# The rhinos from the Middle Pleistocene of Neumark-Nord (Saxony-Anhalt)

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## Zusammenfassung

### Die Nashörner der mittelpleistozänen Fundstelle von Neumark-Nord (Sachsen-Anhalt)

*In Neumark-Nord (Sachsen-Anhalt, Deutschland) wurden die Ablagerungen eines kleinen interglazialen Sees überliefert, die mit einem Alter von etwas mehr als 200.000 Jahren in das Isotopenstadium OIS 7 gestellt werden können. Diese Sedimente enthalten eine große Anzahl an Skelettmaterial von verschiedenen Hirschen, Waldelefant, Auerochsen, mehreren Nashornarten und anderen Tieren, oft vergesellschaftet mit Steinartefakten.*

*Die Nashörner aus der Fundstelle wurden drei verschiedenen Arten zugewiesen: dem Waldnashorn* Stephanorhinus kirchbergensis, *dem Steppennashorn* Stephanorhinus hemitoechus *und dem Wollhaarnashorn* Coelodonta antiquitatis. *Von allen Arten blieb mindestens ein kompletter Schädel erhalten; von* S. hemitoechus *ist außerdem ein Teilskelett überliefert, das kräftiger gebaut ist als der von derselben Art bekannte Fund aus Bilzingsleben.*

Coelodonta *kennt man hauptsächlich als »glaziale« Art, in Neumark-Nord wurde sie aber in interglazialen Ablagerungen gefunden, die auch den Eurasischen Altelefanten* Elephas antiquus, S. kirchbergensis, *den Auerochsen* Bos primigenius *und den Rothirsch* Cervus elaphus *enthalten. Das häufigste Großsäugetier in den Sedimenten ist der Damhirsch* Dama. *Auch in anderen Fundstellen kennt man das Wollhaarnashorn aus interglazialen Ablagerungen, so z. B. in Ehringsdorf und La Fage. Beide Fundorte gehören einer ähnlichen Zeitstellung wie Neumark-Nord an, was nahelegt, dass während dieser Periode in großen Teilen Europas eine andere Umwelt oder ein anderes Klima vorherrschte als während anderer Interglaziale.*

*Die stratigraphische Verbreitung der westeuropäischen pleistozänen Nashörner wird dargelegt. Die stratigraphischen Reichweiten von* S. etruscus *und* S. hundsheimensis *überschneiden sich. Schrittweise ersetzten die stratigraphisch jüngeren Formen* C. antiquitatis, S. kirchbergensis *und* S. emitoechus *diese beiden Arten. Die drei jüngeren Arten haben mehr hypsodonte (hochkronigere) Zähne, mehr Zahnzement auf den Kronen und schmalere Prämolaren als die unter- und frühmittelpleistozänen Arten (*S. hundsheimensis *und* S. etruscus*). Diese Eigenheiten im Zahnbau legen nahe, dass ihre Nahrung in einem größeren Maße aus hartem Futter bestand, das zu einem starken Zahnabrieb führte. Möglicherweise begünstigten die sich häufig ändernden Klimabedingungen während der eiszeitlichen Perioden Arten, die daran angepasst waren, unter unterschiedlichen Umweltbedingungen zu leben, und die sich in diesen Zeiten daher erfolgreich ausbreiten konnten.*

## Summary

*At Neumark-Nord (Saxony-Anhalt, Germany) sediments of a little interglacial lake are preserved with an age of slightly more than 200 ka, which corresponds to OIS 7. The sediments contained a large number of skeletons of deer, elephants, auerochs, rhinos etc., many of which associated with lithic industry.*

*The Rhinocerotidae from this locality are described and assigned to the »forest rhino«* Stephanorhinus kirchbergensis, *the »steppe rhino«* Stephanorhinus hemitoechus *and the »woolly rhino«* Coelodonta antiquitatis. *All species are represented by at least a complete skull and* S. hemitoechus *also by a partial skeleton, which is more robust than in the same species from Bilzingsleben.*

Coelodonta *was believed to be mainly a »glacial« species, but at Neumark-Nord it has been found in an interglacial environment in direct association with* Elephas antiquus, S. kirchbergensis, Bos primigenius *and* Cervus elaphus, *while* Dama *is the most abundant large mammal in the sequence. Other localities where the woolly rhino was found in an interglacial environment are Ehringsdorf and La Fage. These localities are of a similar age, which suggests that during this period a different environment or climate prevailed in a large part of Europe, than in other interglacial periods.*

*The stratigraphic distribution of the west European Pleistocene rhinos is discussed. The stratigraphic ranges of* S. etruscus *and* S. hundsheimensis *overlap. The replacement of these rhinos by* C. antiquitatis, S. kirchbergensis *and* S. hemitoechus *occurred stepwise. These three species are more hypsodont, have more cementum on their crowns and have smaller premolars than the Early and early Middle Pleistocene species they replaced (*S. hundsheimensis *and* S. etruscus*). These dental features suggest that they had diets that included a greater proportion of hard or abrasive food. Possibly, the frequently changing environments during the glacial cycles favoured species, that were adapted to living in a wider range of environments and that therefore were better colonisers.*

## 1. Introduction

Neumark-Nord is a late Middle Pleistocene archaeological and palaeontological locality in sediments of a small interglacial lake (Mania et. al. 1990). Whereas most authors place the locality in an »Intra-Saale warm period« (equivalent to Oxygen Isotope Stage 7 - or OIS 7)[1], some place the locality in the Eemian (or OIS 5) (e. g. Litt 1994). The Ehringsdorf site is not far away and is similarly either placed in an »Intra-Saale warm period« or in the Eemian. Radiometric dates are in favour of the older age (Mallik et al. 2000; Mania et. al. 2003).

The geological situation of Neumark-Nord was described by M. Thomae (1990) and the pedology by M. Altermann (1990). Various archaeological aspects of the locality were described by D. Mania (1990; 1990a), U. Mania (1988) and E. Brühl (2001) with a general overview by D. Mania (1992; 1996) and the locality was treated in the regional context by D. Mania (Mania 1991; Mania 1997; Mania/Mai 2001).

An overview of the palaeontology of the locality, including plants, ostracods, molluscs and vertebrates, is given by Mania (2000). The palynology is described by M. Seifert (1990; 1990a and T. Litt (1994) and the macrofloral remains by D. H. Mai (1990) and Mania and Mai (Mania/Mai 2001). The ostracods were described by R. Fuhrmann and E. Pietrzeniuk (Fuhrmann/Pietrzeniuk 1990), the insects by G. Böhme (2001), the molluscs by Mania and Mai (Mania/Mai 2001), *Emys orbicularis* by V. Karl (1996) and Böhme indicated the presence of *Elaphe longissima*.

The locality is peculiar in the large number of articulated skeletons of large mammals (Mania 1990), in particular deer. The huge accumulation of deer skeletons was explained as due to cyanobacterial intoxication (Braun/Pfeiffer 2002). A pathology in *Elephas antiquus* was described by K. Fischer (2003). The reptiles and amphibians were described by Böhme (2003). Small mammals were described by W.-D. Heinrich (1990; 2001), *Bos primigenius* by H.-J. Döhle (1990) and the cave lion by Fischer (2001). For the fallow deer the name *Dama dama geiselana* was introduced, while also the red deer *Cervus elaphus* is present (Pfeiffer 1995; Pfeiffer 1997; Pfeiffer 1998; Pfeiffer 1999; Pfeiffer 1999a). The red deer from Neumark-Nord has been assigned to the subspecies *Cervus elaphus spelaeus*, while the fallow deer is seen as part of a long lineage in Europe (Van der Made 2001). The few remains belonging to *Megaloceros* were described by Van der Made (2003). In addition there are several species that have not yet been described in detail. After the literature cited above and the present paper, the list of mammals from Neumark-Nord is:

- Insectivora
  - *Talpa europea*
  - *Sorex* ex gr. *araneus*
- Rodentia
  - *Apodemus maastrichtiensis*
  - *Apodemus* sp.
  - *Clethrionomys glaerolus*
  - *Arvicola* sp.
  - *Microtus* ex gr. *arvalis/agrestis*
- Carnivora
  - *Ursus arctos*
  - *Panthera leo spelaea*
  - *Canis lupus*
  - *Vulpes vulpes*
- Proboscidea
  - *Elephas antiquus*
- Perissodactyla
  - *Equus* sp.
  - *Stephanorhinus kirchbergensis* (Fig. 1a–b)
  - *Stephanorhinus hemitoechus*
  - *Coelodonta antiquitatis*
- Artiodactyla
  - *Megaloceros giganteus antecedens*
  - *Dama dama geiselana*
  - *Cervus elaphus spelaeus*
  - *Bos primigenius*

## 2. Methods

The methods applied in this paper are the conventional methods in palaeontology. Metrical data are important, but only if accompanied by a clear statement of how they were obtained.

### *Measurements and their abbreviations*

All measurements are given in mm. Whenever possible, the measurements are taken in a way that is comparable to the measuring of Suoidea and ruminants as indicated by Van der Made (1989; 1996). General abbreviations are:

DAP = antero-posterior diameter.
DT = transverse diameter.
H = height.
L = length.

The way of measuring the **skull** is indicated in Fig. 2. These measurements are given here, using C. Guérin's numbers, as well as other measurements[2].

1) Distance from the tip of the premaxillary to the posterior surface of the occipital condyles in rhinos where the nasal septum is not ossified, identical to measurement 2 in rhinos with an ossified nasal septum.
2) Distance from the tip of a nasal to the posterior surface of an occipital condyle on the same side.
3) Distance from the tip of nasals to the occiput.
4) Length of the nasal-incisive notch.
5) Minimal width at the postorbital constriction.
6) Distance from the postorbital process to the occiput (cannot be taken if the postorbital process is not well developed).
7) Distance from the superorbital process to the occiput.

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[1] E. g. Mania 1994; Mania 1995; Mania 1997; Heinrich 2000; Heinrich 2001; Van der Made 2001; Van der Made et. al. 2004.

