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The horses (Mammalia, Equidae) from the early Wuermian of Villa Seckendorff, Stuttgart-Bad Cannstatt, Germany

By Ann Forsten, Helsinki, and Reinhard Ziegler, Stuttgart

With 1 Plate, 10 Figures, 6 Tables

Summary

The horses of Villa Seckendorff, an early Wuermian fauna from Stuttgart-Bad Cannstatt, are presented. The bigger *Equus germanicus* is the most common large mammal species of the fauna. *Equus hydruntinus* is represented by one of the richest samples from Germany. By means of morphological and metrical comparisons with several European samples the relationships to these and closely related species are discussed. Both horses of Villa Seckendorff represent well-known species, often found in sympatry.

Zusammenfassung

Die Pferde der Villa Seckendorff, einer frühwürmzeitlichen Fauna aus Stuttgart-Bad Cannstatt, werden vorgestellt. Das größere *Equus germanicus* ist die häufigste Großsäugetierart der Fauna. *Equus hydruntinus* ist durch eine der umfangreichsten Stichproben aus Deutschland repräsentiert. Mittels morphologischer und metrischer Vergleiche mit vielen europäischen Stichproben werden die Beziehungen dieser und nahe verwandter Arten diskutiert. Beide Pferde von der Villa Seckendorff sind bekannte Arten, die oft sympatrisch vorkommen.

1. Introduction

History. – The Stuttgart area is well known for its Pleistocene fossiliferous sites. Quaternary paleontology has a nearly 300 years old tradition here. Thus, already in the year 1700 fossil remains were found near Uffkirche. Duke Eberhard Ludwig initiated excavations, which resulted in lots of bones and teeth of mammoth and other Wuermian large mammals.

The Pleistocene finds in the Stuttgart area mainly derive from two types of sediments: periglacial sediments, such as loesses, and interglacial travertines. The interglacial mammal faunas of Stuttgart all derive from travertines as side products of commercial travertine mining in quarries in Untertürkheim, Bad Cannstatt, and Münster, presently incorporated in greater Stuttgart. Close to the present level of the River Neckar are the Eemian travertines of Untertürkheim and Cannstatt-Ganz-

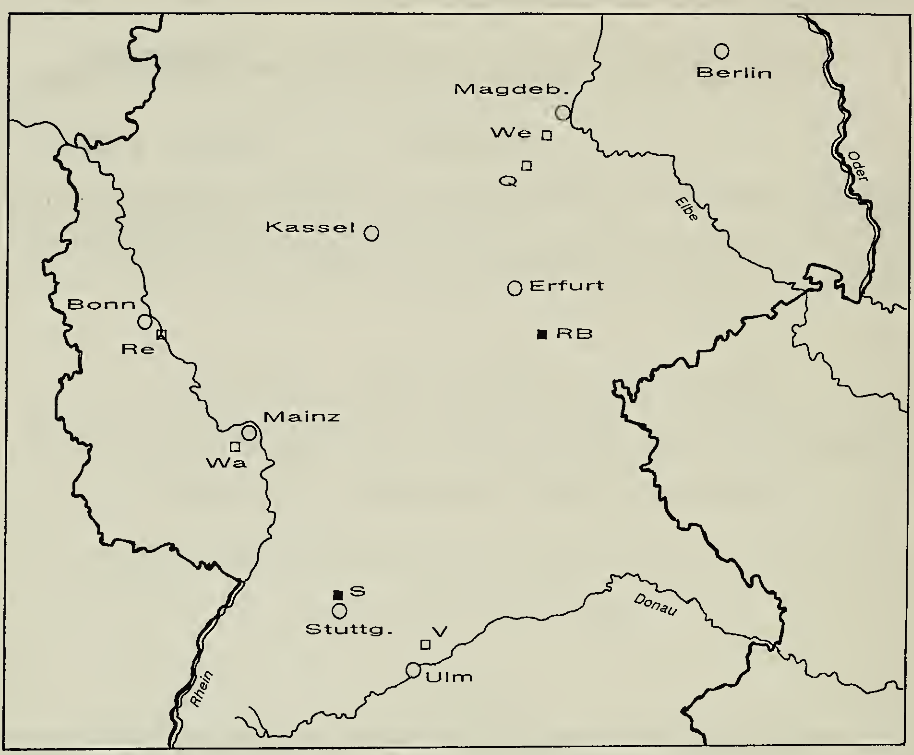

Fig. 1. Map of Germany with the equid sites treated in this volume. Empty squares: *Equus germanicus*; full squares: *Equus germanicus* and *Equus hydruntinus*.

hornstrasse, which have yielded faunas and human artifacts. The higher travertines, still exploited in quarries between Cannstatt and Münster, have yielded Holsteinian faunas and human artifacts.

In 1957, when excavating the foundation for an old people's home, the Villa Seckendorff on Freiligrathstrasse 3 in Bad Cannstatt, a fissure filling and a small cave in the karstic travertine were cut. The travertine dates from the Holsteinian (Reiff 1986, Table 2), but the fissure was filled only in the early Wuermian glacial (Reiff 1965, Adam 1966). A field campaign in the same year, initiated by the Staatliches Museum für Naturkunde Stuttgart, unearthened a rich fauna of small and large mammals, birds, and lower vertebrates in the fissure loam (for a list of the large mammals in the Seckendorff fauna, see Table 1). Hundreds of jaws and bones of mammoth, woolly rhino, horses, bison, aurochs, deer, and carnivores were found closely packed. Many bones were gnawed by cave hyaenas and Adam (1966) interpretes the site as a hyaena den. Reiff (1981) believes the broken bones of the large mammals to be the result of human activity. The small mammals, the herptiles and fish were evidently accumulated by owl pellets.

The micromammals from Seckendorff have been published by Koenigswald (1985) and the herptiles and fish by Böttcher (1994). In the present paper we report on the two species of horse. With an estimated 52 individuals, the horses constitute more than one third of the large mammal fauna. The sample of *Equus hydruntinus* Regalia is one of the largest from Germany.

Tab. 1. List of large mammals from Villa Seckendorff, with minimum number of individuals (MNI) based on most common element, all age groups.

