

## A preliminary note on the rhinos from Bilzingsleben

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*Abstract.* - Two species of Rhinocerotidae (rhino's) are found in Bilzingsleben: the small *Stephanorhinus hemitoechus* and the large *Stephanorhinus* aff. *kirchbergensis*. The *S. kirchbergensis* lineage is characterized by increase in size in the third molar; in Bilzingsleben (Holstein complex) this tooth is still relatively small, in Ehringsdorf (intra Saale interstadial or oxygen isotope stage 7) it is larger and in Taubach (Eemian or stage 5) it is even larger. The smaller rhinos of the genus *Stephanorhinus* were represented in Europe by *S. aff. etruscus* with small  $P_2$  in the late early Pleistocene, the slightly larger *S. hundsheimensis* with relatively large  $P_2$ , which dispersed into Europe during the early Middle Pleistocene and evolved into *S. hemitoechus*, with small  $P_2$ , which ranged from the late Middle into the Late Pleistocene.

*Zusammenfassung.* - Erste Mitteilungen über die Nashörner von Bilzingsleben. Zwei Arten von Nashörnern (Rhinocerotidae) wurden in der altpaläolithischen Fundschicht von Bilzingsleben gefunden: der kleine *Stephanorhinus hemitoechus* und der große *Stephanorhinus* aff. *kirchbergensis*. Die *S. kirchbergensis*-Evolutionlinie ist durch eine Zunahme in der Masse des dritten Molars gekennzeichnet. Bei den Bilzingslebener Individuen (Holstein-Komplex) ist dieser Zahn noch ziemlich klein, bei den Ehringsdorfer Individuen (Intrasaale-Warmzeit bzw. Sauerstoffisotopen-Stadium 7) ist er bereits größer und bei den Taubacher Individuen (Eem-Warmzeit bzw. Stadium 5) ist er noch größer.

Die kleinen Nashörner von der Gattung *Stephanorhinus* waren in Europa durch *S. aff. etruscus* mit kleinen  $P_2$  vertreten. Im späteren Frühpleistozän wurde diese Art durch den Einwanderer *S. hundsheimensis* ersetzt. Dieser war etwas größer und hatte auch einen bereits größeren  $P_2$ . Er evolvierte im späten Mittel- bis Spätpleistozän zu *S. hemitoechus* mit einem wiederum kleinen  $P_2$ .

### Introduction

The locality of Bilzingsleben is well known for its human remains, archaeological remains and fossils and for the geological information it contains (VLČEK, 1978; MANIA et al. 1980, 1986, 1997; MAI et al. 1983; FISCHER et al. 1991; MANIA 1990a, 1990b etc.). Systematic and annual excavations since 1969 by D. Mania yielded huge collections of mammal fossils. Since 1997, I am involved in this project through the study of the cervids (VAN DER MADE, 1998a) and rhinos. By now, approximately half of the rhino material has been studied. It is the aim of this paper to give some of the first results and to discuss the evolution of these rhinos.

### Collections

Rhino material was studied in a number of collections, and some of this material is used here for comparison. Where this is the case, this is indicated by the following abbreviations.

NHML	Natural History Museum, London (formerly British Museum (Natural History)).
FBFSUJB	Forschungstelle Bilzingsleben, Friedrich Schiller-Universität Jena, Bilzingsleben.
IPUW	Institut für Paläontologie der Universität, Wien.

### Measurements and their abbreviations

All measurements in mm.

DAP	Antero-posterior diametre of a tooth or bone.
DAPp	DAP of the proximal end of a bone.
DT	Transverse diametre (width).
DTa	DT of the anterior lobe of a tooth.
DTmax	Maximal DT of a bone.
DTp	DT of the posterior lobe of a tooth, or of the proximal end of a bone.
L	Length of a bone.
Lext	Length of the astragalus, measured at the external side.

### Pleistocene *Stephanorhinus* in the literature

The rhinos (family Rhinocerotidae OWEN 1845) from Bilzingsleben have been assigned to two species of the genus *Dicerorhinus*: *D. hemitoechus* and *D. kirchbergensis* (eg. MANIA 1983). These species, as well as *D. etruscus* and *D. kirchbergensis*, were commonly placed in that genus (eg. STAESCHE 1941; KAHLKE 1965, 1966, 1975, 1977; LOOSE 1975; GUÉRIN 1980; MAZZA 1988) and some paleontologists continue to do so (eg. GUÉRIN 1996). However, currently they are all placed in *Stephanorhinus* KRETZOI 1942 (eg. FORTELIUS et al. 1993; CERDEÑO 1990, 1993). The recent *Dicerorhinus* has incisors, whereas the European forms placed in, or related to, *Stephanorhinus* lost the incisors already in the Late Miocene. In addition there are numerous morphological differences between both genera. *Stephanorhinus* must have separated millions of years ago from the lineage leading to the living *Dicerorhinus*. Some authors (eg. GUÉRIN 1980) prefer to use the name *Dicerorhinus mercki* (KAUP 1841) instead of *S. kirchbergensis* (JÄGER 1839) in spite of the fact that the latter name has priority. GUÉRIN (1980, 1982a, 1982b) proposed a model of evolution and stratigraphical distribution of, what is called here, *Stephanorhinus* from western Europe. He considered *D. etruscus etruscus* (FALCONER 1868) of the Pliocene and early Pleistocene to evolve into *D. e. brachycephalus* (SCHROEDER 1903) from the early Middle Pleistocene and later into *D. hemitoechus* (FALCONER 1868) of late Middle and Late Pleistocene. This evolution should have occurred in Europe. *D. mercki* was considered to be a migrant from Asia, that lived during the Middle and Late Pleistocene in Europe.

FORTELIUS et al. (1993) assigned most of what GUÉRIN (1980) called *D. etruscus brachycephalus* to *Stephanorhinus hundsheimensis* (TOULA 1902), except for the type, that was placed in *S. kirchbergensis*. They also indicated problems in understanding the phylogeny of the group. Their cladogram unites *S. etruscus* and *S. hundsheimensis*, these are grouped with *S. hemitoechus* and these three again with *S. kirchbergensis* (omitting, two Pliocene species that are not discussed here). This seems to preclude an evolution of *S. hundsheimensis* to *S. hemitoechus*. FORTELIUS et al. (1993), MAZZA et al. (1993) and RUSTIONI et al. (1995) considered *S. etruscus* typical of the Early Pleistocene, but also occurring in the Middle Pleistocene, a small form called *S. aff. hundsheimensis* typical of the latest Early Pleistocene, the larger *S. hundsheimensis* typical of the early Middle Pleistocene and *S. hemitoechus* of the early Middle to Late Pleistocene. Most of these species were thus supposed to have

overlapping ranges, implicitly contradicting Guérin's evolutive and stratigraphic model. *S. kirchbergensis* was believed to be typical of the Middle and Late Pleistocene. A small late Early Pleistocene rhino, very likely identical to that was assigned to *S. aff. hundsheimensis* by MAZZA et al. (1993), was also reported from Spain and was assigned to *S. etruscus* (CERDEÑO 1993; VAN DER MADE 1998b, in press). GUÉRIN (1980), nor FORTELIUS et al. (1993) included the large collections from Thuringia in their studies. As we will see below, the material from Bilzingsleben belongs to *S. hemitoechus* and *S. aff. kirchbergensis*. A study of this material and a comparison with material from other localities in Thuringia is expected to resolve some of the problems, or at least define them more clearly.

### **Brief description and comparison of selected material from Bilzingsleben**

The rhino postcranial material from Bilzingsleben can be separated into two fairly well separated size groups. Most of the dental elements can be separated into two groups on the basis of morphology and size. Though the separation in size is not as clear, as in the bones, it coincides well with the separation based on morphology.

No complete skulls are found. There are many small fragments. Isolated nasals are wide and have extensive rugose areas, suggesting large horns.

All dental elements are represented. In this preliminary note, only the permanent lower dentition is described and compared. As a general rule, it can be stated that the enamel is smooth and that there is no important formation of cementum in *S. aff. kirchbergensis*, whereas the enamel is slightly more rugose and there may be some more cementum in *S. hemitoechus* (eg. compare Plate 3, figures 1 and 3 and Plate 1, figures 1 and 2). The cheek teeth do not show the angular morphology as in *Coelodonta*.

The  $P_2$  can be separated metrically into two groups (Figure 1). The smaller ones (Pl. 1, fig. 1; Pl. 2, fig. 1) tend to have relatively low crowns, and are assigned to *S. hemitoechus*. The length tends to be less at the base than in the upper half of the crown. One specimen from Weimar-Ehringsdorf in a mandible shows that *S. hemitoechus* occasionally may have large  $P_2$ , that are within the range of *S. kirchbergensis*. The specimens from Bilzingsleben are small compared to those of *S. hundsheimensis* from Voigtstedt, Süssenborn and Soleilhac (Figure 3). The  $P_2$  of *S. aff. kirchbergensis* (Pl. 1, fig. 1) are large, have high crowns and tend to have a greater length at the base than in the upper half of the crown.

The  $P_3$  and  $P_4$  have similar morphologies. There are gradual morphological differences between the two premolars, for instance the first fossid is more clearly developed in the fourth premolar. The first lobe is wider than the second lobe in both, the difference being greater in the third premolar. However there is important overlap between the  $P_3$  and  $P_4$  in this character. The third premolar is smaller than the fourth premolar, moreover both species differ in size. In *S. aff. kirchbergensis* (Pl. 2, fig. 3), the bottom of the second fossid of the fourth premolar may have a U-shaped bottom as in the molars, or a V-shaped bottom. In *S. hemitoechus*, this bottom is always V-shaped. In the latter species, the first fossid may occasionally be closed (Pl. 6, fig. 2). Because none of the characters is usually decisive, isolated  $P_4$  of the small species and  $P_3$  of the large species are difficult to tell apart.

The  $M_1$  and  $M_2$  are similar in morphology, though the former seems to have a slightly higher crown and relatively wider second lobe. The second molar is slightly larger, but there is an important overlap in sizes within each of the two species. There are two morphological types; one with a second fossid with a V-shaped bottom and with a first fossid that tends to have this morphology as well and another one, where these fossids have a U-shaped bottom.

