THE TAXONOMIC POSITION OF THE CHALICOTHERIID PERISSODACTYL *KYZYLKAKHIPPUS ORLOVI* FROM THE OLIGOCENE OF KAZAKHSTAN

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ABSTRACT. The type of *Kyzylkakhippus orlovi*, reaffirmed as probably teeth dp^2–dp^4 from Oligocene deposits at Kyzyl-kak, Kazakhstan, is compared to upper deciduous teeth of *Schizotherium priscum*. This comparison, and the known presence of *S. turgaicum* in the Kyzyl-kak fauna, suggest that *K. orlovi* is a junior synonym of *S. turgaicum*. Upper teeth of *S. turgaicum* are otherwise poorly known. Because '*K. orlovi*' is thereby referable to the Schizotheriinae, there is no definite evidence of the Chalicotheriinae in the Old World prior to the Aquitanian or Burdigalian. *Chalicotherium* and *Nestoritherium* alone can at present be included in the Chalicotheriinae.

IN 1964 Gabunia and Belyaeva erected a new genus and species, *Kyzylkakhippus orlovi*, for a deciduous upper dentition from middle Oligocene deposits at Kyzyl-kak, Kazakhstan. They identified the type, from the collection in the Palaeontological Institute of the Academy of Sciences of the U.S.S.R., Moscow (specimen no. PIN 2259-330), as dp^2–dp^4 of an anchitheriine equid. Thenius (1968), however, noted morphological differences between the type dentition and that of known horses, and the zoogeographic difficulties of suggesting that an equid or palaeotheriid had existed in Kazakhstan in the middle Oligocene; he correctly referred the genus to the Chalicotheriidae. Thenius also reinterpreted the type dentition as dp^3–M^1 and suggested especially close affinity to the Chalicotheriinae. Malcolm C. McKenna, who also questioned the referral of *Kyzylkakhippus* to the Equidae (pers. comm.), made the cast of the type specimen shown in text-fig. 2. My study of this cast and of the drawing of the type figured by Gabunia and Belyaeva (1964, fig. 6) leads me to accept the original identification as dp^2–dp^4 but also to accept Thenius's placement of *Kyzylkakhippus* in the Chalicotheriidae. However, I consider that it belongs to the Schizotheriinae rather than to the Chalicotheriinae.

The family Chalicotheriidae is thought to have arisen in the late Eocene or early Oligocene from members of the family Eomoropidae (Radinsky 1964). Two subfamilies, the Chalicotheriinae and Schizotheriinae, are recognized. Generally speaking, the Chalicotheriinae, consisting only of the genera *Chalicotherium* and *Nestoritherium*, have undergone quite pronounced changes in foot structure, and on this basis are easily distinguished from all known schizotheriines. Chalicotheriine dentition is conservative, however, and the upper molars remain low-crowned and quadrate. In the Schizotheriinae (*Schizotherium*, *Borissiakia*, *Moropus*, *Phyllotillon*, *Ancylotherium*) postcranial modifications have occurred much more gradually than in the Chalicotheriinae, and never attain the derived state seen in even the most primitive known representatives of *Chalicotherium* (*C. pilgrimi*, *C. rusingense*). Schizotheriines modify the dentition more than do chalicotheriines, elongating the

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molars and increasing the crown height, but they do so gradually. Over a short span of time, changes in schizotheriine dentitions are relatively few. *Schizotherium* lacks the derived foot structure of the Chalicotheriinae, but its teeth are less elongated than in most other schizotheriines. The exact relationship of *Schizotherium* to chalicotheriines and other schizotheriines is not clear, but it is probably very near the common ancestry of all schizotheriines. It is possible also that ancestry of the Chalicotheriinae is close to *Schizotherium* and perhaps lay within a species which at the present state of knowledge would be placed within *Schizotherium*.