[2] Guérin 1980, Tab. 1,4a–f; indicated measurements numbered 1 to 32, though numbers 10–12 and 24 are lacking in his table.

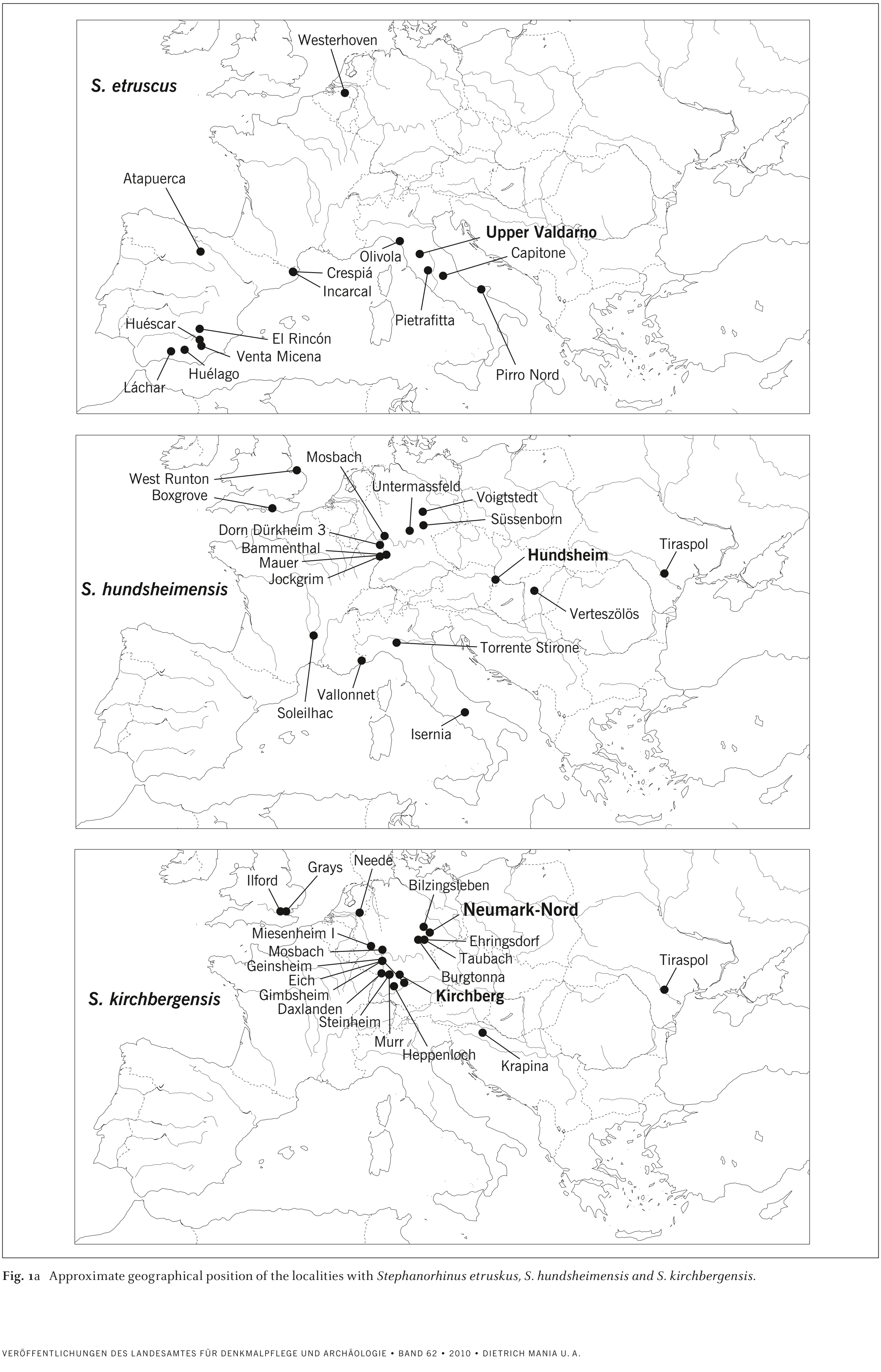


**Fig. 1a** Approximate geographical position of the localities with *Stephanorhinus etruskus, S. hundsheimensis and S. kirchbergensis.*

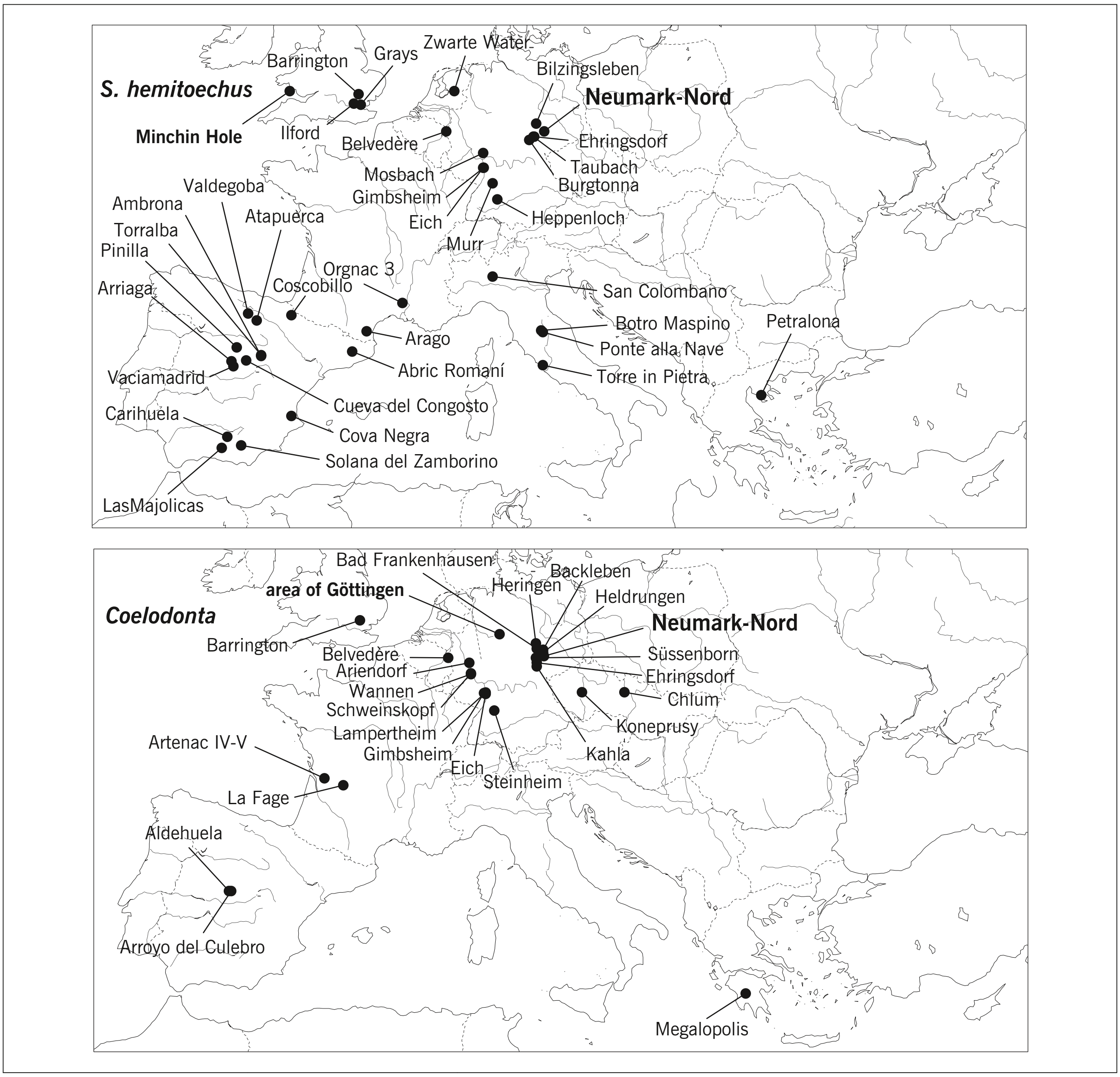


**Fig. 1b** Approximate geographical position of the localities with *Stephanorhinus hemitoechus* and *Coelodonta antiquitatis*.

8) Distance from the preorbital process to the occiput.
9) Distance from the nasoincisive notch to the anterior rim of the orbit.
13) Distance from the posterior border of the M$^3$ to the posterior end of the occipital condyle of the same side.
14) Distance from the tip of a nasal to the anterior border of the orbit.
15) Width of the occiput.
16) Width of the skull at the mastoid apophyses.
17) Minimal distance between the fronto-parietal crests.
18) Width at the postorbital processes.
19) Width at the supraorbital processes.
20) Width at the preorbital processes.
21) Maximal width at the zygomatic arcs.
22) Width of the entrance of the nasal cavity.
23) Distance of the foramen magnum to the occipital crest.
25) Height of the skull just anterior to the P$^2$, measured parallel to the medial plane.
26) Height of the skull above P$^4$–M$^1$, measured parallel to the medial plane.
27) Height of the skull above the M$^3$, measured parallel to the medial plane.
28) Width of the palate, measured just anterior to the P$^2$.
29) Width of the palate at the level of P$^4$–M$^1$.
30) Width of the palate, measured just anterior to the M$^3$.
31) Width of the foramen magnum.
32) Width of the occipital condyles.
33) Width of the nasals.
34) Height of the nasal aperture.
35) Width of the choanae.
36) Minimal width of the skull in the area of the pterygoid process of the basisphenoid.
37) Distance between the caudal alar foramina.
38) Distance between the lacerum foramina.