Occasionally the bottom might be «parabolus-shaped» (the valley being narrower), but there is never a sharp line at the bottom. The first morphology occurs in small molars and the second in large molars. This dimensional and morphological separation into two groups is taken as a separation of the molars of the two species; the small molars with V-shapes being assigned to *S. hemitoechus* (Pl. 3, fig. 3; Pl 6, fig. 2) and the large ones with U-shapes to *S. aff. kirchbergensis* (Pl. 2, fig. 2; Pl 3, fig. 1; Pl. 4, fig. 1). In *S. kirchbergensis* from Ehringsdorf, the fossids are narrower than in Bilzingsleben and frequently a V-shape is present, however the V-shape is wider than in *S. hemitoechus* from Ehringsdorf. It seems thus that the V-shape developed convergently in later populations of the *S. kirchbergensis* lineage. Apart from these morphological characters, there are others that can be used to separate both species, but the shape of the fossids is by far the best character in the Bilzingsleben sample.

The  $M_3$  tend to have relatively low crowns, an anterior fossid with a low bottom, posteriorly directed roots and a different morphology of the distal loph and never have distal facet. None of the large specimens in Figure 2 has V-shaped fossids and none of the small ones has U-shaped fossids. The lingual side of the posterior lobe is more square in *S. hemitoechus*, whereas in *S. aff. kirchbergensis* it is more undulating, projecting more lingually below the posterior loph than below the posterior fossid.

**Mandible** fragments that preserve the symphysis are invariably without incisors or alveoles for the incisors and no isolated incisors have been found.

The **postcranial skeleton** shows clear differences in size between the smaller *S. hemitoechus* and the larger *S. aff. kirchbergensis*. Virtually all bones are represented in the sample, but it is not the intention to describe and discuss all elements here.

The **astragalus** has the typical morphology as in rhinos. Pleistocene *Stephanorhinus* seems to occur roughly in three size groups: the small *S. etruscus* (*S. aff. hundsheimensis* of some authors) of the Early Pleistocene, the intermediate *S. hundsheimensis* and *S. hemitoechus* of the Middle and Late Pleistocene and the large *S. kirchbergensis* of the Middle and Late Pleistocene (Fig. 5). Within each species and even within each sample, the length of the astragali seems to be much more variable than the width. This is particularly clear in samples from localities with only one species (eg. Süssenborn and Atapuerca TDW4). Two small juvenile specimens from Taubach are relatively very wide. These specimens show that the length of the astragalus tends to increase more than the width during the life of the individual. If the specimens indeed belong to *S. kirchbergensis* (as is supposed here), the length increases more than the width, if the specimens belong to *S. hemitoechus*, only the length is to increase. It is to be expected that length varies much more with the age of the individual than the width and that length/width ratios of astragali are to some degree age dependent. The result is that for a given length, the astragali of *S. kirchbergensis* or *S. aff. kirchbergensis* are relatively wider (length-width ratio) than those of the *S. hundsheimensis* - *S. hemitoechus* group and these in turn are wider than in the *S. etruscus* group. However, if the range of length-width ratios is considered, there is probably no important difference. A specimen assigned to *S. aff. kirchbergensis* (Pl. 5, fig. 1) is relatively much wider than the specimen assigned to *S. hemitoechus* (Pl. 5, fig. 2), the distance between proximal and distal articulation facets is less, etc. However, the differences might be individual, or age dependent, rather than specific. If in samples with more than one species, the proportions are taken as a basis for specific assignation of the astragali, any later analysis will show differences between both species in proportions. Here, the proportions are considered less reliable, because they seem to be variable in monospecific samples. In any case, one has to be cautious in the interpretation of any character related to the length and width proportions of the astragalus for the study of taxonomy and/or locomotory adaptation.

There are but few complete **metapodials**. The few available specimens suggest that *S. aff. kirchbergensis* has more robust third metacarpals than *S. hemitoechus*. The third metatarsals of the smaller form are more gracile than the few complete specimens of *S. hemitoechus* from Neumark Nord and Ehringsdorf.

The **first central phalanx** is more or less symmetrical and is a wide tooth. The lateral phalanges are narrower and more asymmetrical. Most of the specimens are large (Figure 6) and are believed to belong to *S. aff. kirchbergensis* (Plate 7); the smaller specimens are believed to belong to *S. hemitoechus* (Plate 6, fig. 1). In the larger phalanges, the DAPp-DTp plot (Figure 6) shows a good correlation, but the L-DTp plot suggests a separation in more robust anterior phalanges and more gracile posterior phalanges. *S. hemitoechus* might be expected to be more cursorial and therefore to have more elongate phalanges; however, the available data do not support such an assumption.

The **second central phalanx** and second lateral phalanges differ in the same way as the first phalanges. Again the large specimens are assigned to *S. aff. kirchbergensis* (Plate 8, fig. 2) and the small ones to *S. hemitoechus* (Plate 8, fig. 1). There is no evidence for more gracile posterior phalanges, nor for a greater gracility of one of the two species (Figure 7).

## Discussion

The genera *Coelodonta* and *Stephanorhinus* are the common rhinos of the Pleistocene of Europe. Both lack incisors. *Coelodonta* has more cementum and enamel that is more rugose than *Stephanorhinus* and its cheek teeth have a more angular morphology. This confirms the assignation of the material from Bilzingsleben to *Stephanorhinus*.

There is a good agreement in size between the large form from Bilzingsleben and material from Ehringsdorf and Taubach in the IQW that has been assigned to *D. kirchbergensis* (KAHLKE 1975, 1977). There are however also differences. The lower molars from Bilzingsleben have U-shaped fossids, while the molars from Ehringsdorf and Taubach tend to have V-shaped fossids. The third molars from Bilzingsleben are relatively small, whereas those from Ehringsdorf are larger and those from Taubach are still larger.

Increase in the size of the M3 relative to that of other teeth is very common among ungulates. The M3 may just become larger, maintaining its shape, or may become more elongate through the addition of distal lobes. Such trends are interpreted as adaptations to diets that include greater amounts of food of a poorer quality. Generally, this means that an omnivore shifts to a more herbivorous diet or that a herbivore ingests a greater amount of plant material with a lower nutritive value. These trends are frequently connected with a tendency towards greater crown heights, thinner enamel and the formation of cementum. These trends, in particular M3 length has often been used as a stratigraphical tool. (VAN DER MADE 1999.)

The fauna from Bilzingsleben is an interglacial fauna, placed on biostratigraphical grounds within the Holstein complex (HEINRICH 1991; MANIA 1995, 1997), time equivalent to stage 11. Ehringsdorf is placed in an intra-Saale interglacial (HEINRICH 1991; MANIA 1997), or oxygen isotope stage 7. Taubach is placed in the Eemian (HEINRICH 1991), or oxygen isotope stage 5. Heinrichs models of evolution of *Arvicola* and *Castor* that imply a sequence from old to young: Bilzingsleben - Ehringsdorf - Taubach, is corroborated by the tendencies in the *Stephanorhinus kirchbergensis* lineage. The ages of the localities and the morphological and metrical differences in the samples of the large *Stephanorhinus* lead to the following model of evolution: M<sub>3</sub> size increased from stage 11 to stage 7 and further to stage 5 and U-shaped fossids in the molars were replaced by V-shaped fossids between stages 11 and 7.

The differences between the large *Stephanorhinus* of the different ages are such, that it is convenient to reflect this in taxonomy. FORTELIUS et al. (1993, p. 65) suggested that

*S. kirchbergensis* could be divided into two species, the smaller Middle Pleistocene *S. brachycephalus* and the larger *S. kirchbergensis*. *S. brachycephalus* was first published as a variety of *D. mercki*, but later GUÉRIN (1980) considered it a subspecies of *D. etruscus*. The type of *S. brachycephalus* is a skull from Daxlanden (figured by LOOSE 1975). This skull looks much like a larger skull from Mosbach assigned to *S. kirchbergensis* and many authors consider it conspecific, or at least related (eg. LOOSE 1975; MAZZA 1988). Whereas «*brachycephalus*» is an available name, a study of the type material should reveal, whether the Bilzingsleben material can be assigned to this taxon.

In order to place the small rhino from Bilzingsleben in its context we have to bear in mind the phylogenetic and stratigraphic models of GUÉRIN (1980, 1982a, 1982b), proposing a single lineage consisting of different forms typical of a particular time, and FORTELIUS et al. (1993), who supposed a more complex phylogeny and overlapping ranges of the taxa.

The small species *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus* are very similar in size and morphology, differing in details rather than in ecologically important characters. Sympatric related species differ usually in size and/or in some adaptation that is clearly reflected in morphology of bones, skull or dentition. Therefore, it seems unlikely that two of the three species, or all three, lived at the same time at the same place. For instance, citations of *S. etruscus* from Mosbach (see FORTELIUS et al. 1993), are probably either based on material from the Early Pleistocene Mosbach I, or on an underestimation of the variability of *S. hundsheimensis*. Similarly the citation of *S. hemitoechus* from Mosbach (see FORTELIUS et al. 1993) is questionable, maybe it does come from Mosbach 3 after all, though no *Stephanorhinus* was reported from this level (VON KOENIGSWALD & TOBIEN 1987). In order to demonstrate overlapping ranges, the assignation of the material should be beyond discussion, which is difficult in such similar species, as well as the stratigraphical provenance. In addition, Guérin's model of subsequent forms is from an ecological point of view more attractive than a model with very similar forms that overlap in time and space.