Species	MNI (n)	%
Carnivora		
Canis lupus L.	8	5.6
Vulpes vulpes L.	5	3.6
Ursus arctos L.	1	0.7
Ursus spelaeus ROSENM. & HEINROTH	1	0.7
Mustela eversmanni L. s. *putorius* LESSON	1	0.7
Crocuta crocuta spelaea (GOLDFUSS)	16	11.6
Panthera leo spelaea (GOLDFUSS)	3	2.2
Proboscidea		
Mammuthus primigenius (BLUMENBACH)	8	5.8
Perissodactyla		
Equus germanicus NEHRING	43	31.2
Equus hydruntinus REGALIA	9	6.5
Coelodonta antiquitatis (BLUMENBACH)	8	5.8
Artiodactyla		
Megaloceros giganteus (BLUMENBACH)	4	2.9
Cervus elaphus L.	7	5.1
Rangifer tarandus (L.)	2	1.4
Capreolus capreolus (L.)	4	2.9
?Rupicapra rupicapra (L.)	1	0.7
Bos primigenius BOJANUS	18	13.0
Bison priscus ssp.	2	1.4

Biostratigraphy. – The age of the Seckendorff fauna is mainly based on the small mammals (KOENIGSWALD 1985). Already at a first glance their species composition reflects the late Pleistocene age of the assemblage, but only a few taxa allow a more precise age determination within the late Pleistocene. The relative enamel thickness of the molars of *Arvicola* clearly show their affiliation to the recent species *A. terrestris* (L.). Accordingly, the fauna cannot be earlier than the last glacial.

The early Wuermian faunas (> 30000 BP) are characterized by their diversity of large mammals. In the late Wuermian (< 20000 BP) of Southern Germany, *Crocuta* and *Megaloceros* disappeared and *Ursus spelaeus* ROSENMÜLLER & HEINROTH, *Mammuthus*, and *Coelodonta* became rare. The late Wuermian faunas also differ from the earlier ones in the dominance and derived evolutionary level of the collared lemming *Dicrostonyx*. The presence of the less derived subspecies *D. gulielmi rotundus* AGADJANIAN & KOENIGSWALD and the equal frequency of *Dicrostonyx* and *Lemmus* in the fauna of Seckendorff evince its early Wuermian age. In the mid-Wuermian, the small suslik, *Spermophilus citelloides* (KORMOS), present at Seckendorff, is replaced by the larger *S. superciliosus* (KAUP), the earliest record of which in Southern Germany dates from a. 40000 BP.

The early Wuermian is characterized by the appearance of steppe elements, such as *Cricetus cricetus major* (WOLDRICH), *Spermophilus citelloides*, *Lagurus lagurus* (PALLAS), *Allactaga major* (KERR), and *Hystrix vinogradovi* (ARGYROPULO). A classical fauna, comprising some of these elements, is Roter Berg, near Saalfeld, Germany (NEHRING 1880, STEHLIN & GRAZIOSI 1935). In the Seckendorff fauna, steppe elements occur together with typical glacial species, such as *Dicrostonyx*, *Lemmus*, *Rangifer, Coelodonta* and *Mammuthus*, and with mountain taxa, such as *Marmota* and *Microtus nivalis* (MARTINS). The absence of *Cricetus* and *Lagurus* may be due to local ecological factors.

The Seckendorff fauna is probably slightly younger than the interstadials Saint-Germain I and II, corresponding to the Brörup and Odderade interstadials, dated > 69000, respectively 64000 and 60000 B.P. (WOILLARD & MOOK 1982), and between 110000–75000 B.P. (MANGERUD 1991, MENKE 1991), but no exact correlation is as yet possible.

Ecology. – In the Seckendorff fauna, mammalian species of a temperate character, such as *Clethrionomys, Apodemus,* and *Capreolus,* occur only in low numbers and thus do not reflect interglacial conditions. Typical arctic forms, represented by *Mammuthus, Coelodonta, Rangifer, Dicrostonyx,* and *Lemmus,* and the mountain taxa *Microtus nivalis* and *Marmota,* rather indicate a cold climate. *Allactaga major* and *Spermophilus citelloides* are dwellers of open ground in a steppic environment. The co-occurrence of arctic, mountain, and steppe elements is typical of the cold stages of the middle and late Pleistocene (STORCH 1969).

KOENIGSWALD (1985), on the basis of the micromammals, believes that the annual mean temperature may have been less than 0° C, resulting in permafrost conditions. The presence of moist biotopes, even open water, is demonstrated by such taxa as *Talpa, Arvicola, Lemmus,* and *Microtus oeconomus* (PALLAS). Permafrost conditions do not exclude open water, which may occur due to low temperatures and low evaporation.

The lower vertebrates (BÖTTCHER 1994) affirm the glacial character of the Seckendorff fauna, but some species cannot endure permafrost although they may withstand winter mean temperatures down to −16° C. The mean July temperature must have been a. 17° C, judging from the present northernmost distribution of these species, reflecting the lower limits of their reproduction. According to BÖTTCHER (1994), permafrost is not necessary to explain the co-existence of animals requiring moist, respectively arid, conditions, as open water occurs even in steppe environments. The Villa Seckendorff is situated in the transitional area between the Neckar valley with its moist pastures and the more arid altiplane of the Schmidener Feld. The fossil fauna may have been brought together by predators from different biotopes of the surroundings.

Aims and methods. – In this paper we want to analyse and to compare the horses from Seckendorff with similar finds from elsewhere in Europe. Fossil samples of horses are best compared using quantitative methods based on measurements of the teeth and skeleton. Before the comparisons, the samples have to be analysed for homogeneity, e.g. in scatter plots and frequency diagrams. The statistical parameters, particularly the mean, standard deviation (s.d.), and coefficient of variation (V), are calculated. For comparison of samples we used scatter plots with major axises and 95% equiprobability ellipses (DEFRIESE-GUSSENHOVEN 1955) and UPGMA (= unweighted pair-group method using arithmetic averages) phenograms (see SNEATH & SOKAL 1973). The ellipses, which give the confidence limits for the samples plotted, allow their direct statistical comparison. The phenograms are constructed using the Euclidean distance between the samples compared. As in all statistical comparisons the interpretation of the diagrams is tentative at best, when sample size is small, i. e. N < 25. For abbreviations of local samples used in the comparisons, see Table 2.

Tab. 2. Abbbreviations for local samples used in the comparisons.