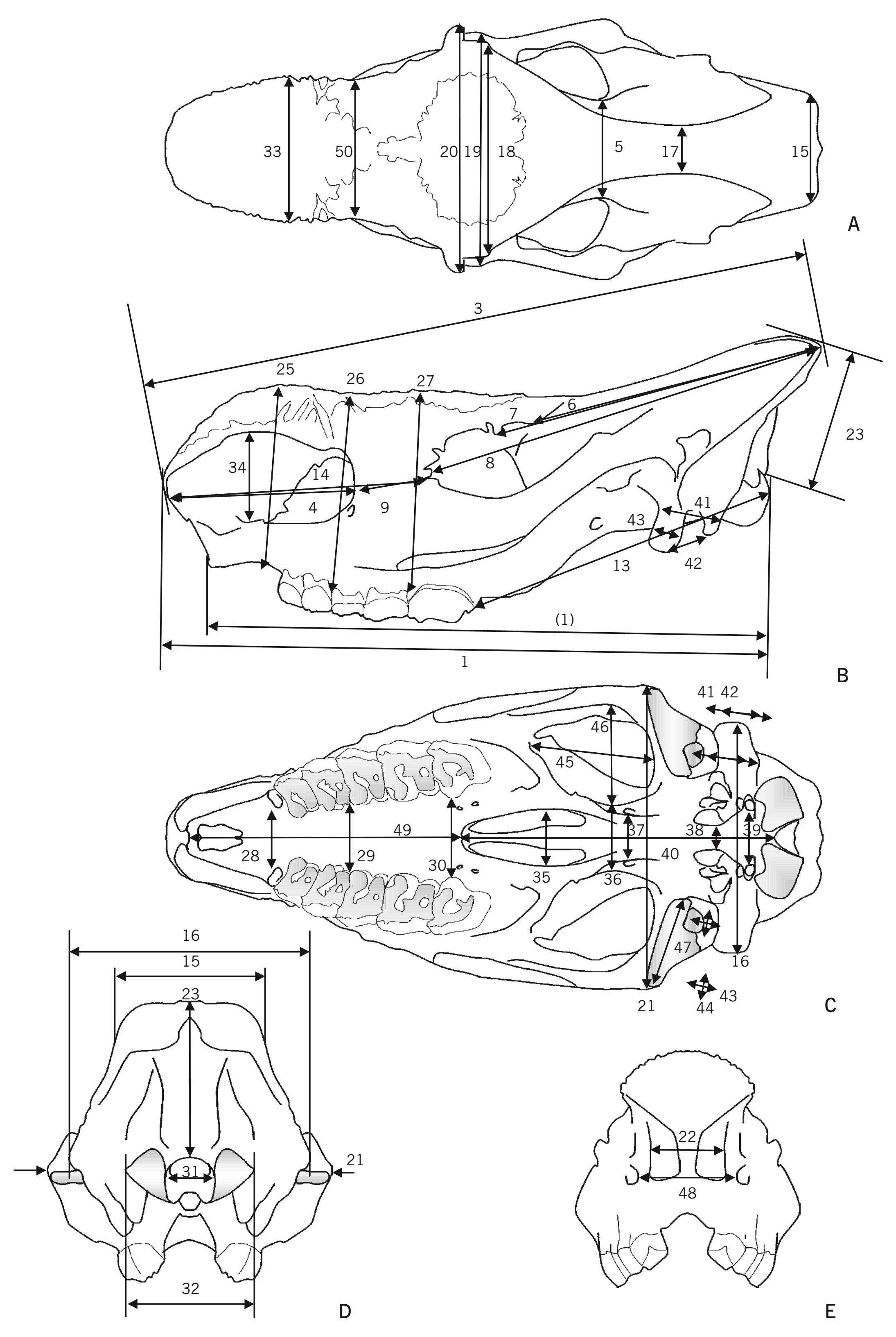


**Fig. 2** The way of measuring the skull: A) dorsal view, B) left lateral view, C) inferior view, D) posterior view, E) anterior view. Numbers and abbreviations as given in the text.

39) Distance between the hypoglossal foramina.

40) Distance between the posterior limit of the palate and the foramen magnum.

41) Distance of the front of the retroarticular process to the back of the jugular process.

42) Distance of the tip of the retroarticular process to the tip of the jugular process.

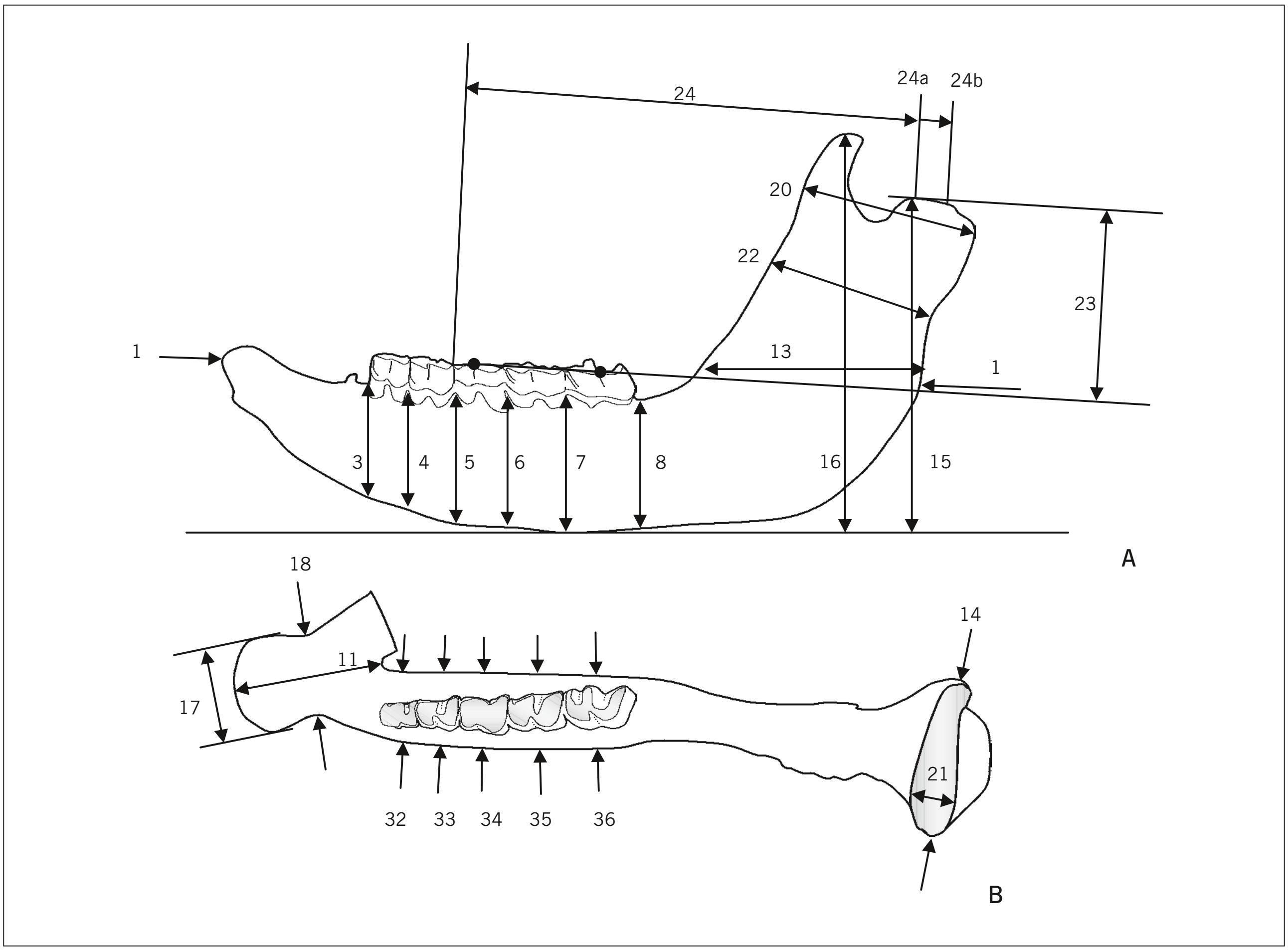


**Fig. 3** The way of measuring the mandible: A) buccal view, B) occlusal view. Measurements 1–16 after Guérin (1980).

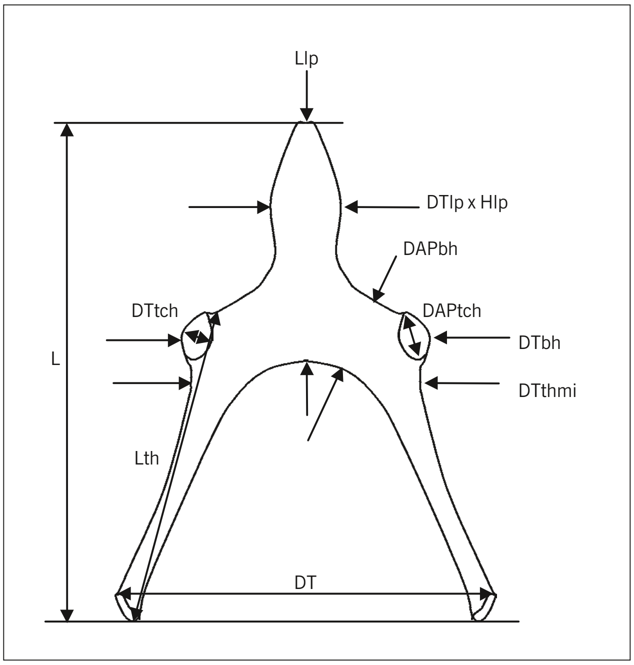


**Fig. 4** The way of measuring the hyoid.

43) DAP of the retroarticular process.
44) DT of the retroarticular process.
45) Length of the space medial to the zygomatic arc.
46) Width of the space medial to the zygomatic arc.
47) Width of the facet.
48) Distance between the infraorbital foramina.
49) Length of the palate measured in the median plane.
50) Minimal width of the nasals behind the area of origin of the nasal horn.

The way of measuring the **mandible** is indicated in Fig. 3. Guérin's (1980, Tab. 3,4g) measurements are numbered 1 to 16. Most of them are included here (using their original numbers), and others are added.