Astragali from the Early Pleistocene, that have been assigned to *S. etruscus* or to *S. aff. hundsheimensis* are on average a little smaller than Middle and Late Pleistocene specimens assigned to *S. hundsheimensis* (*S. e. brachycephalus*) and *S. hemitoechus* (Figure 5; VAN DER MADE, in press, figure 4). Similarly, Early Pleistocene cheek teeth are on average smaller (Figure 4). In a way this groups all Early Pleistocene forms, despite that some have been assigned to *S. aff. hundsheimensis*. More important, it is suggestive of a break near the Early Middle Pleistocene boundary. The earliest Middle Pleistocene *Stephanorhinus* have relatively larger  $P_2$  than the Early Pleistocene ones. Reduction of the size of premolars is a common tendency, that is often related to an increase in size of the posterior molars, particularly in artiodactyls (eg. VAN DER MADE 1999). The early Middle Pleistocene *S. hundsheimensis* seems thus to be more primitive than the Early Pleistocene *Stephanorhinus* and, if this is correct, *S. hundsheimensis* is no likely descendant of *S. etruscus*. *S. hundsheimensis* may be an immigrant that replaced *S. etruscus* at, or close to, the Early-Middle Pleistocene boundary. Apart from a discrepancy in the position of the break, this is more in line with the model of FORTELIUS et al. (1993), that does not derive *S. hundsheimensis* from *S. etruscus*, than with GUÉRIN's (1980) model, that supposes a continuous evolution.

Soleilhac has a particularly large  $P_2$ , Voigtstedt, Süssenborn and Cesi have large  $P_2$ , and Bilzingsleben, Pinilla del Valle, Neumark Nord and Ehringsdorf have small  $P_2$  (Figure 3). This suggests a gradual decrease in size, though the possibility of one or two breaks exists. Comparing Bilzingsleben and Ehringsdorf, there seems to be a difference in  $M_1$  size. However, considering Süssenborn, Voigtstedt and Soleilhac, it appears difficult to explain this as a tendency, moreover, virtually all variation is within the ranges of Süssenborn.

*S. hemitoechus* is often considered to be more heavily built than *S. hundsheimensis* (eg. RUSTIONI et al. 1995). The postcranial material from Bilzingsleben, seems to be rather gracile. The small rhino from Bilzingsleben is thus more like *S. hemitoechus* in its dentition and seems to be more like *S. hundsheimensis* in its skeleton. Both species are considered here as a lineage, in which first changes in dentition are seen and later changes in the skeleton. This is largely in line with GUÉRN's (1980) model of evolution, as well as with his stratigraphy, though the taxonomy is different. The small rhino from Bilzingsleben is assigned to *S. hemitoechus*, though it is likely to represent a primitive form.

### Conclusions

Though much material Bilzingsleben remains to be studied and many more specimens from the Thuringian localities and elsewhere should be included in the comparisons, a number of preliminary conclusions can be drawn and, as a working hypothesis, a model of evolution of Pleistocene European *Stephanorhinus* can be presented.

The rhinos from Bilzingsleben are assigned to *S. aff. kirchbergensis* and *S. hemitoechus*.

The *S. kirchbergensis* lineage entered Europe during the early Middle Pleistocene. Its evolution towards larger M3 is of stratigraphic value and corroborates earlier findings on rodents that Bilzingsleben is older than Ehringsdorf which in turn is older than Taubach. This is consistent with a correlation of Ehringsdorf to an intra-Saale interglacial (isotope stage 7). The smaller *Stephanorhinus* is represented in the Early Pleistocene by *S. etruscus*, which is replaced at, or close to, the Early-Middle Pleistocene transition by *S. hundsheimensis*, which is an immigrant. This species evolved into *S. hemitoechus*.

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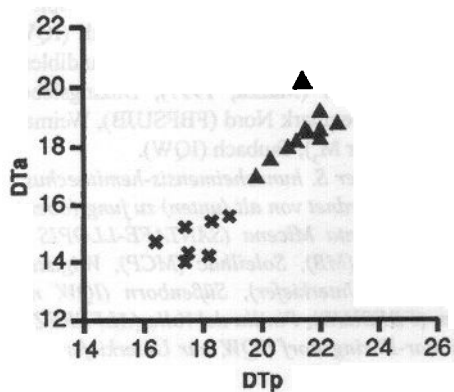


Fig. 1 Bivariate plot of the  $P_2$  of *Stephanorhinus* from Bilzingsleben. DTa = anterior width, DTp = posterior width. Crosses = *S. hemitoechus*, triangles = *S. aff. kirchbergensis*.

Abb. 1 Bivariater Plot des  $P_2$  von *Stephanorhinus* von Bilzingsleben. Dta = vordere Breite, Dtp = hintere Breite. Kreuze = *S. hemitoechus*, Dreiecke = *S. aff. kirchbergensis*

M/3 Bilzingsleben

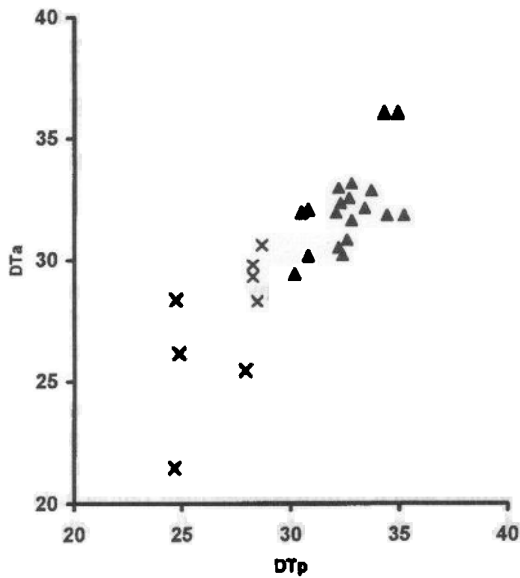


Fig. 2 Bivariate plots of the M<sub>3</sub> of *Stephanorhinus* from Bilzingsleben. DTa = anterior width, DTp = posterior width. Crosses = *S. hemitoechus*, triangles = *S. aff. kirchbergensis*.

Abb. 2 Bivariate plots des M<sub>3</sub> von *Stephanorhinus* von Bilzingsleben. DTa = vordere Breite, DTp = hintere Breite. Kreuze = *S. hemitoechus*, Dreiecke = *S. aff. kirchbergensis*

▲ *S. aff. kirchbergensis*  
X *S. hemitoechus*

Fig.3 Size in the cheek teeth of *S. etruscus* (crosses) and the *S. hundsheimensis* - *hemitoechus* lineage (dots). The localities are in approximate stratigraphical order from old (bottom) to young (top): Valdarno (IQW), Pietrafitta (Mazza et al. 1993), Venta Micena (Santafé-Llopis & Casanovas-Cladellas 1987), Atapuerca TDW4b (MB), Soleilhac (MCP), Voigtstedt (IQW; only specimens in mandibles), West Runton (NHML; only specimens in mandibles), Süßenborn (IQW; only specimens in mandibles), Cesi (Mazza, 1997), Bilzingsleben (FBFSUJB), Pinilla del Valle (Alferez & Iñigo 1990), Neumark Nord (FBFSUJB), Weimar-Ehringsdorf (IQW; only specimens in mandibles, save for M<sub>3</sub>), Taubach (IQW).

Abb. 3 Größe der Backenzähne von *S. etruscus* (Kreuze) und der *S. hundsheimensis*-*hemitoechus* - Linie (Punkte). Die Fundstellen sind stratigraphisch geordnet von alt (unten) zu jung (oben): Valdarno (IQW), Pietrafitta (MAZZA et al. 1993), Venta Micena (SANTAFÉ-LLOPIS & CASANOVAS-CLADELLAS 1987), Atapuerca TDW4b (MB), Soleilhac (MCP), Voigtstedt (IQW, nur Unterkiefer), West Runton (NHML, nur Unterkiefer), Süßenborn (IQW, nur Unterkiefer), Cesi (MAZZA 1997), Bilzingsleben (FBFSUJB), Pinilla del Valle (ALFÉREZ & INIGO 1990), Neumark-Nord (FBFSUJB), Weimar-Ehringsdorf (IQW, nur Unterkiefer ohne M<sub>3</sub>), Taubach (IQW)



