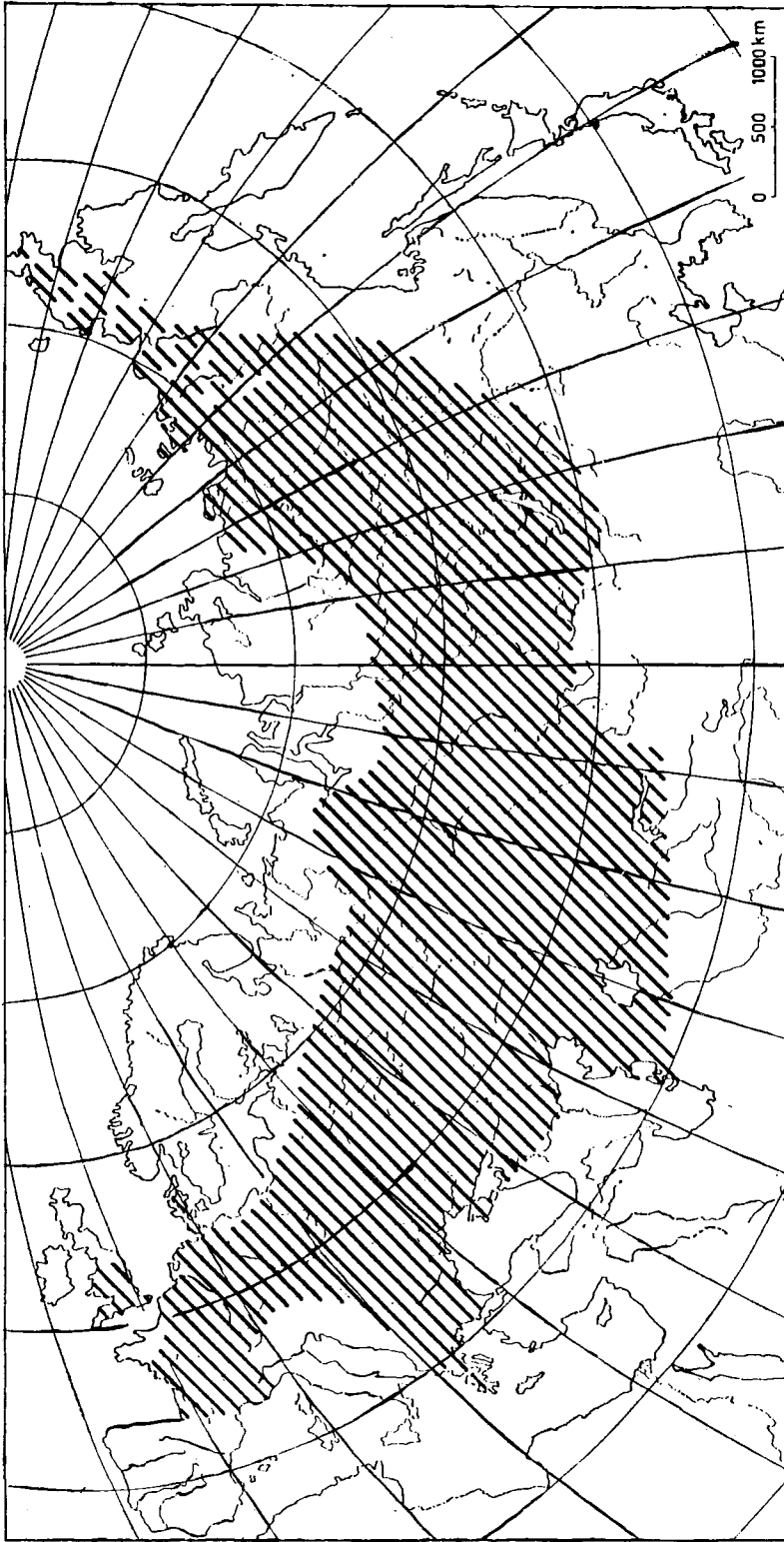


Fig. 1 Sketch of the maximal distribution of saiga (*Saiga tatarica borealis* (Čerskij, 1876)/*S. tatarica tatarica* (Linnaeus, 1766)/*S. tatarica* ssp.) in the Palaeartic during the Last Cold Stage, based on the existing fossil record (from R.-D. Kahlke 1990, with additions)

were assumed to come from a late Pleistocene horizon. More recently, the Siberian finds have been reassigned to the older, Olyorian horizon, and their specific referral left open (Sher 1986, p.100).