Abbreviation	Locality
Caballoid horses	
B	Brundon Pit, UK
Et	Romania (data Samson 1975)
Hof	Hofstade I, Belgium (Germonpré 1994)
K12	Kostenki 12, Russia
K12I	Kostenki 12 I, Russia
K14	Kostenki 14, Russia
Ki	Kiskevely, Hungary
Q	Quedlinburg, Germany
RB	Roter Berg, Germany
Re	Remagen, Germany
S	Seckendorff, Germany
Sip	Sipka, Chechia
VV	Vogelherd layer V, Germany
VVII	Vogelherd layer VII, Germany
Wa	Wallertheim, Germany
We	Westeregeln, Germany
Wi	Willersin, Germany
Z	Zemst IIB, Belgium (Germonpré 1994)
Small caballoid horses	
J	Jaurens, France
Mz	Mezin, Russia (Belan 1985)
NU	North Ural, Russia
Pek	Pekarna, Czechia
PU	Pred-Ural, Russi
Sol	Solutré, France
ZU	Za-Ural, Russia
Equus hydruntinus	
Bin	Binagadi, Azerbaijan (Gadziev 1953)
D	Dorog, Hungary
E	Erd, Hungary
HB	Holodnaja Balka, The Crimea, Ukraina
Kop	Kopacine, Croatia
LV	Lunel-Viel, France (Bonifay 1993)
RB	Roter Berg, Germany
S	Seckendorff, Germany
SS	Staro Selje, Crimea, Ukraina

We measured the teeth and bones according to classical methodology, following mainly Gromova (1949, 1952). All measurements are given in cm, except in Fig. 9 where the logs are of measurements in mm to avoid negative values. Length and breadth of the teeth were measured both at the base (not 1 cm above) and at the occlusal surface excluding cement. In the latter case we did not differentiate wear classes, since coefficients of variation calculated on the total sample of a tooth category are normal for homogeneous samples (e.g. V's between 1–10), but we excluded the little worn M1–2 from the calculations because of their aberrant occlusal proportions. We pooled P^{3-4}, respectively P_{3-4}, and M^{1-2}, respectively M_{1-2}, since these tooth pairs cannot be objectively differentiated. The plication count is a single number per tooth to facilitate statistical handling of data. The plication count and protoconal length given in Tables 3 and 4 are calculated on P^3–M^2.

All the material from Villa Seckendorff is stored in the Staatliches Museum für Naturkunde Stuttgart (SMNS) under the catalogue-numbers: *Equus germanicus* 31362, 31428–464, 31466–481, 31483–489, 31491–596, 31598–610, 31622–683, 31687–719, 31723–738, 31740–745, 31750, 31753–974, 31980–987, 32069–72, 32240–242, 32249–252, 32262–263, 32351, 32493–32495, 32507–508, 32514–515, 32547–550, 32743–32745. *Equus hydruntinus* 31465, 31482, 31490, 31597, 31611–31621, 31684–31686, 31721–722, 31746–749, 31751–752, 31975–979, 32397, 32521–526, 32546.

Acknowledgements

Our sincere thanks are due to all colleagues in charge of collections studied and used here for comparison.

We are also indebted to Mrs. R. Harling (SMNS) for taking the photos and to Dr. G. Bloos for critically reading the manuscript.

2. Description of the horses and comparisons

Equus germanicus Nehring

(Medium-sized to large caballoid horse)
Pl. 1, Figs. 1–2, Textfigs. 2–7, Tabs. 3, 4

Synonyms: *E. latipes* Gromova
E. transilvanicus Teodoreanu
E. remagenensis Skorkowski
E. remagensis Nobis

We compared the large caballoid horse from Villa Seckendorff with samples from Remagen, the type locality of *E. germanicus,* and from Quedlinburg, Westeregeln, Roter Berg, Wallertheim, and Vogelherd levels V and VII, all Germany, from whence *E. germanicus* has been referred to (Nehring 1884, Schmidtgen & Wagner 1928, Lehmann 1954). The age of these samples is believed to be Mousterian/early to mid-Wuermian (e.g. Schmidtgen & Wagner 1928, Lehmann 1954). In addition we compared with samples of *E. transilvanicus* Teodoreanu (data Samson 1975, tables), Romania, *E. remagensis* Nobis not Skorkowski from Zemst IIB and *E.* cf. *remagensis* from Hofstade I (data Germonpré 1993, tables), Belgium, and *E. latipes* Gromova from the type locality Kostenki, Russia. While *E. transilvanicus* and *E. remagensis* are early Wuermian (Samson 1975: 243, Germonpré 1993), *E.* cf. *remagensis* is middle and *E. latipes* late Wuermian (Germonpré 1993, Gritchuk 1984, Markova 1984). We also compared with the mid-Wuermian sample from Sipka Cave (horizon II and without exact stratigraphic provenance), Czechia, identified as *E. germanicus* (Musil 1965).

From other parts of Europe have been described similarly medium-sized to large and robust horses. David & Prat (1962) described a new subspecies, *E. caballus piveteaui* (often referred to as a separate species, *E. piveteaui*) from the Mousterian of La Chaise, France. The referred MC III (David & Prat 1962, Pl. III) resembles those from Seckendorff, while the short and massive MC III of "a typical *E. germanicus*" from the same site falls just outside the 95% equiprobability ellipse calculated on the MC III from Seckendorff. Of the English sites, the sample from Brundon Pit, believed to be pre-last interglacial in age (Currant, pers. comm.), compares well with that from Seckendorff.

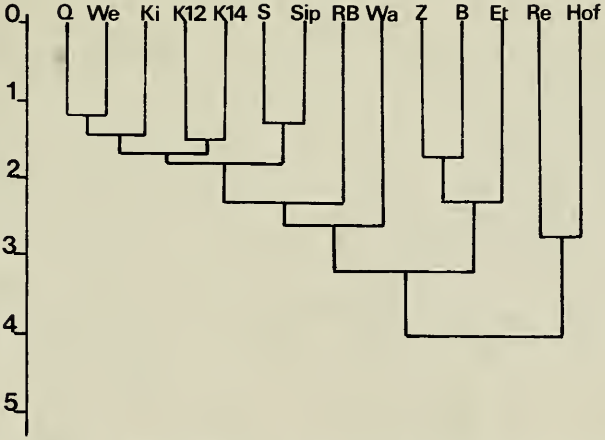

Fig. 2. *Equus germanicus*, a phenogram of UPGMA clustering constructed using 12 measurements on the metapodials of fourteen local samples. Scale to the left is in standard deviation (s.d.) units.