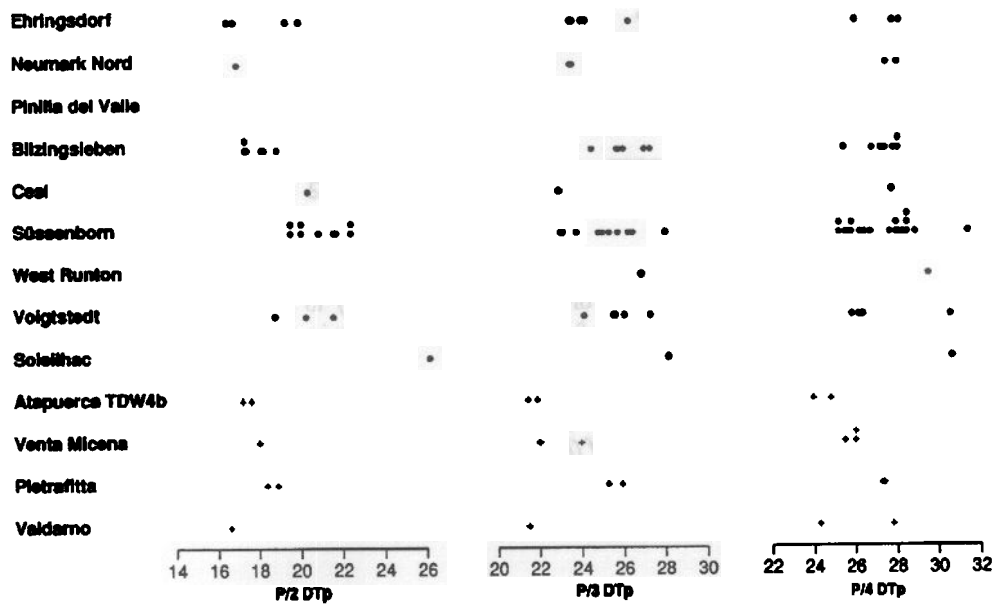


Fig. 3 A

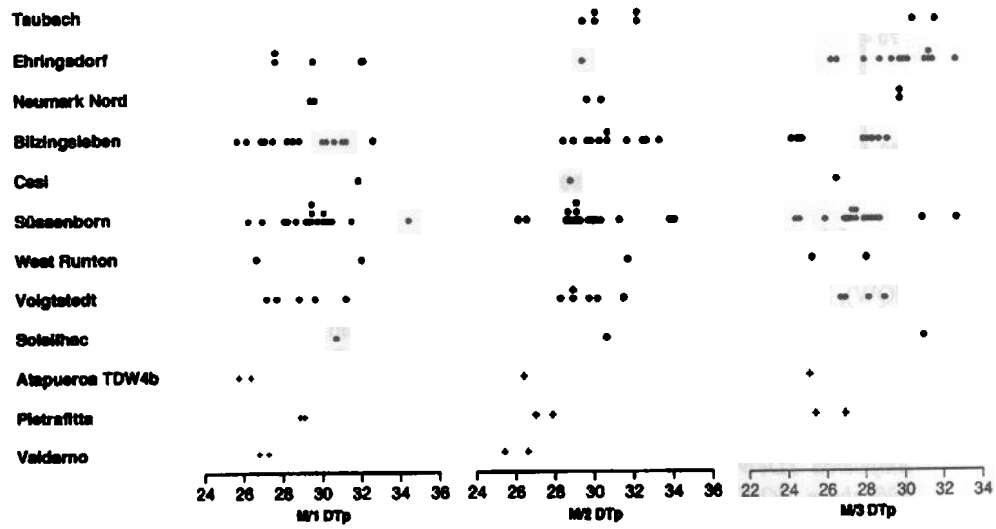
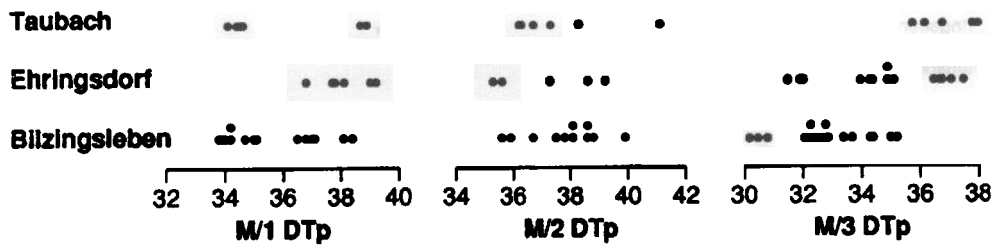


Fig. 3 B



Size increase in the lower molars of *Stephanorhinus kirchbergensis* lineage. The localities are in approximate stratigraphical order from old (bottom) to young (top): Bilzingsleben (FBFSUJB), Weimar-Ehringsdorf (IQW; only specimens in mandibles), Taubach (IQW; specimens in mandibles).

Abb. 4 Größenzunahme der unteren Molaren der *Stephanorhinus kirchbergensis* -Linie. Die Fundstellen sind stratigraphisch geordnet von alt(unten) zu jung (oben): Bilzingsleben (FBFSUJB), Weimar-Ehringsdorf (IQW, nur Unterkiefer), Taubach (IQW, nur Unterkiefer)

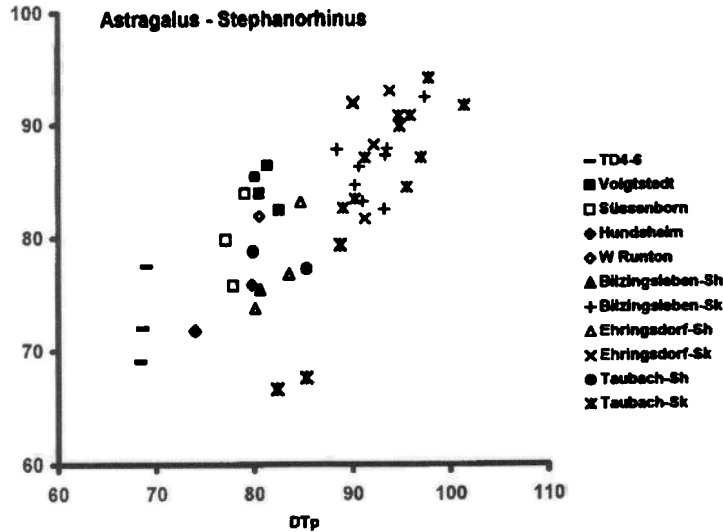


Fig. 5 Size of the astragalus of *Stephanorhinus* from various localities: *S. etruscus* from Atapuerca TD4W4b and TD6 (MB, MNCN), *S. hundsheimensis* from Voigtstedt (IQW), Süßenborn (IQW), Hundsheim (IPUW) and West Runton (NHML), *S. hemitoechus* from Bilzingsleben («Sh»; FBFSUJB), Weimar-Ehringsdorf («Sh»; IQW) and Taubach («Sh»; IQW), *S. aff. kirchbergensis* from Bilzingsleben («Sk»; FBFSUJB), *S. kirchbergensis* from Weimar-Ehringsdorf («Sk»; IQW) and Taubach («Sk»; IQW). Lext is the length measured at the external side and DTp is the proximal width.

Abb. 5 Größe des Astragalus von *Stephanorhinus* verschiedener Fundstellen: *S. etruscus* von Atapuerca TD4W4b und TD6 (MB, MNCN), *S. hundsheimensis* von Voigtstedt (IQW), Süßenborn (IQW), Hundsheim (IPUW) und West Runton (NHML), *S. hemitoechus* von Bilzingsleben („Sh“, FBFSUJB), Weimar-Ehringsdorf („Sh“, IQW) und Taubach („Sh“, IQW), *S. kirchbergensis* von Weimar-Ehringsdorf („Sk“, IQW) und Taubach („Sk“, IQW). Lext = an der äußeren Seite gemessene Länge, Dtp = proximale Breite

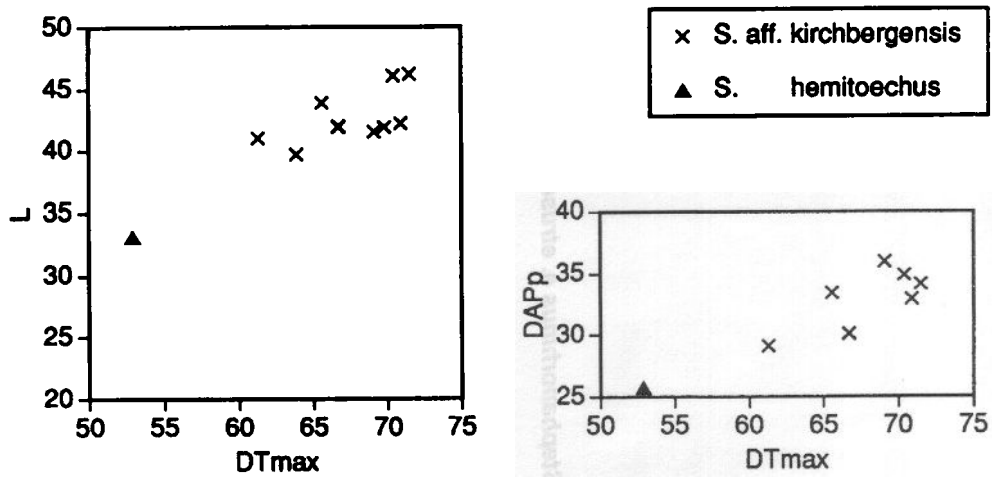


Fig. 6 Bivariate plot (L = length, DTmax = maximal width of the first central phalanx of *Stephanorhinus hemitoechus* (triangles) and *S. aff. kirchbergensis* (crosses) from Bilzingsleben.

Abb. 6 Bivariater Plot (L = Länge, DTmax = maximum Breite) der ersten mittleren Phalanx von *Stephanorhinus hemitoechus* (Dreiecke) und *S. aff. kirchbergensis* (Kreuze) von Bilzingsleben

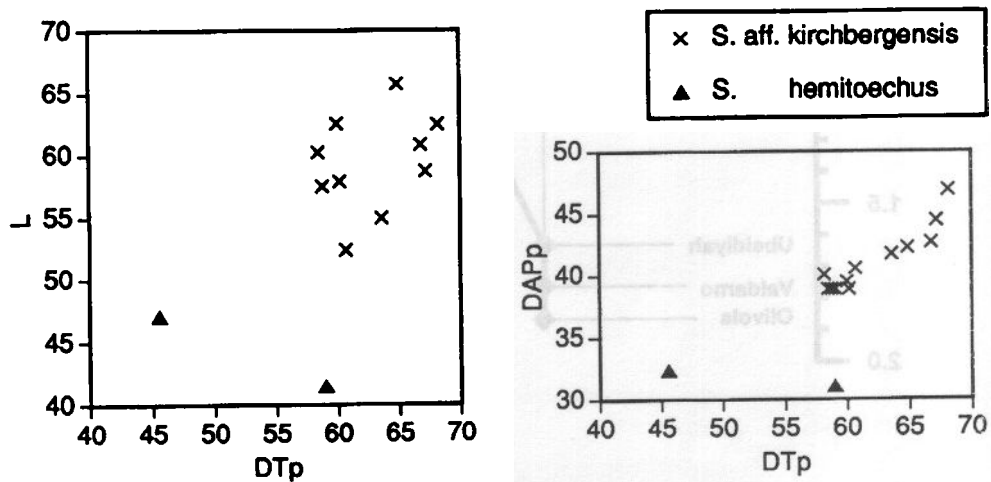


Fig. 7 Size of the second central phalanx of *Stephanorhinus hemitoechus* (triangles) and *S. aff. kirchbergensis* (crosses) from Bilzingsleben.