The best-known species of *Schizotherium*, *S. priscum* and *S. turgaicum*, are represented by both dental and postcranial remains. Postcranial elements provide the most certain means both for allying and differentiating the two species. Compared to elements of other schizotheriine genera, the footbones are of smaller absolute size, metatarsals are longer compared to their width (see, for example, Coombs 1974, table 1), metacarpals and metatarsals are not so closely interarticulated, and fusion between phalanges is unknown. (*Schizotherium* shares the latter three character states with *Borissiakia* but differs from that genus in, among other features, the absence of a cuboid facet from the distal surface of the astragalus.) Among features which differentiate known postcranials of *S. turgaicum* from those of *S. priscum* are the loss or strong reduction of a trapezium in the carpus, and the apparent loss of articulation for the ectocuneiform on metatarsal II in the former species (Coombs, manuscript). Loss or reduction of the trapezium occurs more than once within the Schizotheriinae and seems to allow additional flexion of the manus. *S. priscum* is known primarily from Oligocene fissure fillings in France (Phosphorites of Quercy), and *S. turgaicum* is an element of the middle Oligocene indricothere fauna well known from Kazakhstan.

Lower teeth have been regularly used to differentiate between species of *Schizotherium* (Matthew and Granger 1923; Gabunia 1951; Belyaeva 1954; Dashzeveg 1974), but upper teeth are poorly known, except in *S. priscum*, and have been little used in interspecific taxonomy. Because of their low crowns and lack of obvious elongation, *Schizotherium* upper molars have on occasion been referred to *Chalicotherium* by workers who did not take postcranial characteristics into sufficient account. Gaudry (1875*a*), before the association between chalicothere teeth and postcranials had been recognized, gave the name '*Chalicotherium modicum*' to some upper cheek teeth from the Phosphorites. Filhol (1894) later suggested that '*C. modicum*' might be the same animal as *S. priscum* (which he then referred to *Ancylotherium*), a conclusion with which I fully agree. Similarly, the worn upper molariform tooth of *S. turgaicum* figured by Borissiak (1921, pl. 7, fig. 1) led von Koenigswald (1932, p. 22) to classify the species as *C. turgaicum*. I believe that the same mistake has been made in the case of *Kyzylkakhippus orlovi*, and that this is really a junior synonym of *S. turgaicum*.

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA
Order PERISSODACTYLA
Suborder CHALICOTHERIOIDEA Gill, 1872
Family CHALICOTHERIIDAE Gill, 1872
Subfamily SCHIZOTHERIINAE Holland and Peterson, 1914
Genus SCHIZOTHERIUM Gervais, 1876
Species *Schizotherium turgaicum* Borissiak, 1920

1921 *Schizotherium turgaicum*: Borissiak, p. 43 (English version of Borissiak 1920, above); Matthew 1929, p. 519; Colbert 1935, p. 6; Gabunia 1951, p. 282; Belyaeva 1954, p. 52; Dashzeveg 1974, p. 76.
1932 *Chalicotherium turgaicum*: von Koenigswald, p. 22.
1935 *Macrotherium turgaicum*: Colbert, p. 12.
1964 *Kyzylkakhippus orlovi* Gabunia and Belyaeva, p. 129.
1968 *Kyzylkakhippus orlovi*: Thenius, p. 347.
1969 *Kyzylkakhippus orlovi*: Thenius, p. 573.

Discussion. PIN 2259-330, a deciduous upper dentition, is the holotype and only specimen referred to '*K. orlovi*'. PIN 1442-253, designated as the lectotype of *S. turgaicum* (see Belyaeva 1954), is a lower jaw ramus containing P_4–M_2. The only published upper tooth hitherto referred to *S. turgaicum* is a worn quadrate molariform tooth figured by Borissiak (1921, pl. 7, fig. 1). Although both Borissiak (1921, p. 43) and Belyaeva (1954, p. 52) identified this tooth as an upper molar (?M^2), it is small (17·5 mm long according to Borissiak 1921, p. 43). The lower teeth of the lectotype of *S. turgaicum* are also smaller than their very few known counterparts in *S. priscum*. On the other hand, metatarsals of *S. turgaicum* figured by Borissiak (1921) are in general larger than known metatarsals of *S. priscum*. It is not possible on the basis of limited specimens to reach a conclusion on the relative sizes of feet and teeth in the two species. Size sexual dimorphism in chalicotheriids (Coombs 1975) is a further confusing factor in such a determination. The length of the upper molariform tooth figured by Borissiak (1921) may have been reduced by the wear it shows, but the small size suggests that identification as M^1 or even dp^3 or dp^4 is not unreasonable. In any case, though I detect no particular differentiating features between the two specimens, it is so badly worn that it cannot be meaningfully compared with PIN 2259-330. In the absence of any other published upper teeth of *S. turgaicum*, I have compared PIN 2259-330 with upper teeth of *S. priscum*.