1) Length of the mandible.
2) Distance of back of symphysis to back of the mandible (not indicated in Guérin's Fig. 4g).
3–8) Depth of the mandible behind $P_2$–$M_3$, measured at the internal side of the mandible and perpendicular to the alveolar border (Guérin, Tab. 3), or at the buccal side and perpendicular to the length of the mandible (measurement 1) (Guérin 1980, Fig. 4g).
9–10) Width of the mandible behind $P_4$ and $M_2$. These values are very similar to the »D« values taken here and are not given separately
11) Length of the symphysis. Taken here in a similar way as indicated by Van der Made (1996).
12) Not indicated by Guérin (1980, Tab. 3,4g).
13) DAP ramus at occlusal level and parallel to it.
14) DT condyle.
15) Height of condyle above the lower border of the mandible. It should be taken into account that this meas-

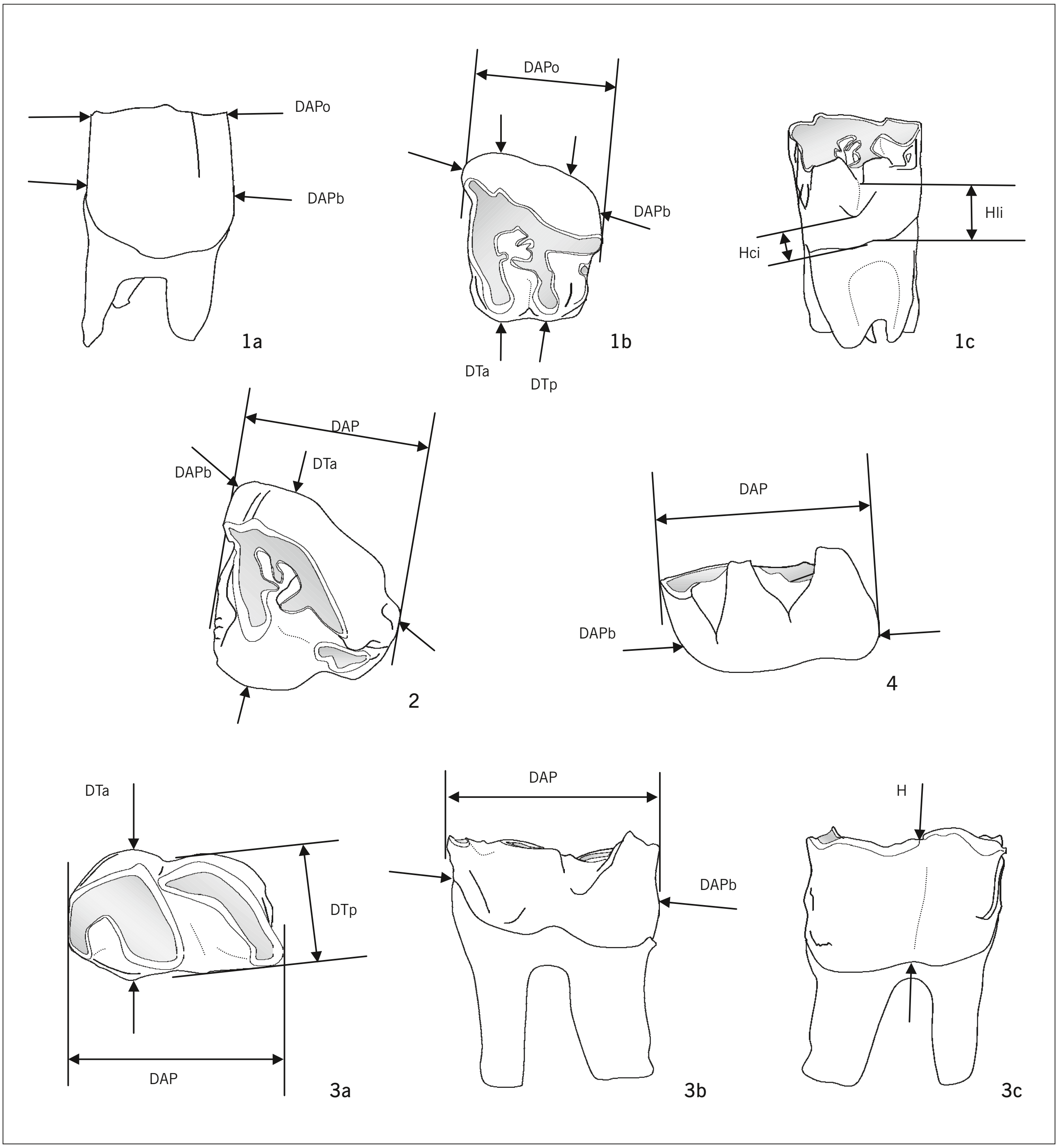


**Fig. 5** The way of measuring the teeth. Given as examples: 1) P3, 2) M3, 3) $M_1$ and 4) $M_3$. Abbreviations as given in the text.

urement is subject to the way the mandible is oriented and thus may be more variable, especially if measurements taken by different persons are compared.

16) Height of coronoid process above the lower border of the mandible. See remark with measurement 15.
17) Maximal width of the anterior part of the mandible.
18) Minimal width symphyseal area at the place of waisting.
19) Height symphysis (see Van der Made 1996).
20) DAP of the ascending ramus at the level of the condyle.
21) Maximum DAP of the facet of the condyle.
22) Minimal DAP of ascending ramus at about half its height.
23) Height of the condyle above occlusal surface. The height is taken perpendicular to the line that that passes through the lowest points of the occlusal surface in the middle of $M_1$ and $M_3$ (indicated by dots).
24) Distance of the condyle (at its highest point - a -, or at its posterior border - b) behind the front of the M1 and measured parallel to the line through the occlusal surface, described above.
25–30) D = depth of mandible at each cheek tooth: D($P_2$) … D($M_3$). It is taken at the lingual side of the mandible and is the shortest distance from the highest point of the mandible below the middle of a tooth to the lower border of the mandible (see Van der Made 1989; Van der Made 1996).

31–36) W = width of the mandible, at each cheek tooth: W($P_2$) … W($M_3$). It is taken perpendicular to D. D and W are comparable to measurements 3–10 by Guérin (1980), but are taken as defined by Van der Made (1989; 1996) for ruminants and suoids and are preferred here.

The way of measuring the **hyoid** is indicated in Fig. 4.

L = length.
DT = transverse diameter.
Llp = length of the lingual process measured from the back of the basihyoid.
Hlp = height of the lingual process.
DTlp = greatest width of the lingual process.
DAPbh = minimal DAP of the section of the body of the basihyoid.
DTbh = DT of the basihyoid, or maximum width of the bone at the place of the tubercles for articulation with the ceratohyoid.
DTthmi = DT of thyrohyoid.
DAPtch = greatest diameter of the tubercle for articulation with the ceratohyoid.
DTtch = width of the tubercle for articulation with the ceratohyoid, measured perpendicular to DTtch.
Lth = length of the thyrohyoid.

The **teeth** are measured as indicated in Fig. 5.

DAP = In the $P^x$ and $M^{1-2}$ the maximum DAP measured on the buccal side, usually more or less equivalent to the occlusal DAP, though occasionally the anteriormost point may be a little below the occlusal surface. Compared to the other upper cheek teeth, the $M^3$ has a different shape and in this case, the DAP is taken close to the base, at the level where the crown extends most posteriorly. In the $M^3$, the measurement is perpendicular to the line through the anteriormost parts of the tooth in the middle and at the buccal side at the same level as the posterior measuring point. In the lower teeth, the DAP is the maximum length measured at the lingual side and parallel to the occlusal surface. Usually this will be more or less the occlusal length. In the $M_3$, the basis of the tooth extends much more posteriorly than the occlusal surface. In such a case, the measurement is taken as indicated in Fig. 5,4.
DTa = The maximum DT of the anterior lobe of the tooth.
DTp = The maximum DT of the posterior lobe of the tooth.
H = In the lower molars, the height of the tooth at the buccal side where the talonid and trigonid meet. It is measured as the distance between the uppermost point of the lower border of the crown and the point where the anterior wing of the hypoconid connects to the back of the protoconid. This measurement is possibly not the best indicator of the functional crown height, but is certainly a measurement that often can be taken, since it is taken at the last point of the upper part of the tooth to be affected by wear. Here the measurement is not taken if wear has affected this point, though it might be used as some indication for the age of the individual.
Hci = In the upper premolars with a lingual cingulum, this is the shortest distance between the cingulum and the lower border of the crown.
Hli = In the upper premolars, this is the distance between the lower border of the crown and the point where the bases of the lingual cusps meet. This measurement is not taken strictly perpendicular to the basis of the crown or occlusal surface (how to determine such a plane?). The measurement is taken here in premolars; although such a measurement might be interesting in molars, it is difficult or impossible to take such a measurement in a constant way.

The **vertebrae** are measured as indicated in Fig. 6.

1 = total height.
2 = height of the vertebral body.
3 = length of the dorsal spine, measured at the posterior side from the upper surface of the vertbral canal to the tip of the spine and more or less perpendicular to the antero-posterior axis of the vertebral canal.
4 = height of the main anterior facet.
5 = height of the main posterior facet.
6 = height of the vertebral canal, measured at the posterior side.
7 = length of the vertebral body, measured in the medial plane as the distance from the line through the ventral and dorsal edges of the main facet to the parallel line that touches the surface of the main anterior facet. This measurement is thus not taken parallel to the lower and lateral surfaces of the vertebral body. Whereas this measurement seems to reflect well in some way the length of the body, in the axis (with its tooth), it seems artificial and the length is measured in the median plane as the distance from the postero-ventral point to the anteriormost point (as indicated by Mazza 1988, Fig. 4,1b).
8 = antero-posterior diameter of the arch in the median plane.
9 = distance of the most cranial point of the cranial articular process to the most caudal point of the caudal articular process. This measurement can be taken on the right or left sides.
10 = distance of the most cranial to the most caudal point of the transverse process. This measurement can be taken on the right or left sides.
11 = maximum width of the vertebra, measured at the transverse process.
12 = width of the »waist« of the vertebra. (In thoracic vertebrae, the transverse process tends to be positioned more dorsally and the articular processes more medially and there is no »waist«; the measurement is not taken.)