Abb. 7 Größe der zweiten mittleren Phalanx von *Stephanorhinus hemitoechus* (Dreiecke) und *S. aff. kirchbergensis* (Kreuze) von Bilzingsleben

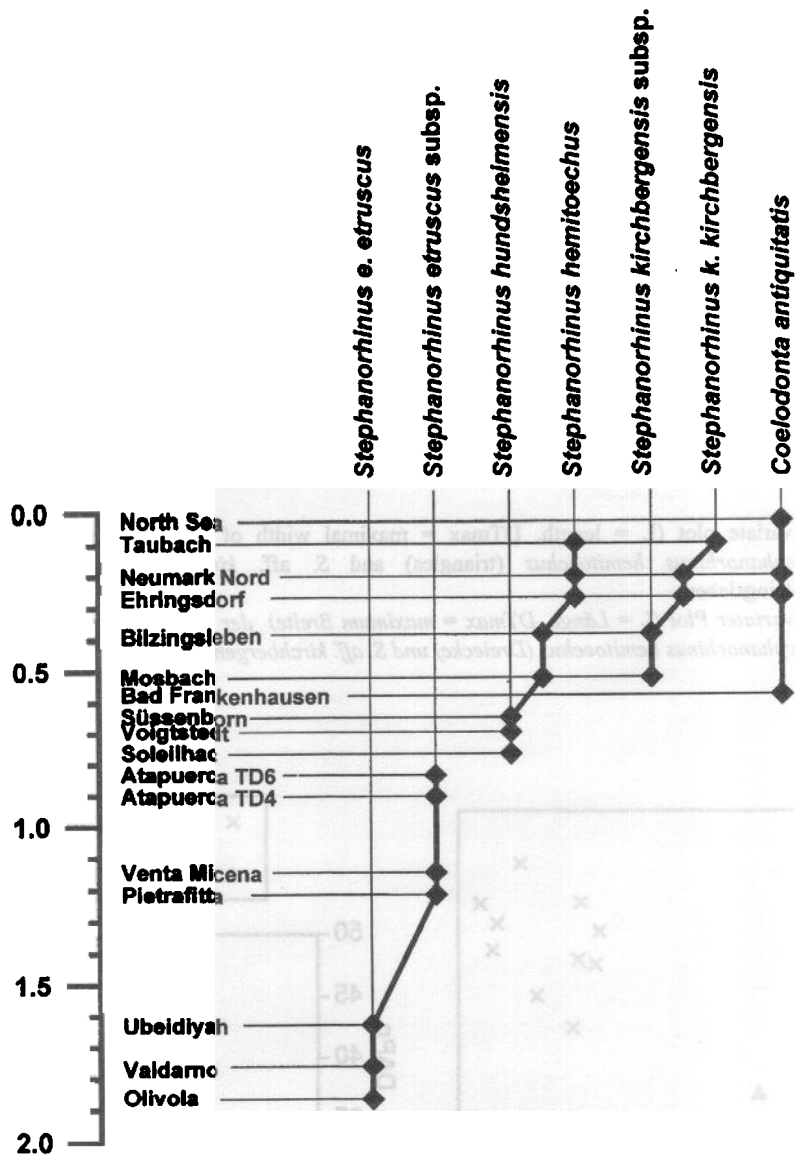


Fig. 8 Stratigraphical distribution of principal Pleistocene European rhinos. A selection of localities is given in approximate stratigraphical order and their estimated age in Ma (millions of years) is indicated on the left.

Abb. 8 Stratigraphische Verbreitung der hauptsächlichsten Nashornarten des europäischen Pleistozäns. Links die Auswahl von Fundorten in ihrer stratigraphischen Abfolge und mit ihrem geschätzten Alter (in Millionen Jahren)

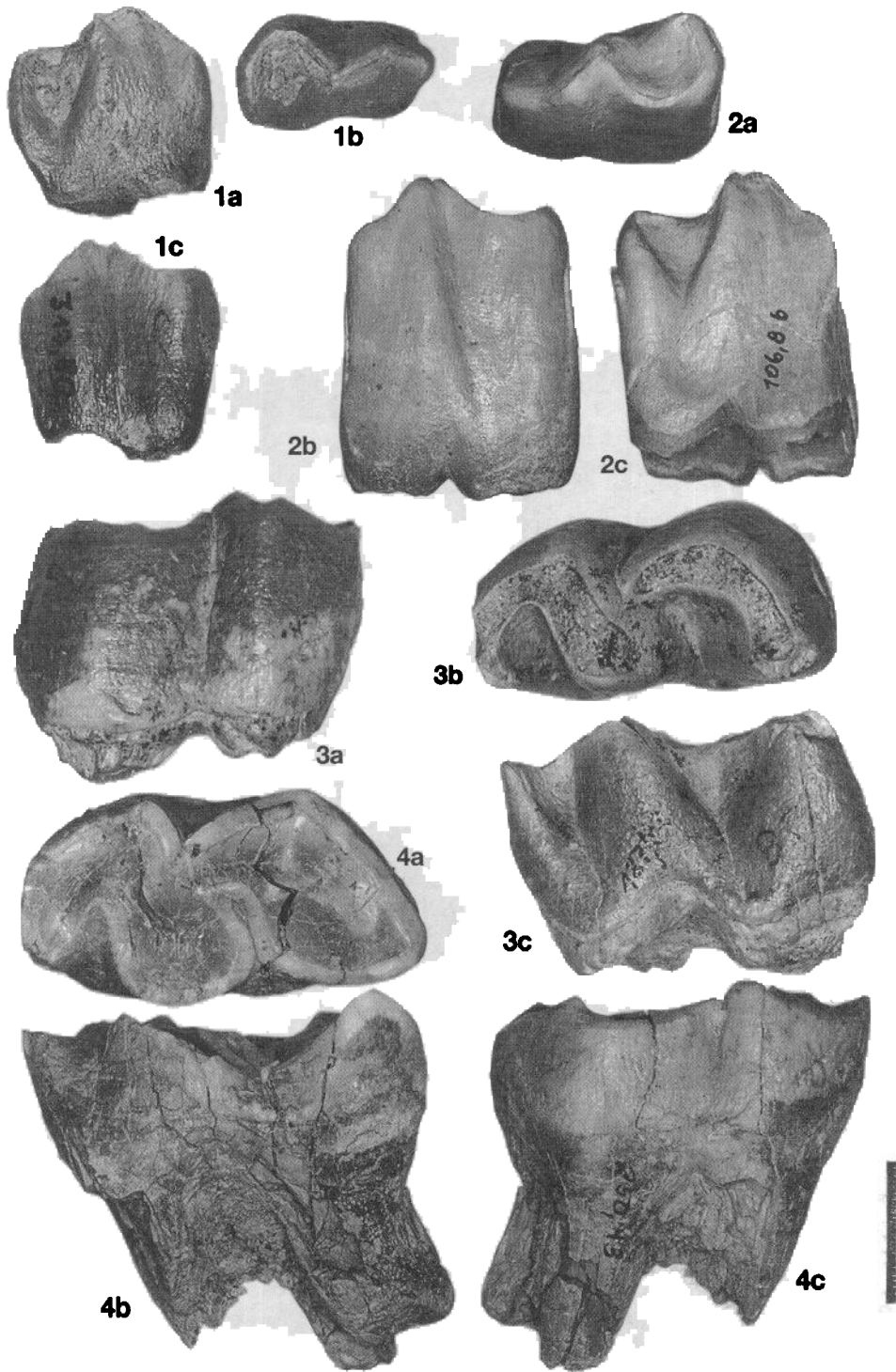
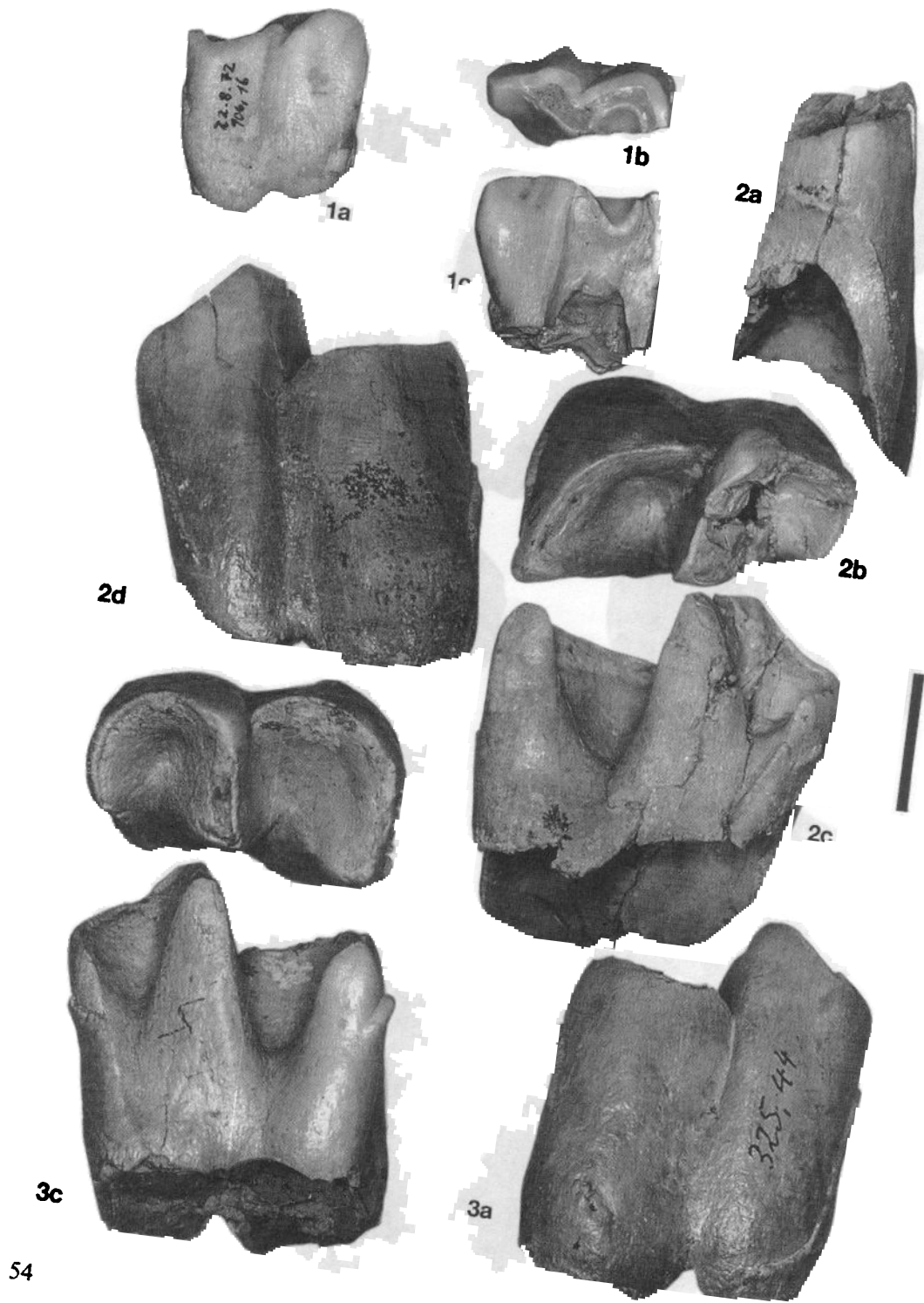
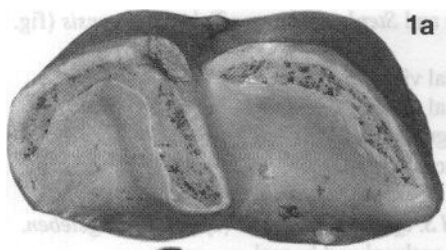