For purposes of comparison with PIN 2259-330, the most useful specimen is a maxilla from the Phosphorites of Quercy; this was given the numbers PQ 359–PQ 362 at the Muséum d'Histoire Naturelle de Lyon, Lyon, France, but was cast as specimen no. AMNH 10494 in the collection of the Department of Vertebrate Paleontology of the American Museum of Natural History, New York. The teeth in this specimen (text-fig. 1) can be identified as dp^2–M^2 and are probably referable to *S. priscum*. The posterior two teeth, M^1 and M^2, are generally similar to M^1 and M^2 on left and right uncatalogued maxillae of *S. priscum* in the Muséum National d'Histoire Naturelle, Paris, figured respectively by Filhol (1877) and Gaudry (1875*b*). (The specimens figured by Filhol and by Gaudry are very similar to one another and, if from the same locality, might be two sides of the same individual; M^2 is slightly

more symmetrical than M^2 of AMNH 10494, but both molars are approximately as quadrate as those of AMNH 10494.) The most posterior tooth of AMNH 10494 is probably not an M^3, because M^3 of *S. priscum* is strongly asymmetrical, with the posterior part of the ectoloph especially reduced (text-fig. 3). The anterior three teeth of AMNH 10494 should therefore be regarded dp^2–dp^4. These teeth are of similar morphology to one another and are all molariform. The molariform structure of dp^2, as thus identified, is remarkable in the sense that dp^2 in *Moropus*, where several immature maxillae are known, is closer in morphology to P^2 than it is to dp^3, dp^4, or to the permanent molars. Permanent premolars, including P^2, of *S. priscum* are generally similar to those of *Moropus*. Lower deciduous teeth known in *Schizotherium* and other schizotheriines are not helpful in elucidating this question. Tooth dp_2 of *Moropus* sp. from Aquitanian deposits of St-Gérand-le-Puy, France, is elongated compared to its width but is clearly not molariform (Coombs 1974). A dp_3 in an uncatalogued specimen of *S. priscum* (Field Lot Bach 1893-11 in the Muséum National d'Histoire Naturelle, Paris) corresponds closely in morphology to dp_3 of *Moropus* and thus suggests a possible correspondence of dp_2^2 as well. Tooth dp_2 of *Ancylotherium* (*Ancylotherium*) *pentelicum* from Samos (AMNH 23001; see Coombs 1973) is, however, partly molariform.

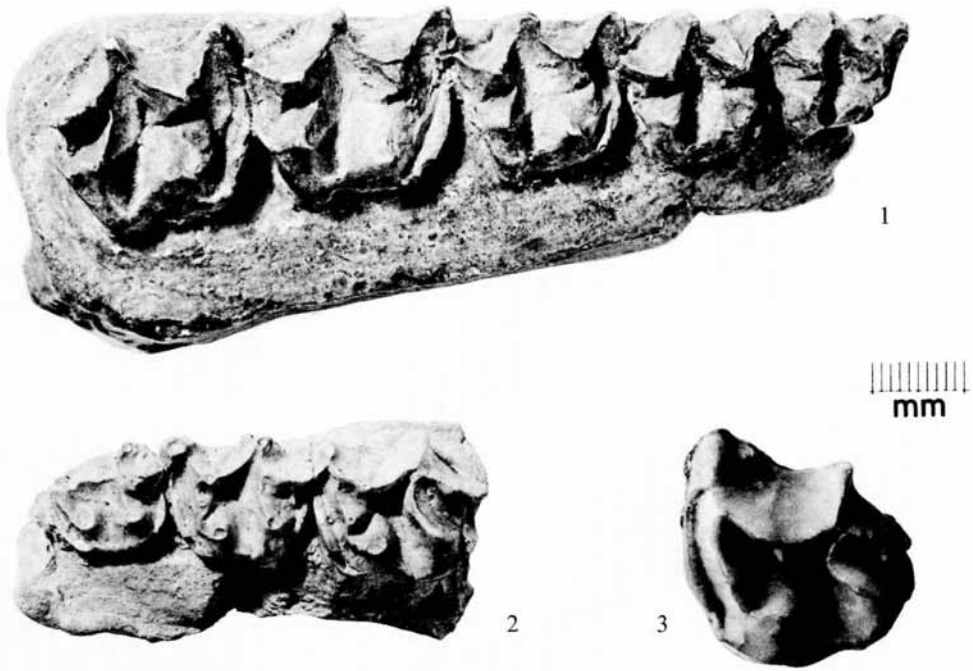
Identification of the upper teeth of AMNH 10494 as dp^2–M^2 makes it more likely that Gabunia and Belyaeva (1964) correctly identified PIN 2259-330, the type of '*K. orlovi*', as dp^2–dp^4. Further examination and comparison with AMNH 10494 suggest that the size difference between the posterior two teeth of PIN 2259-330 is approximately the same as that between dp^3 and dp^4 of AMNH 10494 (see Table 1);