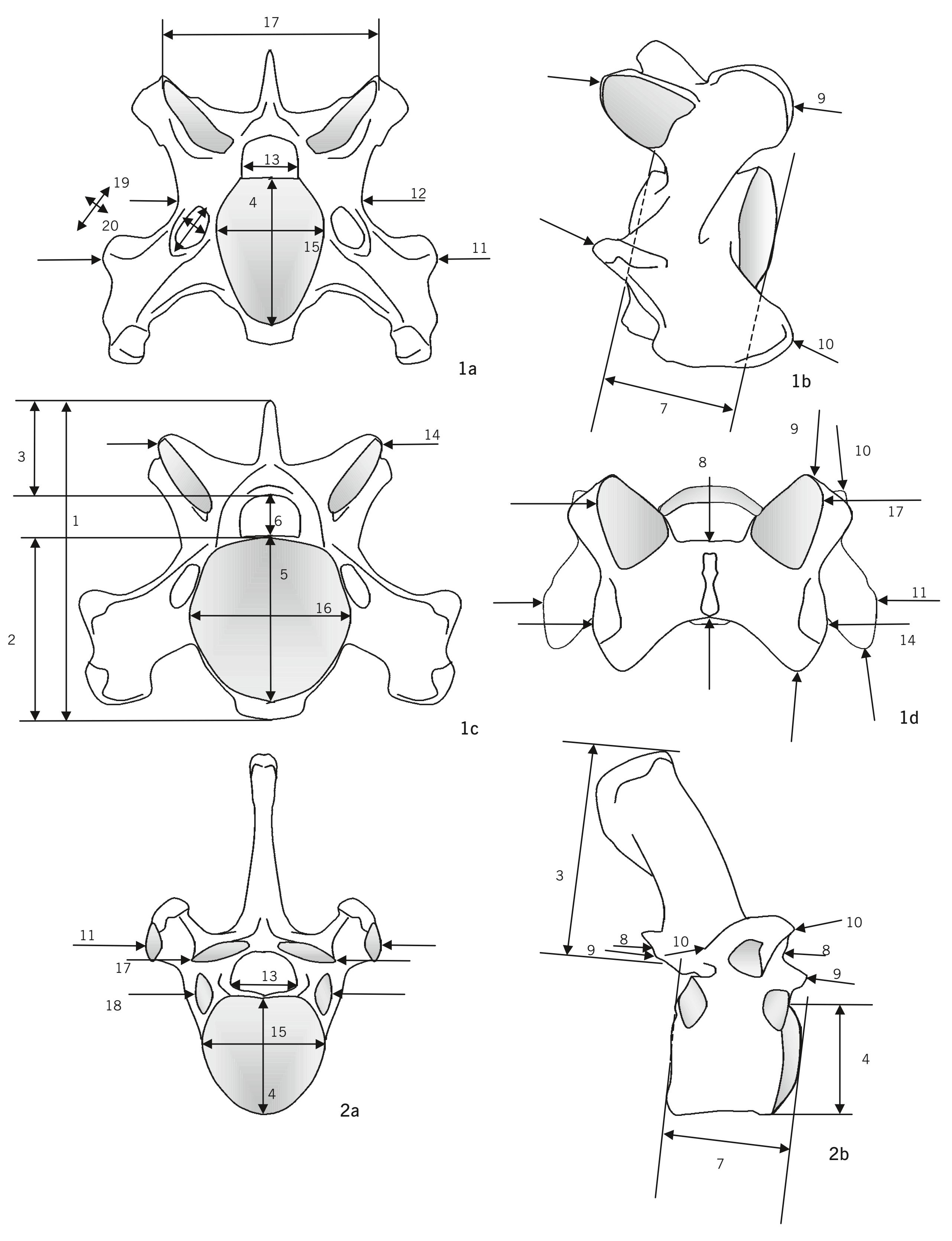


**Fig. 6** The way of measuring the vertebrae. Given as examples: 1) $C_4$, 2) a posterior thoracic vertebra.

13 = width of the vertebral canal, measured at the anterior side.
14 = width measured at the caudal articular facets.
15 = width of the main anterior facet.
16 = width of the main posterior facet.
17 = width measured at the cranial articular facets.
18 = width measured at the anterior costal facets.

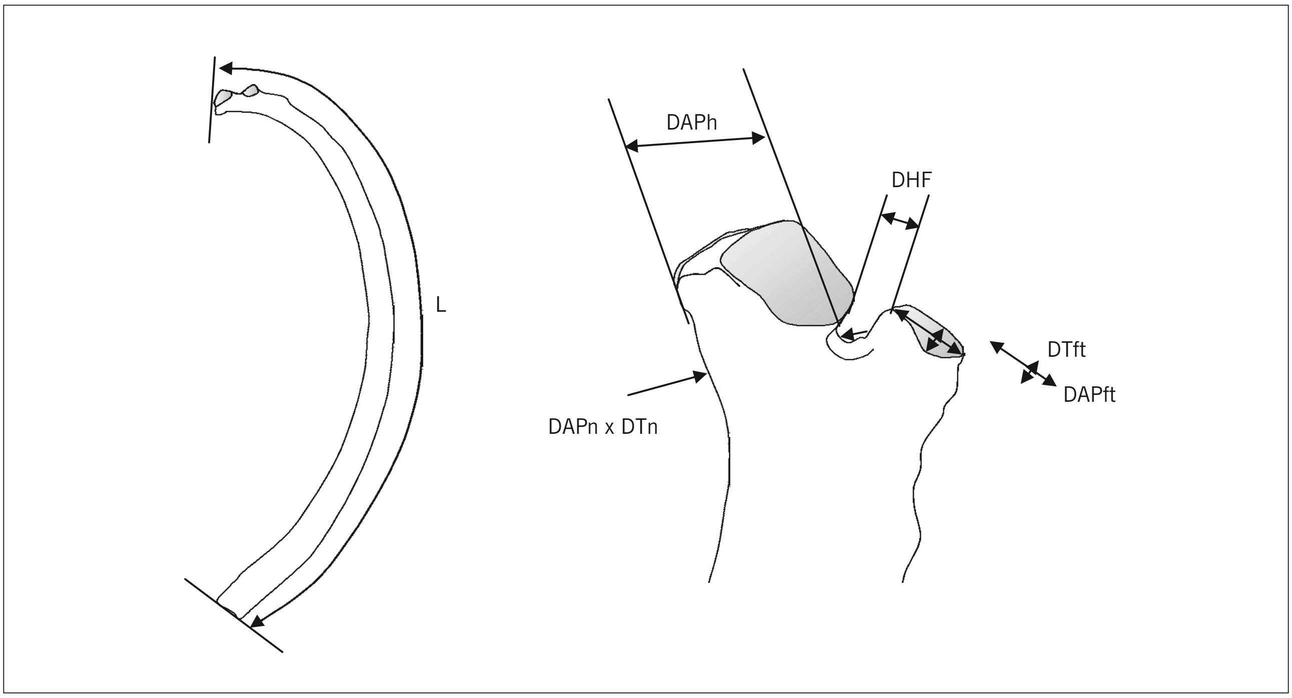


**Fig. 7** The way of measuring the ribs.

19 = long axis of the transverse foramen. This measurement can be taken on the right and left sides in the anterior vertbrae till C7.
20 = short axis of the transverse foramen. This measurement can be taken on the right and left sides in the anterior vertbrae till C7.

The **ribs** are measured as indicated in Fig. 7.

DAPh = DAP of the head, measured at the lower edges of the anterior and posterior facets.
DAPn = DAP of the neck.
DTn = DT of the neck.
DAPft = DAP of the third facet, or facet on the tubercle.
DTft = DT of the third facet, or facet on the tubercle.
DHF = distance from posterior facet on the head to the facet on the tubercle.
L = length measured along the outer side, following the curvature.
DAPsma = maximal DAP of the shaft.
DAPsmi = minimal DAP of the shaft.
DTsma = maximal DT of the shaft (not necessarily measured at the same level as DAPsma).
DTsmi = minimal DT of the shaft (not necessarily measured at the same level as DAPsmi).

The **scapula** is measured as indicated in Fig. 8,2.

DAPd = antero-posterior diameter of the distal part.
DAPdf = antero-posterior diameter of the distal articulation.
DTd = width of the distal part, which is identical to the width of the distal articulation.
DAPn = minimal DAP at the »neck«.
DTn = minimal DT at the »neck«.
L = length.

The **humerus** is measured as indicated in Fig. 8,3.

DAPp = proximal antero-posterior diameter.
DAPp' = an alternative measurement of the proximal antero-posterior diameter.
DTp = proximal width.
DTpf = width of the proximal articular surface.
L = length.
l = an alternative measurement of the length, from the middle of the groove of the distal articulation to the proximal articular surface.
DAPd = distal antero-posterior diameter.
DTd = distal width.
DTdf = width of the distal articular facet.
R1 = medial diameter of the distal articular facet.
R2 = diameter in the middle of the distal articular facet.
R3 = lateral diameter of the distal articular facet.

The **ulna** is measured as indicated in Fig. 8,1.

DAPh = antero-posterior diameter of the head.
DTh = width of the head.
DAPn = antero-posterior diameter of the neck.
DTn = transverse diameter of the neck.
DAPmax = maximum antero-posterior diameter, measured perpendicular to the posterior edge of the bone.
DTmax = maximum width of the bone at the level of the articular facets with the proximal part of the radius.
DTfu = width of the upper part of the facet for articulation with the humerus.
L = total length of the bone.
Lu = length of the upper part measured as the shortest distance between the articular surface for the humerus and the tip of the head.