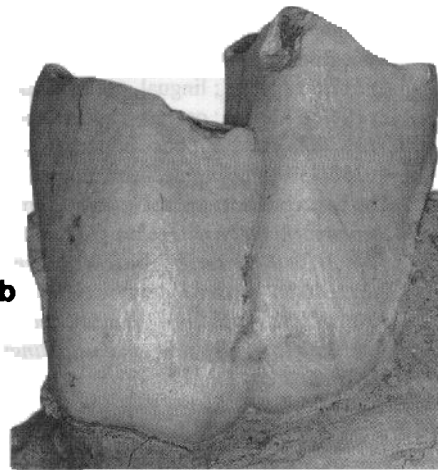
Plate 1 / Tafel 1



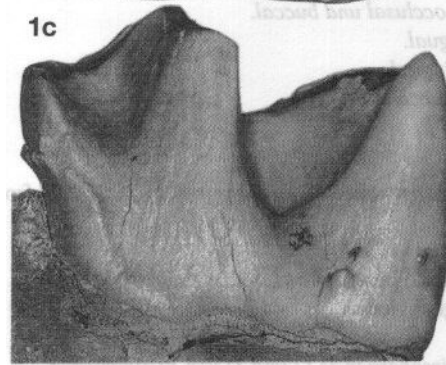
- Plate 1** *Stephanorhinus hemitoechus* (figs. 1, 3 & 4) and *Stephanorhinus* aff. *kirchbergensis* (fig. 2) from Bilzingsleben.
- 1) 317/80 - left  $P_2$ ; lingual, occlusal and buccal views.
  - 2) 106/86 - left  $P_2$ ; occlusal, buccal and lingual views.
  - 3) 187/82 - right  $M_3$ ; buccal, occlusal and lingual views.
  - 4) 250/43 - right  $M_3$ ; occlusal, lingual and buccal views.
- The bar represents approximately 2 cm.
- Taf. 1** *Stephanorhinus hemitoechus* (1, 3 und 4) und *S. aff. kirchbergensis* (2) von Bilzingsleben.
- 1 Nr. 317/80 - linker  $P_2$ , Ansicht von lingual, occlusal und buccal.
  - 2 Nr. 106/86 - linker  $P_2$ , occlusal, buccal, lingual.
  - 3 Nr. 187/82 - rechter  $M_3$ , buccal, occlusal, lingual.
  - 4 Nr. 250/43 - rechter  $M_3$ , occlusal, lingual, buccal.
- Maßstab: 2 cm.
- Plate 2** *Stephanorhinus hemitoechus* (fig. 1) and *Stephanorhinus* aff. *kirchbergensis* (figs. 2 & 3) from Bilzingsleben.
- 1) 106/16 - right  $P_2$ ; buccal, occlusal and lingual views.
  - 2) 345/48 - left  $M_1$ ; anterior, occlusal, lingual and buccal views.
  - 3) 325/44 - right  $P_4$ ; buccal, occlusal and lingual views.
- The bar represents approximately 2 cm.
- Taf. 2** *Stephanorhinus hemitoechus* (1) und *S. aff. kirchbergensis* (2 und 3) von Bilzingsleben.
- 1 Nr. 106/16 - rechter  $P_2$ , Ansicht von buccal, occlusal und lingual.
  - 2 Nr. 345/48 - linker  $M_1$ , anterior, occlusal, lingual, buccal.
  - 3 Nr. 325/44 - rechter  $P_4$ , buccal, occlusal, lingual.
- Maßstab: 2 cm.
- Plate 3** *Stephanorhinus hemitoechus* (figs. 2 & 3) and *Stephanorhinus* aff. *kirchbergensis* (fig. 1) from Bilzingsleben.
- 1) 275/184 - right  $M_1$ ; occlusal, buccal and lingual views.
  - 2) 171/44 - left  $M_3$ ; occlusal, lingual and buccal views.
  - 3) 204/162 - right  $M_2$ ; occlusal, lingual and buccal views.
- The bar represents approximately 2 cm.
- Taf. 3** 3 *Stephanorhinus hemitoechus* (2 und 3) und *S. aff. kirchbergensis* (1) von Bilzingsleben.
- 1 Nr. 275/184 - rechter  $M_1$ , Ansicht von occlusal, buccal und lingual.
  - 2 Nr. 171/44 - linker  $M_3$ , occlusal, lingual, buccal.
  - 3 Nr. 204/162 - rechter  $M_2$ , occlusal, lingual, buccal.
- Maßstab: 2 cm.
- Plate 4** *Stephanorhinus hemitoechus* (fig. 2) and *Stephanorhinus* aff. *kirchbergensis* (fig. 1) from Bilzingsleben.
- 1) 246b/62 - right mandible with  $M_{1,3}$ ; lingual, occlusal and buccal views.
  - 2) 320/122, 320/693, 320/694, 320/695 - left mandible with  $P_4$ - $M_3$ ; buccal, occlusal and lingual views.
- The bar represents approximately 10 cm.
- Taf. 4** 4 *Stephanorhinus hemitoechus* (2) und *S. aff. kirchbergensis* (1) von Bilzingsleben.
- 1 Nr. 246b/62 - rechter Unterkiefer mit  $M_{1,3}$ , Ansicht von lingual, occlusal und buccal.
  - 2 Nr. 320/122, 693-695 - linker Unterkiefer mit  $P_4$ - $M_3$ , buccal, occlusal und lingual.
- Maßstab: 10 cm.