TABLE 1. Greatest length in millimetres along ectoloph of upper molariform teeth of PIN 2259-330 and AMNH 10494. Measurements of PIN 2259-330 from Gabunia and Belyaeva (1964, p. 129).

Tooth	PIN 2259-330	AMNH 10494
dp^2	Broken (approx. 14·0)	16·1
dp^3	17·0	18·0
dp^4	19·5	19·7
M^1	—	22·6
M^2	—	22·8

it is also about the same order of magnitude as the size increment from dp^2 to dp^3. This observation conflicts with Thenius's view that there is a proportionately large size difference between the posterior two teeth. In fact, abrupt size increase does not seem to be a good method of distinguishing dp^4 from M^1 in *Schizotherium*. In AMNH 10494 the increase from dp^4 to M^1 is not much more than the size increments between dp^2, dp^3, and dp^4. In that little-worn specimen there is also a notably small size increase from M^1 to M^2, despite the fact that in many chalicotheriid specimens M^1 is shorter than M^2, possibly because of loss of length by wear during life. The teeth of PIN 2259-330 correspond closely in size to dp^2–dp^4 of AMNH 10494 but, in view of the difficulties mentioned above in making comparisons between *S. priscum* and *S. turgaicum* in tooth and foot size, one must not put undue emphasis on this similarity.

As thus identified, dp^2–dp^4 of PIN 2259-330 and of AMNH 10494 are very similar



TEXT-FIG. 1. Right dp^2–M^2 referred to *Schizotherium priscum*, AMNH 10494, a cast of PQ 359–PQ 362 of the Muséum d'Histoire Naturelle de Lyon. From the Phosphorites of Quercy, Oligocene, of France.

TEXT-FIG. 2. Cast of PIN 2259-330, left dp^2–dp^4, holotype of '*Kyzylkakhippus orlovi*'. From Oligocene deposits of Kyzyl-kak, Kazakhstan.

TEXT-FIG. 3. Left M^3 of uncatalogued specimen (Lot Number Bach 1903-20 at the Muséum National d'Histoire Naturelle, Paris) referred to *S. priscum* from the Phosphorites of Quercy, Oligocene, of France.

All figures ×1·5.

in morphology. Particularly noticeable in both are the complete molarization of dp^2 and the presence of a crista on at least dp^4. On PIN 2259-330, dp^4 is less worn than that of AMNH 10494, and therefore the origin of the metaloph from the ectoloph is closer to the mesostyle; such a variation as a result of differential wear is also seen within a single species of *Moropus*. Other minor differences between the two specimens, for example the stronger protoconule on dp^4 of PIN 2259-330, are also attributable to individual variation or differential wear. The small cuspule near the anterolabial base of the mesostyle on dp^3 and dp^4 of PIN 2259-330 is of uncertain significance. Clearly M_1 had not yet erupted in PIN 2259-330, for the posterior part of dp^4 is unworn. This is consistent with the relative lack of wear on the other teeth. In general, few differences occur between AMNH 10494 and the type of '*K. orlovi*', and most of the differences that do occur can be interpreted in the light of wear. Even if the two specimens were to be identified respectively (after Thenius) as dp^3–M^3 and dp^3–M^1, the basic similarity between them would not be changed. Certainly the generic identity of *Kyzylkakhippus* cannot be maintained.