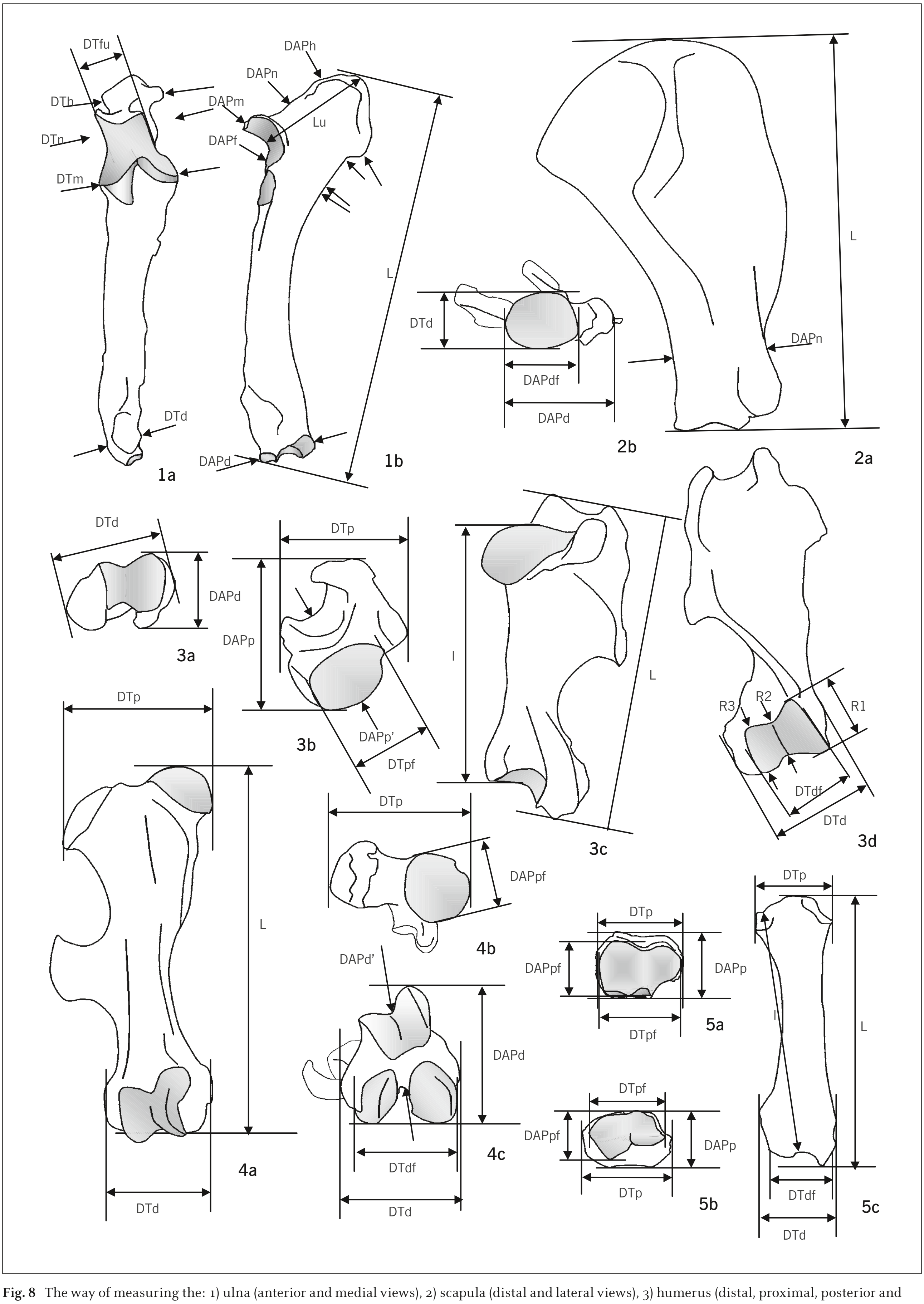


**Fig. 8** The way of measuring the: 1) ulna (anterior and medial views), 2) scapula (distal and lateral views), 3) humerus (distal, proximal, posterior and anterior views), 4) femur (anterior, proximal and distal views, 5) radius (proximal, distal and anterior views).

DAPd = antero-posterior diameter of the distal part of the bone.
DTd = width of the distal part of the bone.

The **radius** is measured as indicated in Fig. 8,5.

DAPp = antero-posterior diameter of the proximal end of the bone.
DAPpf = antero-posterior diameter of the proximal facet.
DTp = transverse diameter of the proximal end of the bone. Is frequently close to DTpf.
DTpf = transverse diameter of the proximal facet.
L = length.
l = an alternative measurement of the length, that frequently can be taken even if the distal ends are eroded or broken.
DAPd = antero-posterior diameter of the distal end of the bone.
DAPdf = antero-posterior diameter of the distal facet.
DTd = transverse diameter of the distal end of the bone.
DTdf = transverse diameter of the distal facet.

The **scaphoid** is measured as indicated in Fig. 9,3.

DAP = measured approximately perpendicular to H.
DT = measured at the widest point, which is the proximal articulation surface.
H = the height, measured as the distance between the line that passes through the two most proximal points and the point of the bone that is most distal to this line.
h = alternative H, measured as the minimal distance between the proximal and distal articular surfaces.

Of the **pelvis** only the maximal diameter of the articular surface of the acetabulum is measured, since usually not much more is preserved.

The **femur** is measured as indicated in Fig. 8,4.

DAPpf = antero-posterior diameter of the articular surface of the head.
DTp = width of the proximal part of the bone.
L = total length, which coincides with the physiologic length, since the greater trochanter is lower than the articular surface.
DAPd = shortest distance of the line that passes through the two posteriormost points of the bone, at the distal end, and the anterior most point of the bone.
DAPd' = distance from the intercondyloid fossa, at the back of the bone, to the depression in the middle of the trochlea. (The medial ridge of the trochlea is often broken or eroded, and the normal DAPd cannot be measured).
DTd = maximal width of the distal part of the bone.

The way of measuring the **patella** is indicated in Fig. 9,7.

DAP = antero-posterior diameter.
DT = width.
H = height.
DTf = width of the facet.
Hf = height of the facet.

The way of measuring the **astragalus** is indicated in Fig. 9,4.

Lext = length, measured at the lateral side.
Lm = minimum length, measured in the middle.
Lint = length, measured at the medial side.
DTpf = proximal DT, or DT of the trochlea.
DT = total DT.
DTdf = DT of the distal articular surface, formed by the facets for navicular and cuboid.
DAPdf = DAP of the distal articular surface.
R (or Rint) = diameter of the trochlea, measured at the medial side.
Rm = minimum diameter of the trochlea, measured approximately at the middle of the trochlea.

The way of measuring the **navicular** is indicated in Fig. 9,6.

DAP = distance between the line that passes through the two posteriormost points of the bone and the anteriormost point.
DT = distance between the medial border of the bone and the point of the bone that sticks out most at the lateral side.

**Third cuneiforme** (Fig. 9,5).

DAP = maximal DAP.
DT = maximal DT, measured approximately perpendicular to DAP.

The way of measuring the **metatarsals** is indicated in Fig 9,1, with the example of the Mt III. Other metapodials are measured in approximately the same way.

L = length, measured parallel to the long axis as the distance from the most proximal and most distal points.
l = an alternative measurement of length, which is the shortest distance between the proximal and distal borders of the bone.
DAPp = DAP, measured at the proximal side.
DTp = DT, measured at the proximal side.
DAPd = DAP of the distal articular surface.
DTd = DT of the distal end of the bone, including the tuberosities just proximal to the articular surface.
DTdf = DT of the distal articular surface.

The **lateral first phalanx** (Fig. 9,2).

DAPp = proximal DAP, measured perpendicular to the axis of the bone.
DTp = proximal DT.

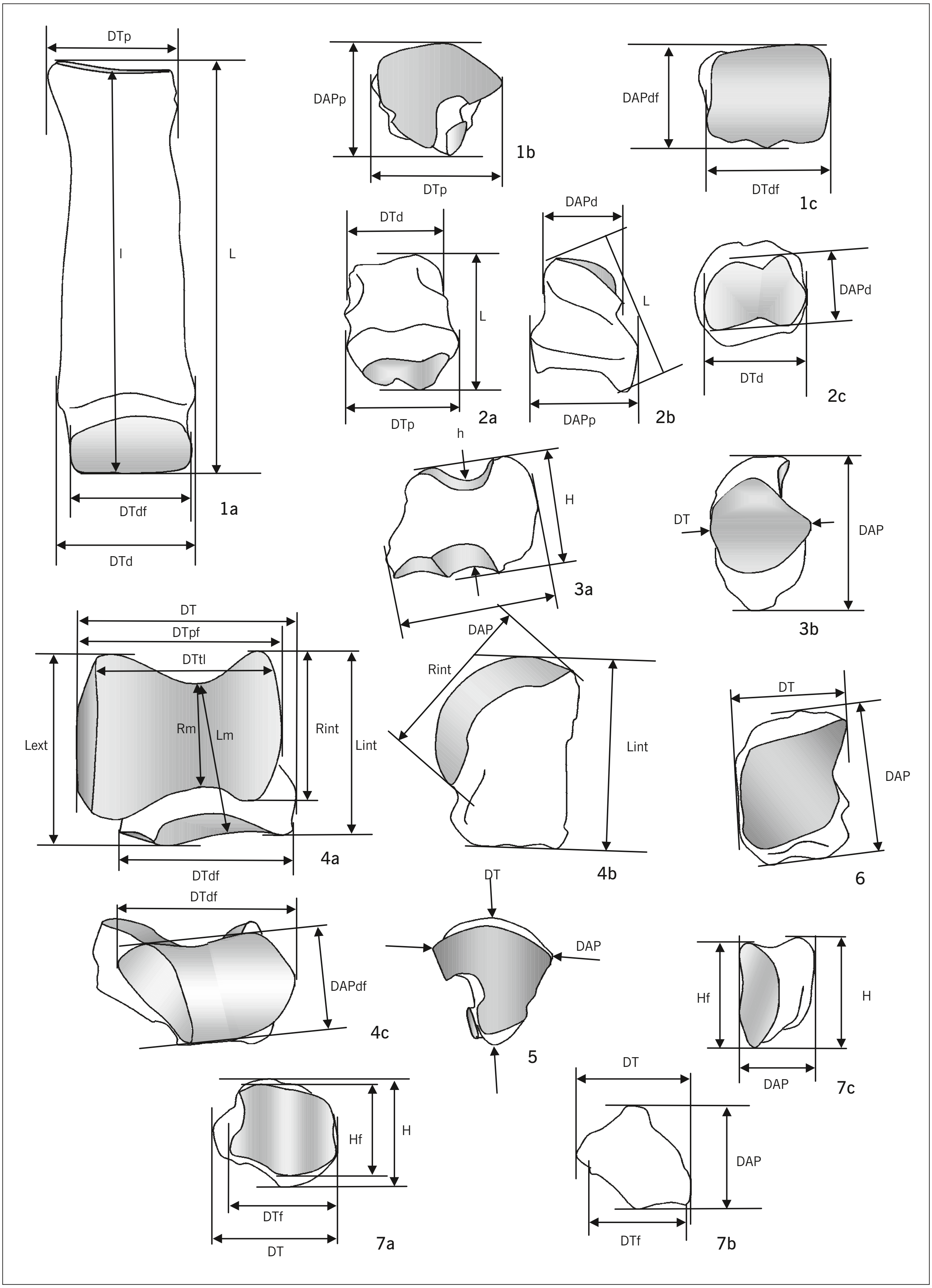


**Fig. 9** The way of measuring the carpals, tarsals, metapodials and phalanges. Given as examples: 1) Mt III, 2) lateral first phalanx, 3) scaphoid, 4) astragalus, 5) cuneiform III, 6) navicular, 7) patella.