Germonpré (1993) reported on a large sample of *E. remagensis* from the early Wuermian of Zemst IIB, respectively of *E.* cf. *remagensis* from the mid-Wuermian of Hofstade I. While the Zemst horse is large, that from Hofstade is a smaller animal, only partly overlapping with that from Seckendorff. *Equus* cf. *remagensis* from Hofstade, in fact, is more similar in metapodial size and proportions to the hypodigm (type sample) of *germanicus* from Remagen, than is *E. remagensis* from Zemst II. The latter, together with the sample from Brundon Pit and *E. transilvanicus*, forms a group of large-limbed forms (Fig. 2: Z, B & Et). The Hofstade and Remagen samples cluster together as the smallest of the forms compared (Fig. 2: Re and Hof).

As for former Yugoslavia, Forsten (1990) referred the dental sample from the late Wuermian of Sandalja II Cave, Croatia, to *E. germanicus* and to this species probably also belong the samples from the Wuerm I of Mala and Velika Klicevica Caves (Benkovac). The early Mousterian horses from the quarry "Siporex“ (Pula) and Crvena Stijena Cave (Montenegro) belong to larger forms. The Hungarian Mousterian and early Wuermian horses are larger and more massive than that from Seckendorff; only in the late Wuermian, e.g. from Kiskevely Cave (Solutréan-Magdalenian; Mottl 1941), did they attain the size of *E. germanicus* (Fig. 2: Ki).

The compared samples are not identical: Roter Berg differs in having relatively long MT III and phalanx I, while the metapodials from the two neighbouring localities Westeregeln and Quedlinburg are short and massive (Figs. 3, 4: RB, resp. We and Q). Unfortunately the hypodigm from Remagen is rather marginal because of the small size of the horse; in the phenograms (Figs. 2, 5, 6: Re) the sample from Remagen joins the others as the last one. This may partly be due to small sample size and chance fluctuations. In a large, homogeneous sample the observations cluster around the mean, while in the calculations based on a small sample aberrant specimens get unmerited weight. In addition, some of the samples (Remagen, Quedlinburg, Westeregeln) seem to be heterogeneous, comprising a small ?caballoid horse together with the larger *E. germanicus* and the morphologically distinct *E. hydruntinus*. Inadvertent inclusion of such small specimens in the calculations may reduce the sample means.

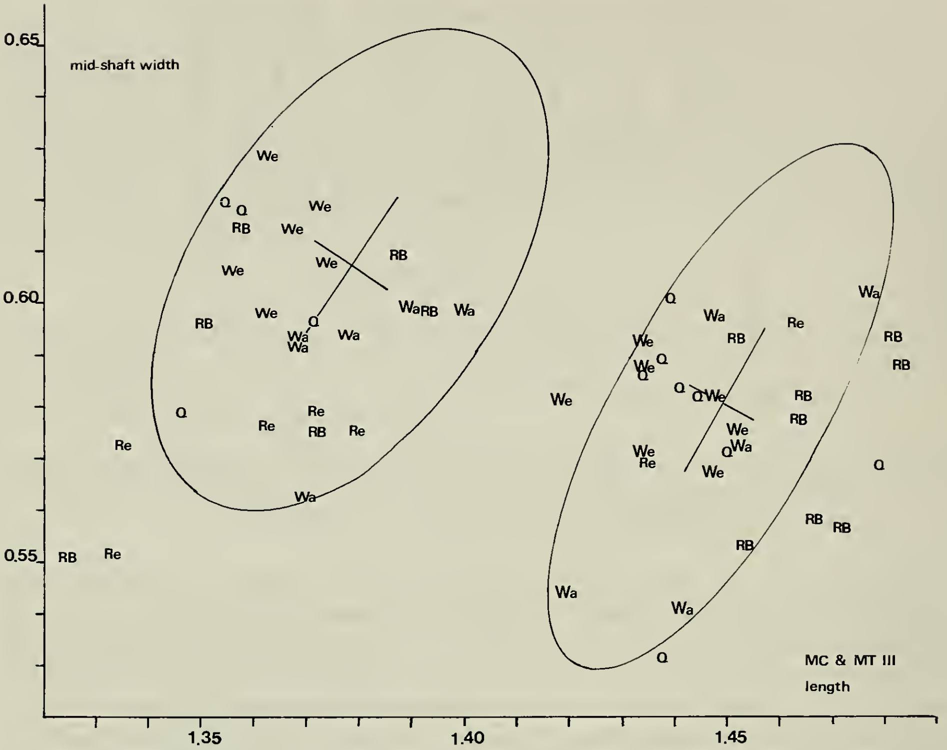

Fig. 3. *Equus germanicus*, metapodial mid-shaft (least) width plotted to total length in local samples. 95% equiprobability ellipses calculated on the material from Seckendorff. Logarithmic data.

Possibly partly for the reasons mentioned, the large samples from the late Wuermian of Kostenki, compared for 14 limb-bone measurements, are more similar to that from Seckendorff than are the contemporaneous ones from Germany (Fig. 5: S, K12, K12I, K14), in spite of a difference in both time and space. Compared for 12 metapodial measurements, the sample from Seckendorff resembles the one from the mid-Wuermian horizon II of Sipka (Fig. 2: S and Sip) and compared for 18 dental measurements it resembles the sample from the mid-Wuermian of Vogelherd V, rather than the early Wuermian one from Vogelherd VII (Fig. 6: S, VV, VVII). This should not be interpreted as indicating a mid- or late Wuermian age of the Seckendorff horse, but should caution against the indiscriminate use of the size (and the proportions, contra Nobis 1981) of fossil horses as stratigraphic markers.

In a wider geograhic context (Fig. 7) Seckendorff, compared for 12 limb-bone variables, clearly belongs in a group of medium-sized to large *germanicus*-horses, distinct from a group of smaller forms typified by the horse from Solutré, France, called *E. caballus gallicus* Prat.