Thenius (1968, p. 348) listed the following members of the Oligocene Indricotherium fauna previously described from Kyzyl-kak, the type locality of '*K. orlovi*': *Cricetodon deploratus*, *C. caducus*, *Hyaenodon aymardi*, Tragulidae indet., *Colodon orientalis*, *Ergilia kazachstanica*, *Indricotherium transouralicum*, *Allacerops* sp., *Schizotherium turgaicum*, and '*K. orlovi*'. The occurrence of *S. turgaicum* is especially important. The lack of described unworn upper teeth of *S. turgaicum* makes it difficult to make a direct comparison with PIN 2259-330, but probably explains why Gabunia and Belyaeva misidentified this specimen as an anchitheriine equid. Clearly the presence of *S. turgaicum* in the Kyzyl-kak faunal assemblage increases the likelihood that '*K. orlovi*' is a junior synonym of *S. turgaicum*. The absence of significant differences from the worn upper tooth of *S. turgaicum* figured by Borissiak (1921) completes the case for synonymy.

Though a full rediscussion of the genus *Schizotherium* would be helpful at the present time, such work is hampered by fragmentary material. In view of Colbert's (1935) conclusion that *S. turgaicum* is an unusually primitive representative of the genus, it is worth pointing out that his notion was based partly on the worn upper tooth figured by Borissiak (1921), and also that upper molars of all *Schizotherium* species are quadrate relative to those of other schizotheriines. *S. turgaicum*, it should be remembered, shows some character states that are clearly not primitive—for example, the loss or reduction of the trapezium in the manus, and the apparent loss of ectocuneiform contact with metatarsal II in the pes. The similarity of PIN 2259-330 to upper deciduous teeth of *S. priscum* adds to the postcranial evidence that *S. turgaicum* clearly belongs to *Schizotherium* and does not represent the separate, primitive genus that Colbert (1935) suggested.

Because '*K. orlovi*' can be referred to *Schizotherium*, there is still no definite evidence of representatives of the Chalicotheriinae prior to the Aquitanian or Burdigalian of the Old World. Skinner (1968, p. 12) attributed *Oreinotherium bilobatum* (Cope, 1891) from the Cypress Hills Oligocene of Saskatchewan, Canada, to the Brontotherioidea *incertae sedis* as a *nomen inquirendum*. After re-examining the heavy mandibular ramus and separate lower deciduous tooth referred to this species, I fully agree with Skinner's assessment. *O. bilobatum* had been previously referred to the

Chalicotheriinae (Cope 1891; Russell 1934), but there is no evidence that the Chalicotheriinae were present in the New World during the Oligocene, or indeed at any other time.

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REFERENCES

BELYAEVA, E. I. 1954. Chalicotheres of the Soviet Union and Mongolia. *Trudy palaeont. Inst. Akad. Nauk SSSR*, **55,** 44–84, pls. 1–3. [In Russian.]

BORISSIAK, A. A. 1920. On the remains of Chalicotherioidea from the Oligocene of Turgai. *Bull. Acad. Sci. St. Petersburg* (6), **13,** (1919), 687–710, 1 pl. [In Russian.]

—— 1921. The remains of Chalicotherioidea from the Oligocene deposits of Turgai. *Ezheg. russk. paleont. Obshch.* **3,** 43–51, pl. 7.

COLBERT, E. H. 1935. Distributional and phylogenetic studies on Indian fossil mammals. III. A classification of the Chalicotherioidea. *Am. Mus. Novit.* **798,** 1–16.

COOMBS, M. C. 1973. The Schizotheriinae (Mammalia, Perissodactyla, Chalicotheriidae), with emphasis on the genus *Moropus*. 1973 Ph.D. thesis, Columbia Univ., 463 pp., Diss. Abstr. 34: 2202B, Univ. Microfilms, Ann Arbor, Michigan.

—— 1974. Ein Vertreter von *Moropus* aus dem europäischen Aquitanien und eine Zusammenfassung der europäischen postoligozänen Schizotheriinae (Mammalia, Perissodactyla, Chalicotheriidae). *Sber. öst. Akad. Wiss., Math.-naturw. Kl.* **182,** 273–288, pls. 1–3.

—— 1975. Sexual dimorphism in chalicotheres (Mammalia, Perissodactyla). *Syst. Zool.* **24,** 55–62.