L = length, measured parallel to the saggital plane of the bone, as the distance between the most proximal and most distal points.
DAPd = measured as the distance between the line that passes through the two plantar-most points of the articulation facet and the dorsal-most point of the bone at this place.
DTd = measured as the greatest DT in the distal part of the bone, as far as the distal facet reaches proximally.

Most of the material is figured in plates. The photographs were made using a 50 mm lens and conventional reflex camera. Processes may appear much larger in one view than in another. This is noted clearly in the dorsal spines of the thoracic vertebrae, which stick out distally; they appear larger in the posterior views and smaller in the anterior views. Occasionally, the effect is noted also in other bones. No measurements should be taken from the plates.

### *Collections and their abbreviations*

The material from Neumark-Nord was kept temporarily in Bilzingsleben when I studied it, but at present it is stored in the Landesmuseum für Vorgeschichte in Halle (LVH). Various numbers have been given to the material. Numbers 186–204b refer to a catalogue by Mania, which gives the position of the finds in plans and sections. Specimens received field numbers (e. g. NN 32), that refer to a find complex (E24, 234 = complex of elephant 24, specimen number 234), to a year or date (e. g. 95'3), or have just the date, and have the catalogue number of the LVH (e. g. HK 88:14). As much information as possible is given here. Some rhino specimens are mentioned in the catalogue but were not seen by me and therefore are omitted here. In others, there are minor discrepancies in identification or dates between the specimens seen by me, or the notes that accompanied them, and the information given by the catalogue.

Material studied for comparison is kept in the following institutions:

| | |
|---|---|
| FISF | Forschungsinstitut Senckenberg, Frankfurt |
| FBFSUJ | Forschungsstelle Bilzingsleben, Friedrich-Schiller-Universität, Jena |
| GIN | Geological Institute, Moscow |
| HGSB | Hungarian Geological Survey, Budapest |
| IGF | Istituto di Geologia, Firenze |
| IQW | Institut für Quartärpaläontologie, Weimar (Senckenberg Forschungsinstitut) |
| LAUT | Laboratori de Arqueologia, Universidad de Tarragona |
| LPTUP | Laboratoire de Prehistoire de Tautavel, Université de Perpignan |
| MB | Museo de Burgos, Burgos |
| MCP | Musee Crozatier, Le Puy-en-Velay |
| MNCN | Museo Nacional de Ciencias Naturales, Madrid |
| NHM | Natural History Museum, London |
| NMM | Naturhistorisches Museum, Mainz |
| NMMa | Natuurhistorisch Museum, Maastricht |
| NMP | National Museum, Prague |
| NNML | Nationaal Natuurhistorisch Museum, Leiden |
| SMN | Forschungsbereich Altsteinzeit Schloss Monrepos, Neuwied (Römisches-Germanisches Zentralmuseum, Forschungsinstitut für Vor- und Frühgeschichte) |
| SMNK | Staatliches Museum für Naturkunde, Karlsruhe |
| SMNS | Staatliches Museum für Naturkunde, Stuttgart |

## 2.1. Taxonomy, description and comparison

All of the rhinos described here belong to the *Stephanorhinus - Coelodonta* group, a group of Rhinocerotinae that is probably monophyletic. In the most recent classifications all five species of living rhinos are placed in the Rhinocerotinae. Genetic data suggest that the living African rhinos (*Diceros bicornis* and *Ceratotherium simum*) and the living Asian species (*Rhinoceros unicornis*, *Rhinoceros sondaicus* and *Dicerorhinus sumatrensis*) form two monophyletic groups that diverged possibly as much as 26 Ma ago (Tougard et. al. 2001). Often, the fossil north Eurasian *Stephanorhinus* and *Coelodonta* are supposed to be more closely related to the living south Asian rhinos than to the living African ones (e. g. Guérin 1980; Heissig 1981; Prothero et. al. 1986). However, a recent cladistic analysis inserted *Coelodonta* between these two groups, but sharing more with the African rhinos (Antoine 2002). Nevertheless, the mainly north Eurasian *Stephanorhinus - Coelodonta* group has probably a very long history independent of the African rhinos, going back far into the Miocene.

*Stephanorhinus* Kretzoi, 1942
**Type species:** *Rhinoceros etruscus* Falconer
**Remarks:** Initially most fossil species of rhinos were described as *Rhinoceros*, but later, a group of mainly north Eurasian Plio-Pleistocene rhinos were placed in *Dicerorhinus*, a genus with type species of the living *D. sumatrensis*. There are numerous morphological differences between the Plio-Pleistocene north Eurasian rhinos and the living *Dicerorhinus* and *Rhinoceros*. M. Kretzoi (1942) introduced the name *Stephanorhinus* for all these rhinos, save *Coelodonta*. It took some time for this name to become widely used, but after W. D. Heissig (1973; 1981) and M. Fortelius et. al. (1993) most authors use the name, though some, including Guérin (1980; 1996), continue to use the name *Dicerorhinus*.

Guérin (1980), in his monumental monograph, indicated (Fig. 115) a Middle Miocene separation between the lineage towards the living *D. sumatrensis* and the group of Plio-Pleistocene north Eurasian species that many others place now in *Stephanorhinus*. Here the use of the name *Stephanorhinus* is believed to be fully justified for a group that has so many morphological differences and that separated since Miocene times from the lineage leading to the type species. Moreover, *Stephanorhinus* shares important characteristics with *Coelodonta* and if not recognised as an independent genus, one might argue to include it in that genus, rather than in *Dicerorhinus*.

Guérin (1980) defined the subgenus *Brandtorhinus* with type species *D. etruscus*, which, having the same type species as *Stephanorhinus*, is thus a junior synonym by definition. Guérin (1980; 1989) rejected Kretzoi's name on the ground that it was not based on a careful study. However, the ICZN does not include any criterion on the scientific quality of a study for a taxonomic name to be available.

*Stephanorhinus kirchbergensis* (Jäger,1839)

**Lectotype:** three specimens which have been figured by. Jäger (1839), Pl. 16,31–33) are kept in the SMNS: number 34000.3, a left upper $M^{1/2}$, probably an $M^2$, number 34000.2, a right $M^3$, and number 34000.1, a right $P_{3/4}$, probably a $P_3$. These specimens are cotypes and from these three specimens K. Staesche (1941, 9) indicated the $M^2$ as a lectotype. This specimen was figured by H. Schroeder (1903, Pl. 9,2).

**Type locality:** Kirchberg an der Jagst, Germany.

**Age of type locality:** late Middle Pleistocene.

**Material:**

193. NN 32 Skull with right and left $P^2$–$M^3$ from the »Untere Uferzone«.
198. Skull, lacking only a fragment of a zygomatic arch, with right and left $P^2$–$M^3$.
200. Found near elephant skeleton no. E 24, remains of probably one individual:
   E 24, 234 = right mandible fragment with posterior half of $P_4$.
   E 24, 248 = right $M_1$ fitting behind E 24, 234.
   E 24, 241 to 243 = skull fragments including maxilla with right $M^{1–3}$.
   E 24, 249 = left mandible fragment with roots of $P_2$ and alveoles for the $P_3$.
200. Found near elephant skeleton no. E 24 (but probably not belonging to the individual listed above):
   - left $P^3$ and left $M^{1/2}$ (probably $M^1$).
   - a fragmentary right $M^3$.

204b. Found together with elephant E I:
   ?E I, 36 = right scapula.
   E I, 39 = left humerus of a juvenile, proximal epiphysis not fused to the diaphysis (and thus not preserved).
   E I, 41 = right humerus, distal part. Little wear on the articular surface shows spongious bone, suggesting that the specimen belonged to a juvenile. The specimen is smaller than E I, 39, and possibly belonged to a different individual.

204b. Excavated 2/9/1996 near elephant skeleton E I four black and one white vertebra:
   - axis ($C_2$).
   - $C_5$.
   - anterior thoracic vertebra, possibly $T_3$.
   - anterior thoracic vertebra, possibly $T_5$.
   - $T_1$ (the white specimen).

   ?NN 50 = distal part of right central metapodial (probably Mc III), found along with other bones (which are also kept under NN 50) in the Körbisdorfer gravels. These beds are believed to be of Holsteinian age and thus from an older interglacial than the previously mentioned remains.

### *Description and comparison*

A first **skull** (Pl. 1) is well preserved and lacks only part of the right zygomatic arch. There is possibly a slight deformation causing the anterior part of the skull to be curved a little to the left. Measurements are given in Tab. 1. The nomenclature of the basicranium is indicated in Fig. 10.