The cheek teeth of all these horses are caballoid with the typical U-shaped inner valley between the metaconid and metastylid of the lowers. Many morphological characters of the cheek teeth are functions of wear: e.g. the development of the pli caballin, although it disappears sooner in the molars than in the premolars; the postfossette in M^3 opening through the hypoconal groove, in later wear becoming iso-

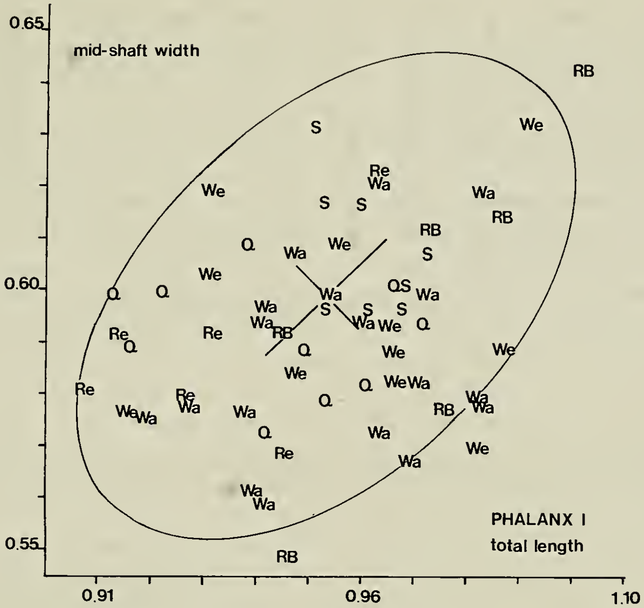

Fig. 4. *Equus germanicus,* Phalanx I mid-shaft (least) width plotted to total length in some local samples. 95% equiprobability ellipse calculated on the sample from Kostenki 12. Logarithmic data.

lated, either including the groove or leaving the groove as an isolated hypoconal lake; the depth of the ectoflexid in the lower molars, often shallow in the little worn teeth but in the worn ones reaching all the way into the double knot; and the development of the "protostylid" plication in P_2. Especially in the upper premolars the hypocone may be lingually indented and there is a strong pli hypostyle overhanging the hypoconal groove. The labial styles are mostly grooved in the upper premolars, often simple in the molars.

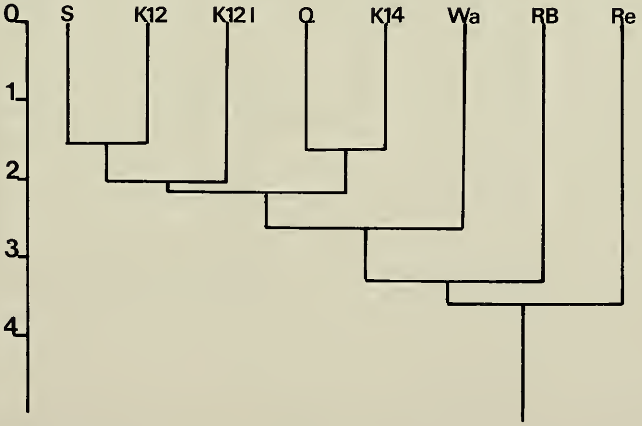

Fig. 5. *Equus germanicus,* a phenogram of UPGMA clustering constructed using 14 measurements on the limb bones in eight local samples. Scale to the left is in s.d. units.

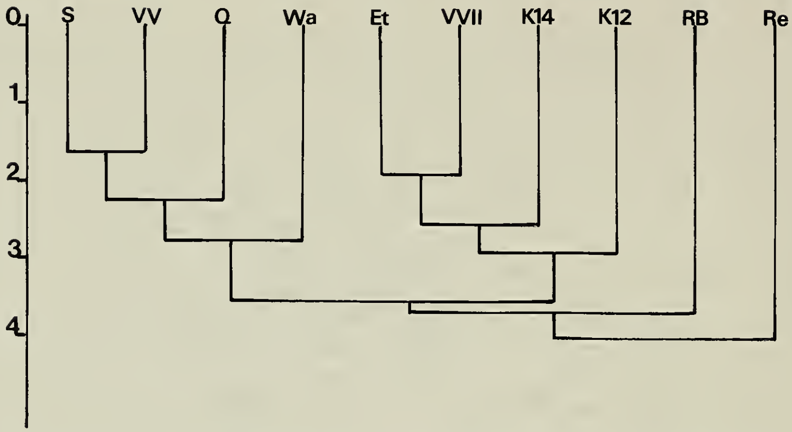

Fig. 6. *Equus germanicus*, a phenogram of UPGMA clustering constructed using 18 dental occlusal measurements of ten local samples. Scale to the left is in s.d. units.

Nehring (1884), in his study of the German Ice Age horses, designated the horses from Remagen, Thiede, and Westeregeln as *Equus caballus fossilis* var. *germanicus* sive *robusta*, characterized as medium-sized and thick-set. He stressed its similarity with Franck's "heavy occidental type" and *E. caballus germanicus* of Sanson and believed it to be the ancestor of these varieties of the domestic horse. The name *E.*

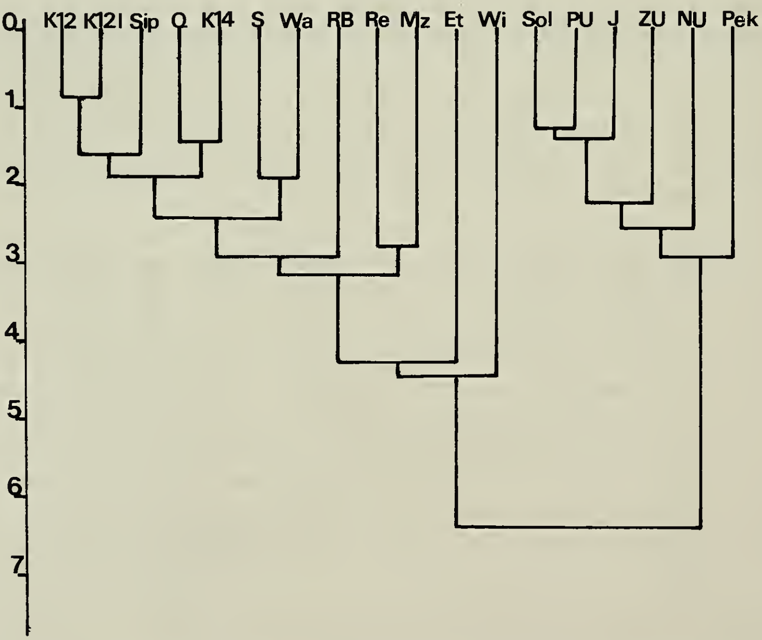

Fig. 7. Caballoid horses, a phenogram of UPGMA clustering constructed using 12 limb bone measurements of eighteen samples of the late Pleistocene. Scale to the left is in s.d. units.

germanicus as of NEHRING (1884) occurs for the first time in WÜST (1900, see LEHMANN 1954), although NEHRING did not use the binominal. According to REICHENAU (1915), NEHRING (1884, foot note on p. 100) explicitely designated a skull of an a. 10 year-old female animal from the loess of Remagen as *E. caballus* var. *germanicus*. This is not correct. Although NEHRING's description and figures are adequate, he did not designate a holotype, nor a type locality.