Unquestioned *Saiga* fossils from the Middle Pleistocene Saalian complex or its equivalents are recorded rarely in both Asia and Europe (e.g. USSR: lower Tobol River (western Siberia); Uluška near Sarepta (central Wolga area); Germany: Zeuchfelder Sander near Freyburg/Unstrut; ? Bottrop (Westfalia); France: Grotte de la Chaise, Abri Suard (Charente); Combe-Grenal (Dordogne) (for literature see H.-D. Kahlke 1975, p. 137)). These records show clearly that *Saiga* sp. (or *Saiga tatarica* ssp.) at that time spread from a central Asian centre of distribution across wide continental areas as far as western Europe.

In the Last Interglacial (Eemian), saiga remains are known from the tar-pits of Binagadi near Baku (Apsheeron peninsula) (Alekperova 1955). The relative richness of the fossil material excludes a merely episodic occurrence in this area during the Eemian, and the geographical position of the site, within the historical range of the species (see below), suggests that this area was a refugium during the Last Interglacial as it is today. Various anatomical features led Alekperova (1955) to distinguish the Binagadi remains as a separate species, *S. binagadensis*. However the differences between this form and *S. tatarica* given by Alekperova (1955), are not greater than those described by Bannikov (1946) for subspecific distinction within modern *S. tatarica* (*S. tatarica tatarica* and *S. tatarica mongolica*). This suggests that the Last Interglacial form from Binagadi should be regarded as a subspecies only, i. e. *S. tatarica binagadensis* Alekperova, 1955. Baryshnikov & Tikhonov (1989, p. 626) regarded *binagadensis* as a southern variant of saiga.

The maximum geographical range of the genus *Saiga* was reached only during the Last Cold Stage (Fig. 1). In the reviews given by Tscherski (1892, p. 188—189), Hescheler & Kuhn (1949, p. 201), Koby (1958, p. 11, 1960, p. 105), Kowalski (1959, p. 43—44, 199—200), Samson & Rădulescu (1959, p. 200—202), Verešagin (1959, p. 441), Toepfer (1964, p. 112), Prat (1966, p. 335), Sher (1967, p. 98), Kožamkulova (1969, p. 92—94), Dinkov *et al.* (1974, p. 5—7), H.-D. Kahlke (1975, p. 139—144), Delpech (1983, p. 207—210), Markova (1984, p. 211) and Musil (1985, p. 76), a total number of more than 180 Palaeartic fossil localities are listed. In Europe, the Pyrenees and the Alps acted as barriers to migration, so that saiga did not reach the Apennine or Iberian peninsulas. Chow *et al.* (1959, p. 82) indicated an absence of fossil *Saiga* from Manchuria, although Verešagin & Baryšnikov (1982, p. 273), without giving details, included northern China within its fossil range. Examination by the author of Pleistocene mammal collections in many museums and institutes in Heilongjiang, Jilin, Liaoning and Shanxi Provinces, and in the Nei Monggol Autonomous Region, revealed no fossils of saiga antelope. Care was taken to distinguish possible *Saiga* skull fragments from those of *Gazella*, on the basis of the stronger sutur-line projections on the skull roof in *Saiga*, and the morphology of their horn cores when complete.