COPE, E. D. 1891. On Vertebrata from the Tertiary and Cretaceous rocks of the North-West Territory. I. The species from the Oligocene or lower Miocene beds of the Cypress Hills. *Contr. Can. Palaeont.* **3,** 1–25, pls. 1–14.

DASHZEVEG, D. 1974. The chalicothere *Schizotherium avitum* Matthew and Granger from the Oligocene of Ergillian-dzo, eastern Gobi, and a review of vertebrates from this locality. *Fauna and Biostratigraphy of the Mesozoic and Cenozoic of Mongolia. In* KRAMARENKO, N. N. (ed.), *Trans. Joint Soviet-Mongolian Paleont. Exped.* **1,** 74–79. [In Russian.]

FILHOL, H. 1887. Recherches sur les Phosphorites du Quercy, Étude des fossiles qu'on y rencontre et spécialement des mammifères. *Annls. Sci. geol.* **8,** 1–340, pls. 1–26.

—— 1894. Observations concernant quelques mammifères fossiles nouveaux du Quercy. *Annls. Sci. nat., Zool.* (7), **16,** 129–150.

GABUNIA, L. K. 1951. Concerning chalicothere remains from Tertiary deposits of Gruzia. *Soobshch. Akad. Nauk. gruz. SSR*, **12,** 279–284. [In Russian.]

—— and BELYAEVA, E. I. 1964. Concerning a representative of the anchitheriines (Anchitheriinae) from the Oligocene of Kazakhstan. *Bull. Acad. Sci. gruz. SSR*, **35,** 125–132. [In Russian.]

GAUDRY, A. 1875*a*. Sur de nouvelles pièces fossiles découvertes dans les phosphorites du Quercy. *C.R. Acad. Sci., Paris*, **81,** 1113–1115.

—— 1875*b*. Sur quelques pièces de mammifères fossiles qui ont été trouvés dans les Phosphorites du Quercy. *J. Zool.* **4,** 518–527, pl. 18.

GERVAIS, P. 1876. *Zoologie et paléontologie générales. Nouvelles recherches sur les animaux vertébrés vivantes et fossiles*. Paris, ser. 2, 72 pp., 12 pls.

GILL, T. 1872. Arrangement of the families of mammals with analytical tables. *Smithson. misc. Collns*, **11,** 1–98.

HOLLAND, W. J. and PETERSON, O. A. 1914. The osteology of the Chalicotheroidea with special reference to a mounted skeleton of *Moropus elatus* Marsh, now installed in the Carnegie Museum. *Mem. Carneg. Mus.* **3,** 189–406, pls. 48–77.

KOENIGSWALD, G. H. R. VON. 1932. *Metaschizotherium fraasi* n. g. n. sp., ein neuer chalicotheriide aus dem Obermiocän von Steinheim A. Albuch. *Palaeontographica, Beitr. Naturg. Vorzeit*, Suppl.-vol. **8** (8), 1–24, pls. 1–3.

MATTHEW, W. D. 1929. Critical observations upon Siwalik mammals. *Bull. Am. Mus. nat. Hist.* **56,** 437–560.

—— and GRANGER, W. 1923. The fauna of the Ardyn Obo Formation. *Am. Mus. Novit.* **98,** 1–5.

RADINSKY, L. B. 1964. *Paleomoropus*, a new early Eocene chalicothere (Mammalia, Perissodactyla), and a revision of Eocene chalicotheres. Ibid. **2179,** 1–28.

RUSSELL, L. 1934. Revision of the lower Oligocene vertebrate fauna of the Cypress Hills, Saskatchewan. *Trans. R. Can. Inst.* **20,** 49–65, pls. 7–10.

SKINNER, M. F. 1968. A Pliocene chalicothere from Nebraska, and the distribution of chalicotheres in the Late Tertiary of North America. *Am. Mus. Novit.* **2346,** 1–24.

THENIUS, E. 1968. Zur systematischen Stellung von *Kyzylkakhippus* (Perisoodactyla, Mamm.) aus dem Oligozän von Kazachstan. *Anz. öst. Akad. Wiss., Math.-naturw. Kl.* **1968,** 347–354.

—— 1969. Stammegeschichte der Säugetiere (einschliesslich der Hominiden). *Handb. Zool.* **8,** 369–722.

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