SKORKOWSKI (1938, cited in THENIUS 1966) considered the name *E. germanicus* preoccupied by *E. caballus germanicus* SANSON 1869, and proposed in its stead the name *E. remagenensis* for the horse from Remagen. NOBIS (1971) erroneously renamed it *E. remagensis*. The name *E. germanicus* cannot be considered validly preoccupied, since SANSON named a breed or variety of domestic horse. Breeds or varieties of domestic animals are not formally named. Thus *E. germanicus* NEHRING is available and valid for the Wuermian horse and has often been used as such in the literature. SKORKOWSKI's name *remagenensis* and NOBIS' *remagensis* are junior synonyms. The female skull from Unkelstein near Remagen (Berlin MB 1972.31.86; NEHRING 1884, Taf. 5, figs. 1, 2) is the lectotype (not holotype, contra MUSIL 1969) of the species. In the collections, e.g. in the Berlin Humboldt Museum, the name *E. adamiticus* SCHLOTHEIM 1820 occurs. That name appears, in fact, to have priority over *germanicus*, but has been little used in the literature and is a nomen nudum; it can therefore be ignored.

Tab. 3. *Equus germanicus*, dental occlusal measurements excluding cement.

Variable	n	Mean ± mean error	s.d.
P^2			
length	18	3.80 ± 0.04	0.151
breadth	18	2.49 ± 0.04	0.187
P^{3-4}			
length	47	2.98 ± 0.02	0.162
breadth	47	2.84 ± 0.02	0.128
M^{1-2}			
length	50	2.62 ± 0.02	0.129
breadth	49	2.67 ± 0.02	0.116
M^3			
length	17	2.84 ± 0.05	0.209
breadth	16	2.26 ± 0.02	0.093
P^3-M^2			
protocone l.	100	1.30 ± 0.01	0.125
plicat. count	92	7,00 ± 0.31	2.99
P_2			
length	14	3.36 ± 0.03	0.108
breadth	14	1.52 ± 0.02	0.084
P_{3-4}			
length	29	2.87 ± 0.03	0.164
breadth	29	1.63 ± 0.02	0.117
M_{1-2}			
length	17	2.75 ± 0.03	0.124
breadth	16	1.46 ± 0.01	0.051
M_3			
length	9	3.16 ± 0.02	0.065
breadth	10	1.32 ± 0.02	0.064

Although the name *E. germanicus*, thus, is formally valid, the question is: does it signify a biologically valid entity and how to delimit this entity from earlier and later ones?

Musil (1975, Fig. 4) believed that *E. germanicus* descended through decrease in body size from the larger *E. taubachensis* Freudenberg of Taubach (Eemian interglacial) and Ehringsdorf (Saale glacial), Germany. Nobis (1971) described the large *E. achenheimensis* from the Saalian glacial horizon of Achenheim, France, and believed it to have given rise, through decrease in size, to the smaller *E. germanicus* (*E. remagensis* in Nobis' terminology) in the younger horizons of the loess sequence of this site. Neither Musil (1975), nor Nobis (1971), gave characters other than size to distinguish the ancestral and descendant species.

The caballoid horses of Eurasia, to which the taxa discussed belong, did indeed decrease in body size with time (Sickenberg 1962, Musil 1977, Fig. 3), but size decrease can seldom be traced in a continuous local sequence, e.g. in a cave. In addition, horses of different size and proportions, but of similar morphology, occur at the same time in different parts of Eurasia, even in Europe as evident above. Thus size decrease appears to have been mainly a geographic phenomenon, not necessarily denoting specific differentiation. On the other hand, at a number of sites two horses, differing in size, seem to occur sympatrically (Musil 1962), indicating true specific differentiation (for alternative explanations, see Forsten 1993).

Sympatry is the only direct evidence for specific differentiation. In addition there is indirect evidence from studies on the mitochondrial-DNA of the extant species of *Equus*. These studies indicate that the living *E. caballus L.* (including *E. przewalskii* Poljakoff) branched off from the latest common ancestor as recently as a. 240000 BP (George & Ryder 1986), although caballoid horses have existed for nearly 1 M years. Caballoids older than a. 240000 years evidently belong to different, ?ancestral, species. To discriminate different fossil species, paleontologists have only the preserved morphology to go by, but in the exceedingly homogeneous caballoid horses, morphology is not diagnostic. Forsten (1988) suggested that among fossil caballoids possibly three taxa succeeded and partly overlapped with one another, but that they can be discriminated only arbitrarily, using metapodial distal articular breadth as a criterion. Due to transgression of body size, there are no hard and fast size limits between the mainly middle Pleistocene large caballoid (*E. mosbachensis* Reichenau), the mainly Eemian interglacial to Wuermian medium-sized to large one (*E. germanicus*), and the Wuermian medium-sized to small *E. caballus* (*E. ferus* Boddaert of authors). The lack of clear differences in morphology and size is reflected in the common use of subspecific names for these categories, e.g. *E. caballus mosbachensis* and *E. c. germanicus*.

The origin of *E. germanicus* is probably to be sought in the large caballoids of the middle and early late Pleistocene, variously called *E. achenheimensis, E. taubachensis, E. steinheimensis* Reichenau, *E. chosaricus* Gromova, *E. insulidens* Samson and *E. mosbachensis* Reich. – *abeli* Antonius. It is uncertain whether these "species" can be differentiated from one another. The myth about the archaism and alledgedly short protocone of the teeth of *E. steinheimensis* should be put to death: the cheek teeth in the sample from Steinheim are fully caballoid and the mean protoconal length is 1.40 cm, which is comparable with other caballoids of equal size. It is also uncertain whether *E. latipes* (originally *E. caballus latipes*) and *E. transilvanicus* can be differentiated from *E. germanicus*. *E. latipes* seems to be an East

Tab. 4. *Equus germanicus,* limb bone measurements.