In the Ural mountains, the range of saiga at times extended to 62°N (Kuz'mina 1971, p.101, 109). Kuz'mina (1977, p.25, 41) further recorded postcranial remains,

which she attributed to Pleistocene saiga, from the course of the Ob River, implying that *Saiga* in western Siberia at times reached as far as the Arctic Circle. Yakutian finds from the basins of the rivers Balyktah, Alazeâ and čukoč, â were published by Lazarey & Tomskaâ (1987, p. 114—115, Tab. XX) as *Saiga borealis*. Since there are a

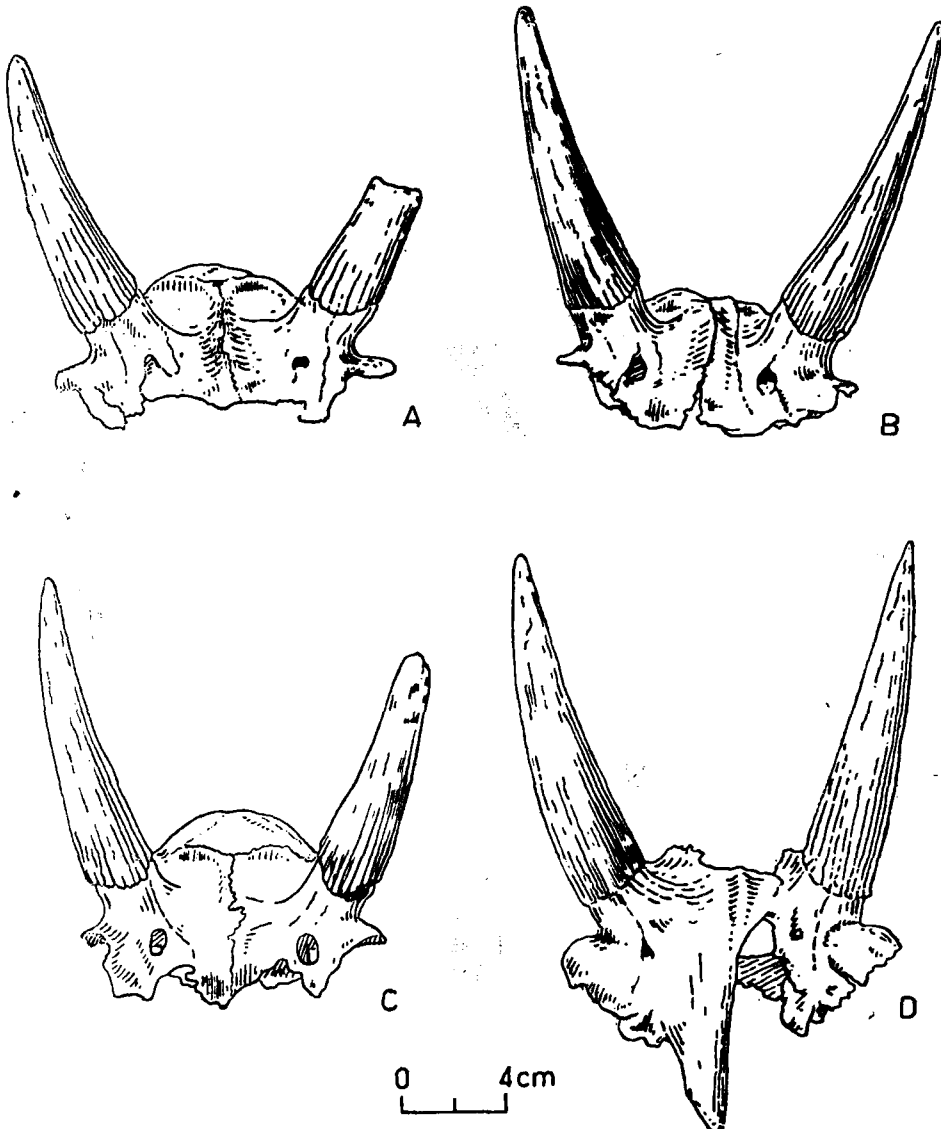


Fig. 2 Skull fragments of Pleistocene saiga, arranged to show the reduction in divergence of the horn core axes:

A-Ušajka River near Tomsk (western Siberia, USSR), stratigraphical position unclear (drawn after Alekseeva 1980, pl. XXX, fig. 1b)

B-Rhein-Herne-Kanal near Bottrop (Germany), Late Middle or Upper Pleistocene (drawn after a cast of the original)