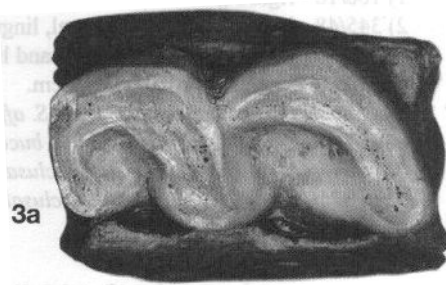
1a



1b



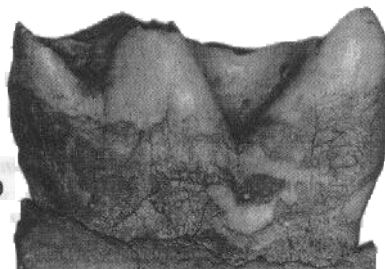
1c



3a



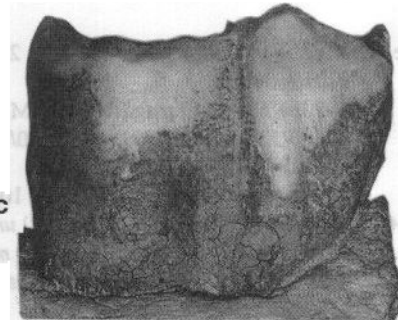
2a



3b



2b



3c



2c



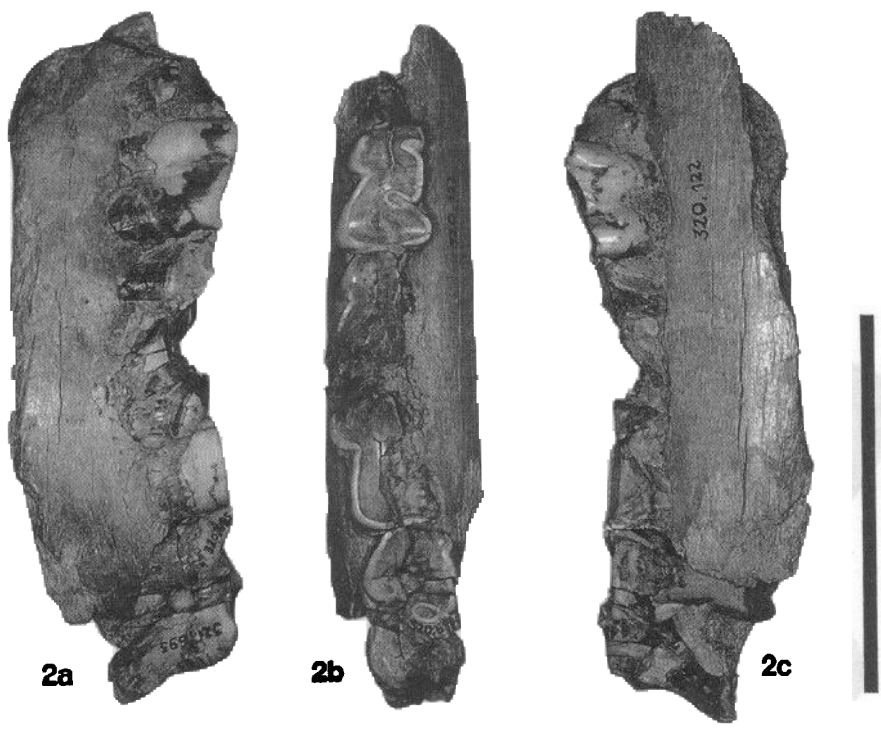
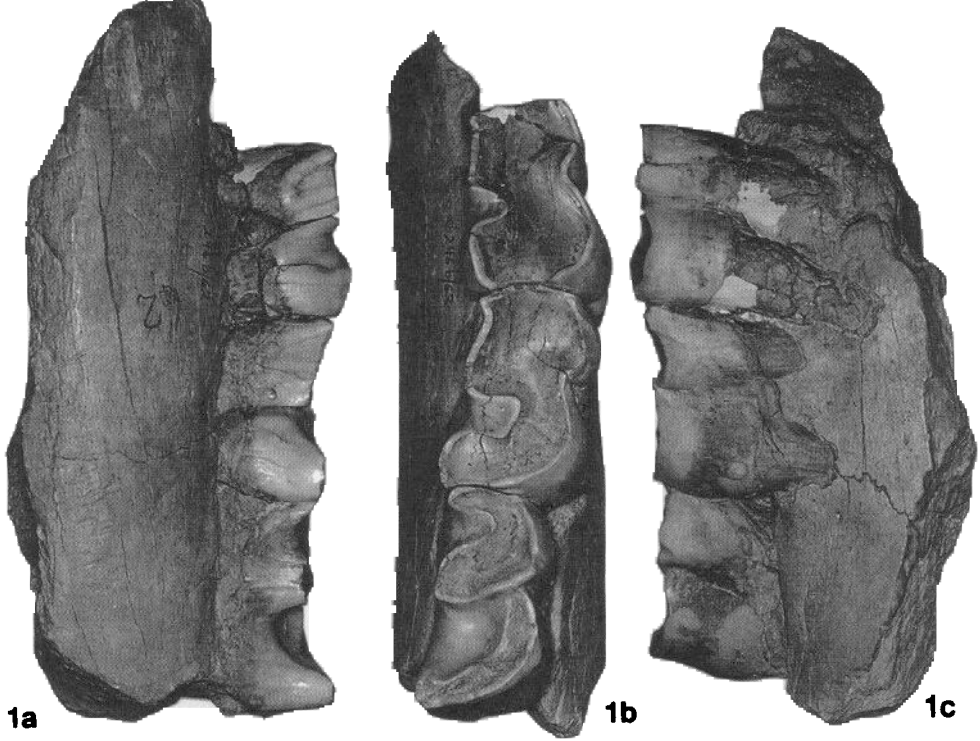
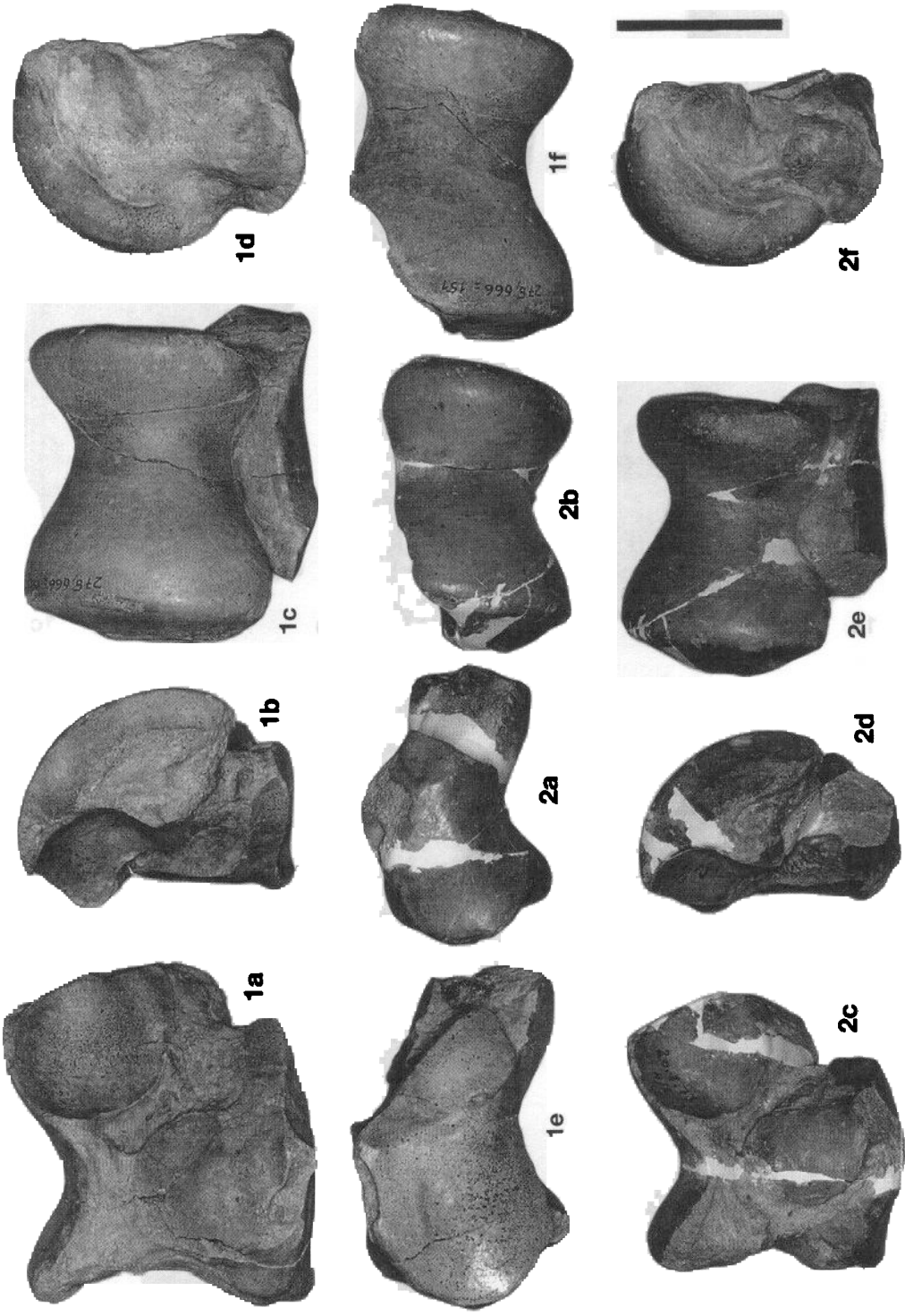
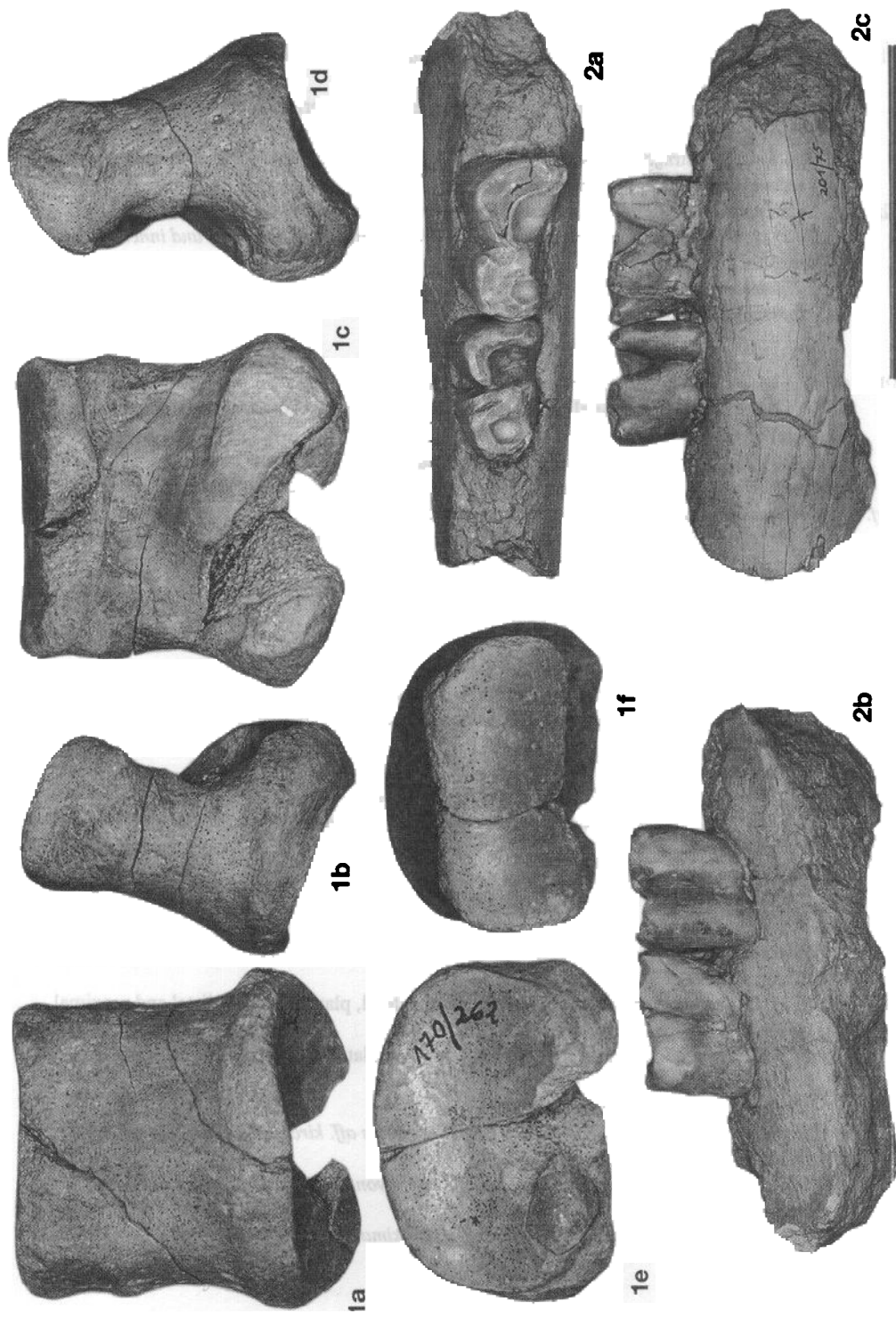
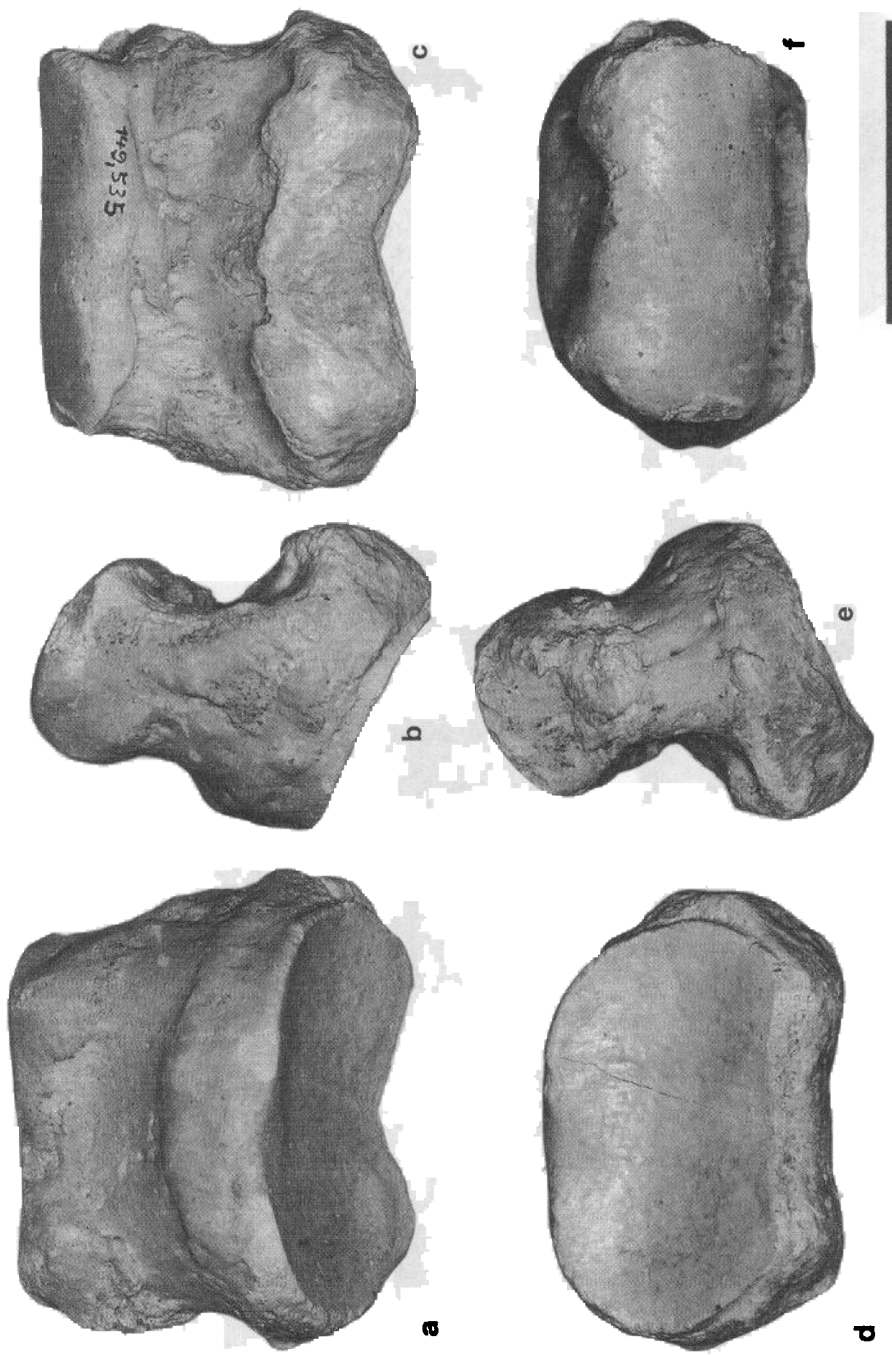