Variable	n	Mean ± mean error	s.d.
Mc III			
length	34	23.86 ± 0.14	0.809
prox. br.	41	5.56 ± 0.04	0.273
prox. diameter	32	3.70 ± 0.04	0.211
dist. art. br.	38	5.44 ± 0.03	0.212
protuber. br.	36	5.29 ± 0.04	0.231
mid-shaft br.	29	4.03 ± 0.03	0.187
Mt III			
length	27	28.15 ± 0.15	0.769
prox. br.	32	5.54 ± 0.05	0.266
prox. diameter	26	4.89 ± 0.05	0.250
dist. art. br.	25	5.50 ± 0.04	0.164
protuber. br.	27	5.39 ± 0.04	0.233
mid-shaft br.	26	3.80 ± 0.04	0.188
Phalanx I			
total length	7	9.14 ± 0.07	0.181
mid-shaft br.	9	4.01 ± 0.06	0.165
Phalanx II			
total length	3	5.32 ± 0.09	0.157
mid-shaft br.	2	4.85	
Astragalus			
dist. art. br.	26	5.63 ± 0.05	0.235
lat. heigth	26	6.48 ± 0.05	0.230
Calcaneum			
height	2	11.72	
tuber a.-p.	10	4.94 ± 0.05	0.157

European vicar of *E. germanicus. E. transilvanicus,* based on material from different Romanian localities, intermediates between the larger middle and smaller late Pleistocene caballoids.

We believe that the caballoid horse from Seckendorff is a rather typical *E. germanicus,* although it is not identical with the type form from Remagen, being larger than the latter.

Equus hydruntinus REGALIA

(Small stenonid horse, not ass)

Pl. 1, Figs. 3–4, Textfigs. 8–10, Tabs. 5, 6

This little stenonid horse is well represented from Villa Seckendorff. The teeth and bones are typical of the species as often described from Europe, the Middle East, the Crimea, and the Caucasus. Primitive features of the upper cheek teeth are the deep postprotoconal groove, ± reaching the prefossette; a faint, soon obliterated pli caballin; the protocone with its short anterior heel; and in the lower molars the small, rounded metaconid and metastylid and ectoflexid reaching all the way into the double knot. In one exceptional specimen from Seckendorff (a lower tooth row, SMNS 31611, see pl. 1, fig. 3) M_2 and M_3 have a shallow ectoflexid. A shallow ectoflexid occurs rarely in *E. hydruntinus*; it can be observed in some lower molars from Roter Berg (The Berlin Humboldt Museum, without numbers, Tübingen Geol. Inst., 1455e), in an M_{1-2} from Lavison and M_3 from La Grotte des Feés and Fontar-

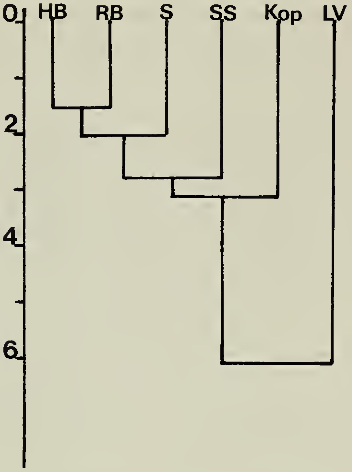

Fig. 8. *Equus hydruntinus*, a phenogram of UPGMA clustering constructed using 18 dental occlusal measurements of six local samples. Scale to the left is in s.d. units.

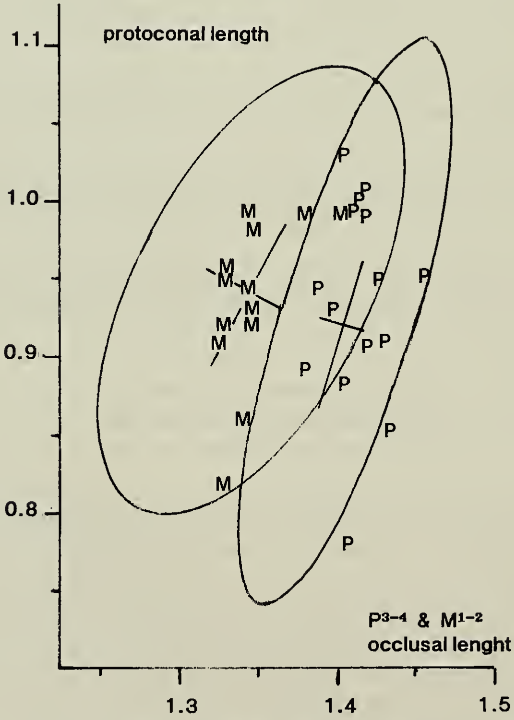

Fig. 9. *Equus hydruntinus*, protoconal length plotted to dental occlusal length in M^{1-2}, resp. P^{3-4}. 95% equiprobability ellipses calculated on the sample from Roter Berg. Logarithmic data.

naud (PRAT 1968, Figs. 91: 2, 94: 11, 96: 16). Usually, but not always, these specimens are little worn. In the lower tooth row SMNS 31611 all the incisors have an infundibulum, although occasionally absent in I_3 (STEHLIN & GRAZIOSI 1935).

We compared the teeth and bones of *E. hydruntinus* from Seckendorff with other samples of the species. Six local samples, i.e. Lunel-Viel, France (data BONIFAY 1991, tables and figures), Holodnaja Balka and Staroselje, the Crimea, Kopacine, Croatia, Roter Berg and Seckendorff, Germany, were compared for 18 dental occlusal measurements in a phenogram (Fig.8). Lunel-Viel is the oldest sample (Holsteinian), Roter Berg early Wuermian, Holodnaja Balka and Staroselje Wuermian, and Kopacine Neolithic. The sample from Lunel-Viel differs from the others at a 6 standard deviation level because of the great occlusal breadth of the teeth, probably due to inclusion of the cement in the measurements. Compared for protoconal length to dental occlusal length, the teeth from Seckendorff correspond well to those from Roter Berg (Fig. 9: 95% equiprobability ellipses drawn for the sample from Roter Berg).