C-Lower Kolyma River (northeastern Siberia, USSR), Olyor faunal complex (redrawn after Sher 1967, p. 107, fig. 2)

D-Binagadi (Apsheron peninsula, USSR), Last Interglacial (redrawn after Alekperova 1955, p. 14, fig. 1)

number of last-glacial (Wisconsin) *Saiga* finds from central Alaska and the arctic coastal area of northwest North America (Frick 1937, p. 546—547, Harington, 1978, p. 48—49, 1981, p. 196ff., 1984, p. 517ff.), *Saiga* in northeast Siberia must at some time have reached the Bering Strait. Further, a rather high absolute date on one Alaskan *Saiga* fossil (37 000+/-900 BP: Harington 1984, p. 520), and evidence of glaciation in the most northeasterly part of Siberia in the Late-glacial. (Sher 1967, p. 98), imply that the maximal extent of *Saiga* distribution must have occurred before the last phase of the Last Cold Stage.

Recently, absolute age determinations have been obtained on Last Cold Stage saiga from the southwestern and northwestern margins of its European range. A horn core from the Grotte de La Salpêtrière (Gard, France), from a horizon da-

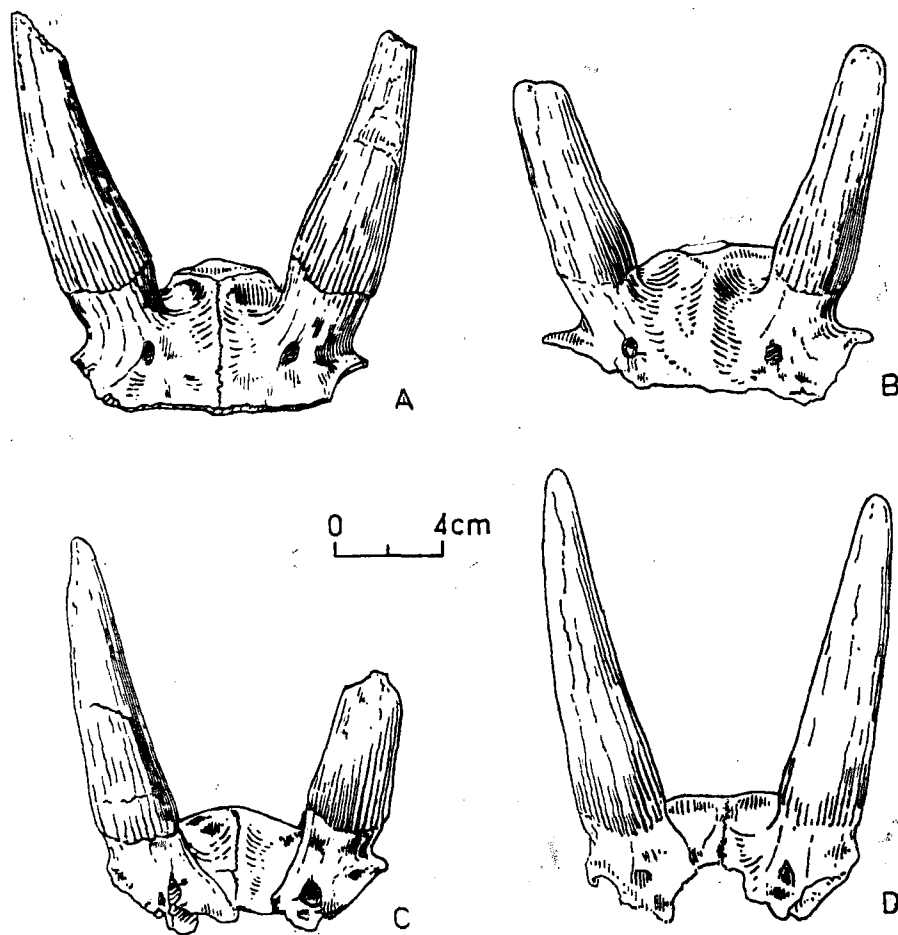


Fig. 3 Skull fragments of Pleistocene saiga, arranged to show the reduction in divergence of the horn core axes:

A-Twickenham (England), Last Cold Stage (drawn after Woodward 1890, p. 614 and after a photo by the British Museum (Natural History) London, A. Carrant)

B-Bernburg (Germany), Last Cold Stage (drawn after Toepfer 1956, pl. I, fig. 1)

C-Königsee/Garsitz (Germany), Last Cold Stage (drawn after Toepfer 1956, pl. I, fig. 2)

D-Pahren (Germany), ?Last Cold Stage (drawn after the original)

ted to 13000+/-200BP, was reported by Crégut-Bonnoure & Gagnière (1981, p. 38). Further, a calcaneum from Gough's Cave (Cheddar, England) was dated to 12 380+/-160BP (Currant 1987, p. 77). Both dates show a maximal extension of the range of saiga in Europe during the Late-glacial. This is supported by Magdalénian (Late Palaeolithic) art from the French sites of La Vache (Ariège), Gourdan (Haute-Garonne) and Rouffignac (Dordogne), which can be interpreted as representations of *Saiga* (Powers & Stringer 1975, p. 286—287). A bone engraving from Gourdan is particularly impressive and is clearly interpretable as *Saiga*. A series of absolute dates on Late Palaeolithic horizons in southwest France, containing fossils clearly identifiable as *Saiga*, was given by Delpech (1983, p. 208—210). These dates suggest that, in this area at least, there were two phases of dispersal of the genus within the Late-glacial.

Although saiga remains from the Late Pleistocene/early Holocene of northeast Siberia have mostly been referred to a special subspecies *S. tatarica borealis* (Cerskij, 1876; see H.-D. Kahlke 1975, p. 138, Veresagin & Baryshnikov 1982, p. 273), finds from palaeolithic localities of the Crimea and the southwestern USSR are identical to the recent form (*S. tatarica tatarica* (Linnaeus, 1766)). The taxa *S. prisca* Nehring, 1891 and *S. ricei* Frick, 1937, from Europe and Alaska respectively, may be younger synonyms of *S. tatarica borealis* (see Harington 1981, p. 213, Baryshnikov & Tikhonov 1989, p. 626).

Evolutionary trends shown by fossil saiga include an increase in the massivity of the horn cores, reduction of their angle of divergence, and lessening of the distance between their bases (R.-D. Kahlke 1990). Because the taxonomy of the genus *Saiga* needs revision, two morphotypes were tentatively suggested by R.-D. Kahlke (1990). The "Bottrop type" (named after the locality of Bottrop (Westfalia, Germany)) includes more primitive forms from the penultimate glacial complex, the Last Interglacial, and possibly the early last glacial complex in Eurasia (Fig. 2, pl. I, 1). The "Pahren type" (named after the locality of Pahren (Thüringia, Germany)) is represented mainly by European skull fragments of Weichselian age (Fig. 3, pl. I, 2)). It should be possible in the future to combine this classification with that suggested by Baryshnikov & Tikhonov (1989) using the length of the nasal and the size of the teeth.

Recent *S. tatarica tatarica* occurs in the steppe and semi-arid zones of the Kalmykian ASSR and Kazakhstan (for data on distributional changes in historical times, see Bannikov 1963, p. 54—59). The smaller Mongolian subspecies (*S. tatarica mongolica* Bannikov, 1946) occurs only as an isolated population in the basin of the Large Western Lakes in Mongolia (Bannikov 1963, p. 59).