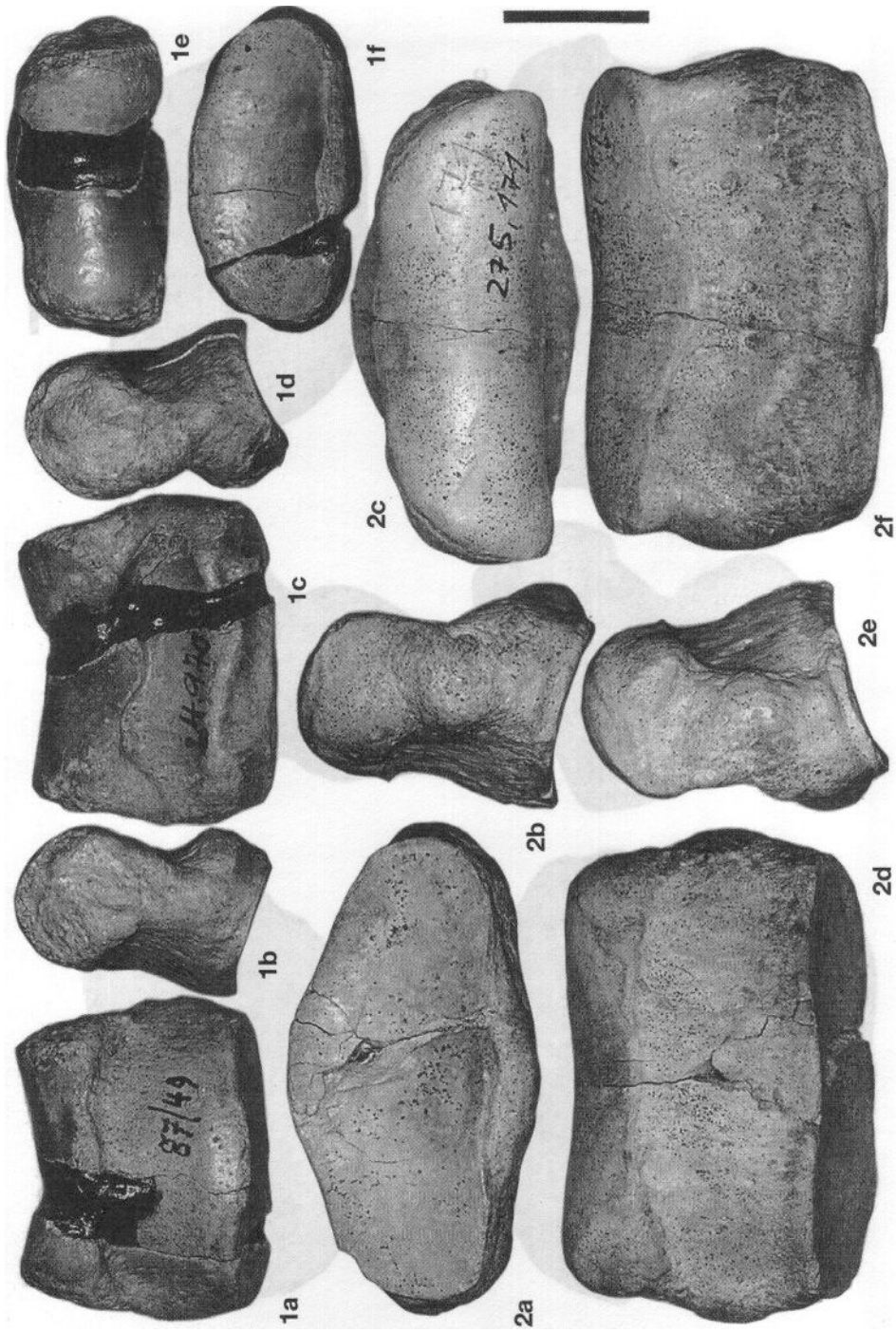
Plate 4 / Tafel 4



- Plate 5 *Stephanorhinus hemitoechus* (fig. 2) and *Stephanorhinus* aff. *kirchbergensis* (fig. 1) from Bilzingsleben.  
 1) 275/666 = 151 - right astragalus; posterior, external, anterior, internal, distal and proximal views.  
 2) 4/3 - right astragalus; distal, proximal, posterior, external, anterior and internal views.  
 The bar represents approximately 5 cm.
- Taf. 5 *Stephanorhinus hemitoechus* (2) und *S. aff. kirchbergensis* (1) von Bilzingsleben.  
 1 Nr. 275/666 = 151, rechter Astragalus, Ansicht von hinten, außen, vorn und innen, distal und proximal.  
 2 Nr. 4/3, rechter Astragalus, Ansicht distal und proximal von hinten, außen, vorn und innen  
 Maßstab: 5 cm.
- Plate 6 *Stephanorhinus hemitoechus* from Bilzingsleben.  
 1) 170/262 - left first central (III) phalanx; dorsal, internal, plantar, external, proximal and distal views.  
 2) 201/75 - right mandible with P<sub>4</sub>-M<sub>1</sub>; occlusal, buccal and lingual views.  
 The bar represents approximately 10 cm for figure 2 and 4.5 cm for figure 1.
- Taf. 6 *Stephanorhinus hemitoechus* von Bilzingsleben.  
 1 Nr. 170/262 - linke erste mittlere Phalanx (III), Ansicht von dorsal, innen, plantar, außen, proximal und distal.  
 2 Nr. 201/75 - rechter Unterkiefer mit P<sub>4</sub>-M<sub>1</sub>, occlusal, buccal, lingual.  
 Maßstab für 2: 10 cm, für 1: 4,5 cm.
- Plate 7 *Stephanorhinus* aff. *kirchbergensis* from Bilzingsleben.  
 149/535 - right (?) first central (III) phalanx; dorsal, external, plantar, proximal, internal and distal views.  
 The bar represents approximately 4 cm.
- Taf. 7 *Stephanorhinus* aff. *kirchbergensis* von Bilzingsleben.  
 Nr. 149/535 - rechte (?) erste mittlere Phalanx (III), Ansicht von dorsal, außen, plantar, proximal, innen, distal.  
 Maßstab: 4 cm.
- Plate 8 *Stephanorhinus hemitoechus* (fig. 1) and *Stephanorhinus* aff. *kirchbergensis* (fig. 2) from Bilzingsleben.  
 1) 87/49 - second central (III) phalanx; dorsal, lateral, plantar, lateral, distal and proximal views.  
 2) 275/171 - second central (III) phalanx; proximal, lateral, distal, dorsal, lateral and plantar views.  
 The bar represents approximately 2 cm.
- Taf. 8 *Stephanorhinus hemitoechus* (1) und *Stephanorhinus* aff. *kirchbergensis* (2) von Bilzingsleben.  
 1 Nr. 87/49 - zweite mittlere Phalanx (III) Ansicht von dorsal, lateral, plantar, lateral, distal und proximal.  
 2 Nr. 275/171 - zweite zentrale Phalanx (III) proximal, lateral, distal, dorsal, lateral und plantar.  
 Maßstab: 2 cm.









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