Six local samples, i.e. Lunel-Viel (data BONIFAY 1991, tables), Seckendorff and Roter Berg (data partly from STEHLIN & GRAZIOSI 1935), Dorog and Erd, Mousterian of Hungary, and Binagadi, Mousterian (?) of Azerbaijan (data GADZIEV 1953, tables), were compared for 12 metapodial measurements (Fig. 10). Here the sample from Lunel-Viel, although dentally large, stands out for the small size of its bones, which has earned it the subspecific name *Equus hydruntinus minor* BONIFAY. The

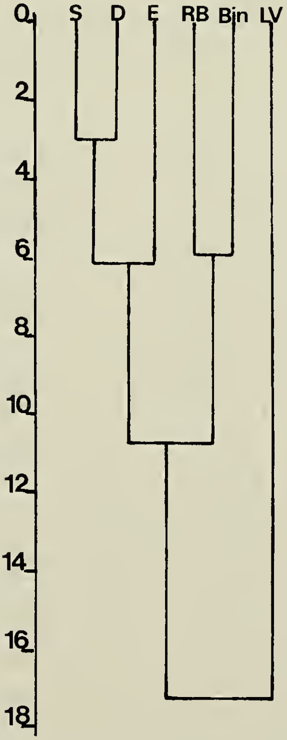

Fig. 10. *Equus hydruntinus*, a phenogram of UPGMA clustering constructed using 12 limb bone measurements in six local samples. Scale to the left is in s.d. units of measures in mm.

sample from Seckendorff resembles the rather large forms from Hungary. *E. hydruntinus* from the early Wuermian of Romania, called *Equus hydruntinus danubiensis* by SAMSON (1975) and believed to be unusually large, is of uncertain validity as a separate taxon. With the exception of some ?early, skeletally small forms, most *E. hydruntinus* were of similar size.

The ecological character of *E. hydruntinus* has often been discussed (GROMOVA 1949, PRAT 1968). Authors regard it as an inhabitant of temperate, arid and stony areas. This opinion is influenced by the notion that the slender-legged and hypsodont *E. hydruntinus* is an ass, related to the African and Asiatic asses. However, molecularly the extant asses are no more closely related to one another than are asses and zebras (GEORGE & RYDER 1986). Also, on dental evidence, *E. hydruntinus* does not appear to be closely related to the extant asses (EISENMANN & PATOU 1980). Its ecological preferences, therefore, must be judged on the basis of the faunas in which it occurs. Although present in temperate faunas, *E. hydruntinus* also occurs in cool to cold faunas (PRAT 1968, DELPECH 1984). Since *E. hydruntinus* is almost always rare when present, irrespective of the climatic character of the assemblage, its absence in a fossil sample cannot be taken as evidence for its absence in the fauna sampled.

Tab. 5. *Equus hydruntinus*, dental occlusal measurements excluding cement.

Variable	n	Mean ± mean error	s.d.
P^2			
length	5	3.12 ± 0.07	0.153
breadth	6	2.27 ± 0.03	0.084
P^{3-4}			
length	15	2.61 ± 0.03	0.126
breadth	15	2.35 ± 0.03	0.120
M^{1-2}			
length	13	2.23 ± 0.03	0.113
breadth	10	2.14 ± 0.03	0.095
M^3			
length	8	2.25 ± 0.04	0.102
breadth	8	1.86 ± 0.04	0.123
$P^3 - M^2$			
protocone l.	30	0.89 ± 0.02	0.126
plicat. count	29	6.98 ± 0.43	2.330
P_2			
length	2	2.72	
breadth	1	1.27	
P_{3-4}			
length	6	2.46 ± 0.02	0.057
breadth	6	1.38 ± 0.03	0.068
M_{1-2}			
length	9	2.25 ± 0.04	0.125
breadth	9	1.23 ± 0.01	0.031
M_3			
length	1	2.62	
breadth	1	1.16	

Tab. 6. *Equus hydruntinus*, limb bone measurements.

Variable	n	Mean ± mean error	s.d.
Mc III			
length	2	22.35	
prox. br.	2	4.28	
prox. diameter	2	2.95	
dist. art. br.	2	3.94	
protuber. br.	2	3.94	
mid-shaft br.	2	2.87	
Mt III			
length	7	26.51 ± 0.18	0.487
prox. br.	7	4.25 ± 0.08	0.205
prox. diameter	7	3.74 ± 0.08	0.214
dist. art. br.	7	3.88 ± 0.04	0.111
protuber. br.	7	3.96 ± 0.04	0.113
mid-shaft br.	7	2.83 ± 0.06	0.147
Phalanx I			
total length	1	7.92	
mid-shaft br.	1	2.47	
Phalanx II			
total length	1	4.27	
mid-shaft br.	1	3.41	
Astragalus			
dist. art. br.	1	4.39	
lat. height	1	5.11	

3. Conclusions

The horse sample from Villa Seckendorff seems to be drawn from two homogeneous populations, representing two species, probably reflecting a short time of deposition of the fossil fauna. A number of faunas of approximately the same age comprise specimens of a third horse taxon. This is the case with the faunas of Remagen, Quedlinburg, Westeregeln, and Wallertheim. These fossil materials may not have been excavated under strict stratigraphic control and may span a considerable time, therefore heterogeneity of the samples is not surprising. On the other hand, MUSIL (1962) showed that there clearly are two sympatric caballoid horses in the late Wuermian of Sveduv Stul, Czechia.

The two horses from Seckendorff represent well-known species, often found in sympatry (e.g. at Westeregeln, Roter Berg and Wallertheim). *Equus hydruntinus* is present in Europe since at least the Holsteinian, possibly even since the Cromerian (MALEZ & al. 1992). A find from Kazakhstan is said to be Mindelian (HISAROVA 1963) and a small calcaneum (Mainz Museum 1949/149) from Mosbach may represent this species from the same time in Europe. The early occurrence of *Equus germanicus* is uncertain due to the lack of characters discriminating this species from earlier caballoid forms. Neither species, thus, is stratigraphically useful.

The horses do not add anything significantly new, neither to the age of the fauna, nor to its ecology. The caballoid horses, including *E. germanicus*, seem to have been ecologically ubiquitous and that appears to be true also for *E. hydruntinus*, the almost constant companion of the former.

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Adresses of authors:
Dr. A Forsten, Zoological Museum, P. B. 17 (Rautatiekatu 13), SF-00014 Helsinki University, Finnland.
Dr. R. Ziegler, Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart.

Plate 1

Fig. 1. *Equus germanicus,* P_2-M_3 sin., occlusal, SMNS 31587.

Fig. 2. *Equus germanicus,* P^2-M^3 sin., occlusal, SMNS 31513.

Fig. 3. *Equus hydruntinus,* P_2-M_3 dext., occlusal, SMNS 31611.

Fig. 4. *Equus hydruntinus,* P^2-M^3 sin., occlusal, SMNS 31604.

All figures in natural size.


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