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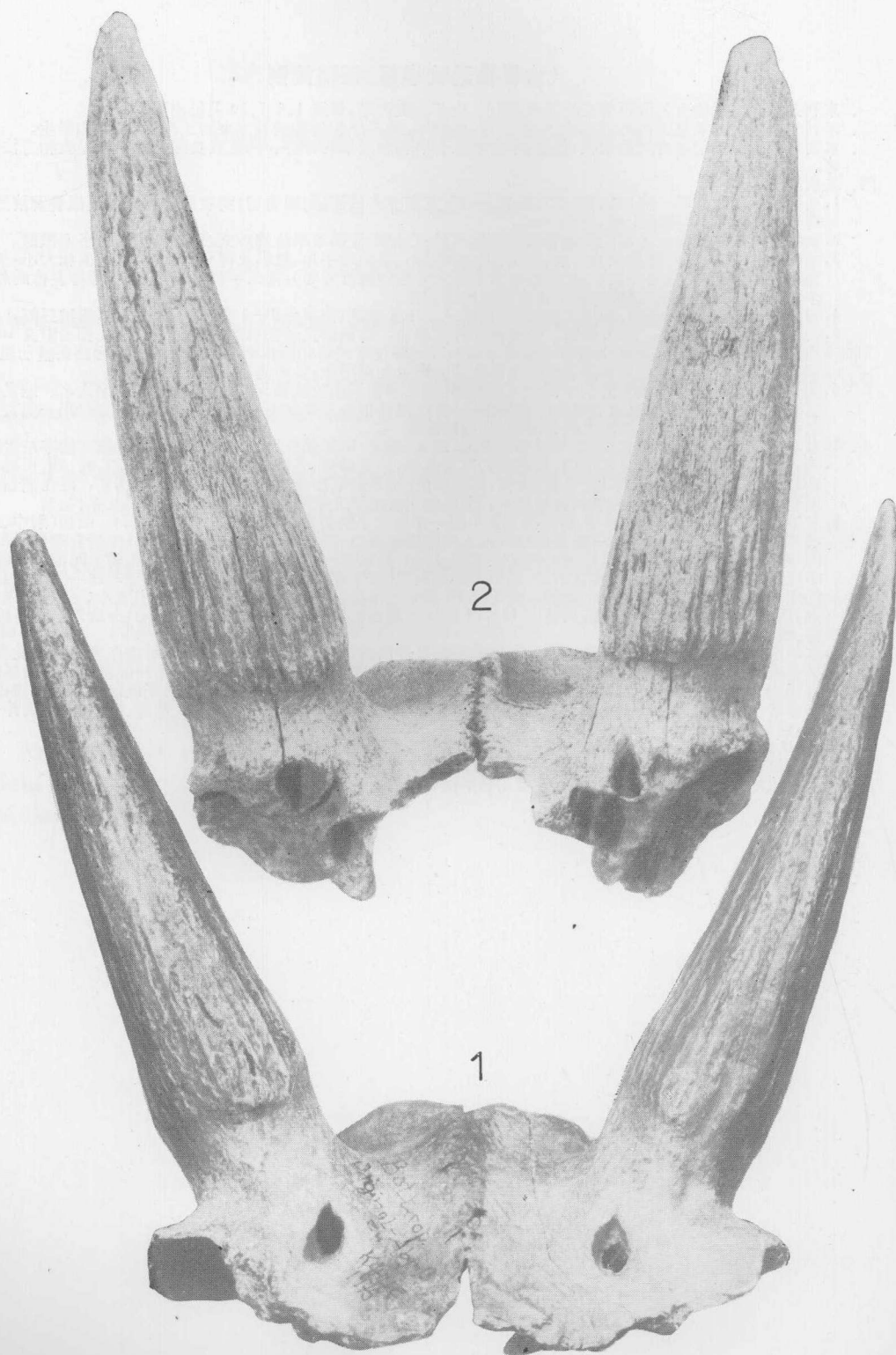
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R.D. 卡尔克: 古北区 *Saiga* 属(偶蹄目、牛科)在更新世时期的地理分布和 图版 I
进化历史



1. *Saiga tatarica* ssp. (frontal view of a skull fragment, cast), Rhein-Herne-Kanal near Bottrop (Germany), original stored in the Museum für Ur- und Ortsgeschichte Bottrop $\times 3/5$
2. *Saiga tatarica tatarica* (Linnaeus, 1766) (frontal view of a skull fragment), Pahren (Germany), stored in the Institut of Quaternary Palaeontology Weimar $\times 3/5$ (photos: T. Korn)