**Tab. 1** Measurements of the skulls of the rhinos from Neumark-Nord.

| | *S. hemitoechus* | | | | *S. kirchbergensis* | | | | | | *Coelodonta* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | HK88:14'3 | | E 21 | E II, 27+29 | 198 | | NN 32 | | E 24 | | 1996, 47 | | HK87:300'610 | |
| | sin | dext | | | sin | dext | sin | dext | sin | dext | sin | dext | sin | dext |
| 1 | 760 | 760 | | | 720 | 720 | -- | | | | 730 | 730 | | |
| 2 | 760 | 760 | | | 721 | 721 | -- | | | | 730 | 730 | | |
| 3 | 840 | | >670 | | 700 | (680) | 780 | 790 | | | 770 | | | |
| 4 | 290.3 | 292.5 | | | 213.1 | 216.3 | -- | -- | | | 248.5 | 247.5 | | |
| 5 | 173.0 | | | | 113.8 | | 60.0 | | ~150 | | 132.8 | -- | | |
| 6 | 384.3 | 375.8 | | | 291.1 | 290.0 | -- | 336.7 | | | 337.1 | 335.9 | | |
| 7 | 414.7 | 416.8 | | | 360.7 | 367.5 | -- | 392.2 | | | 344.3 | -- | | |
| 8 | 450.7 | 452.8 | | | 366.3 | 373.8 | -- | 411.0 | | | 407.9 | 415.6 | | |
| 9 | 129.4 | 131.0 | | | 119.0 | 126.6 | -- | 149.5 | | 139.3 | 140.8 | 141.0 | | |
| 13 | 380.1 | 374.0 | | | 316.4 | 314.6 | -- | -- | | | 373.2 | 375.2 | | |
| 14 | 412.9 | 415.6 | | | 336.6 | 336.7 | -- | -- | | | 401.2 | 389.9 | | |
| 15 | 160.0 | | 189.1 | 148.9 | 156.7 | | 156.5 | | ~161.9 | | 215.5 | | 224.6 | |
| 16 | 281.9 | | | | ~292.8 | | -- | | | | 283.7 | | | |

**Tab. 1** (Continuation).

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 17 | 147.3 | | 55.8 | 72.9 | 65.5 | | ~ 118.5 | | ~55.8 | 102.9 | | 73.4 | |
| 18 | 254.8 | | | | 186.8 | | -- | | | 227.5 | | | |
| 19 | 294.2 | | | | 269.6 | | -- | | | -- | | | |
| 20 | 335.8 | | | | 252.9 | | -- | | | 287.3 | | | |
| 21 | 365.2 | | | | ~381.8 | | -- | | | 344.1 | | 348.9 | |
| 22 | 190.7 | | | | 95.0 | | >155.9 | | | 176.0 | | | |
| 23 | 171.5 | | ~156.7 | | 143.1 | | -- | | | 163.2 | | 175.2 | |
| 25 | 223.1 | 232.9 | | | 192.2 | | -- | 213.7 | | 194.2 | 206.2 | | |
| 26 | 246 | 246 | | | 216.8 | 202.6 | -- | ~230 | | 184 | -- | | |
| 27 | 255 | 249 | | | 204 | 215 | -- | ~ 237.0 | | 187 | 216.4 | | |
| 28 | -- | | | | | | -- | | | 64.3 | | | |
| 29 | 79.7 | | | | 80.2 | | -- | | | 84.6 | | | |
| 30 | 105.9 | | | | 97.6 | | -- | | | ~ 106.3 | | | |
| 31 | 50.5 | | | | 50.7 | | -- | | | 55.4 | | 59.5 | |
| 32 | 147.9 | | | | 140.5 | | -- | | | 154.3 | | ~91.1 | |
| 33 | 187.5 | | ~185.6 | | 166 | | 169.3 | | | 187.7 | | | |
| 34 | 113.4 | 112.4 | | | | | | 100.1 | | 95.1 | 94.3 | | |
| 35 | 62.2 | | | | >32.9 | | | | | 46.2 | | | |
| 36 | 67.4 | | | | 63.7 | | | | | 79.9 | | 83.4 | |
| 37 | 51.4 | | | | 40.1 | | | | | 56.3 | | 51.2 | |
| 38 | 31.6 | | | | 30.9 | | | | | 36.2 | | 43.6 | |
| 39 | 70.2 | | | | 62.8 | | | | | 75.8 | | 90.5 | |
| 40 | 356.5 | | | | 320 | | | | | 374,3 | | | |
| 41 | 72.7 | 80.8 | | <59.0 | | | | 66.1 | 65.2 | 73.7 | | 73.2 | 74.2 |
| 42 | 56.0 | 56.2 | | | 34.5 | | | | ~55.5 | ~59 | | | |
| 43 | 31.7 | 32.5 | <47.2 | | 28.1 | | | | 37.6 | 40.6 | | | |
| 44 | 20.7 | 23.6 | <28.0 | | 21.7 | | | | 36.5 | 23.4 | | 24.4 | 23.1 |
| 45 | 132.9 | 135.5 | | 151.5 | 145.5 | | | | | 133.7 | 134.3 | 19.0 | 15.3 |
| 46 | 101.3 | 103.4 | | | 102.3 | | | | | 65.3 | 69.8 | 93.8 | |
| 47 | 113.7 | 112.4 | | 127.1 | | | | | 132.4 | 102.9 | 96.5 | 94.2 | 99.9 |
| 48 | 171.7 | | | | | | | | | | | | |
| 49 | 305 | | | | 322 | | | | | | | | |
| 50 | | | | | | | | | | | | | |
| 51 | | | | | | | | | | | | | |
| 52 | | | | | | | | | | | | | |
| 53 | | | | | | | | | | | | | |
| 53 | | | | | | | | | | | | | |
| 55 | | | | | | | | | | | | | |

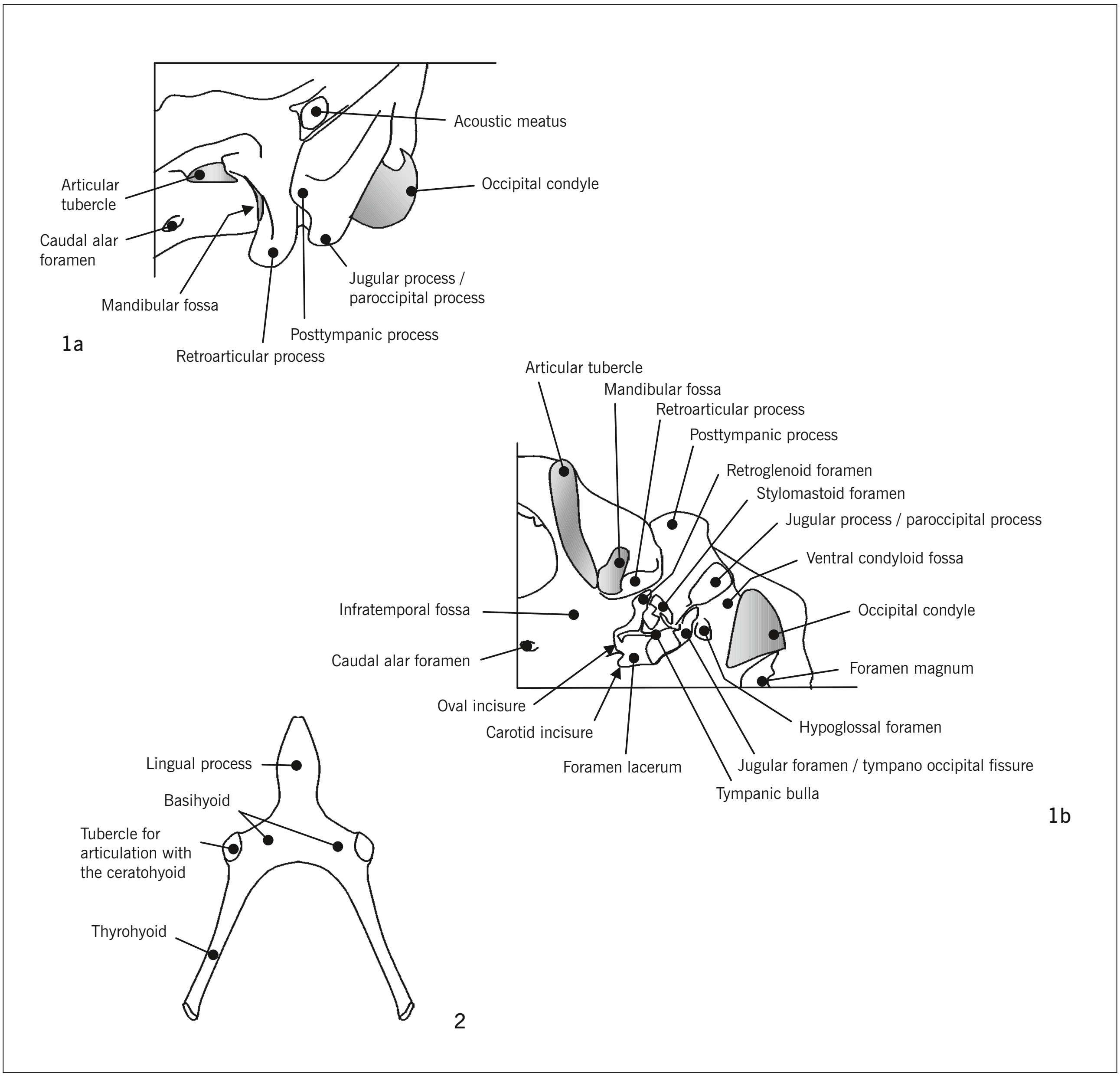


**Fig. 10** The nomenclature of the basicranium and hyoid largely after Koch (1960), Getty (1975) and Evans/deLahunta (1980).

The nasals are slightly widened in the middle and curve down in the anterior part. The dorsal surface is covered with rugose bone with a cauliflower texture from the anterior part to slightly posterior of the widest part. This is where the anterior horn originated. Most of the bone with cauliflower texture faces upward, suggesting that the horn was directed mostly upward and only slightly forward. At the sides the nasals overhang the nasal apertures. There is a relatively extensive bony nasal septum of at least 9 cm length and a maximum thickness of about 27 mm.

The frontals have, like the nasals, an area with a surface with cauliflower texture, which is much more moderately developed than on the nasals. This is where the posterior horn originated. The lesser degree of rugosity suggests that it was considerably shorter than the anterior horn. It has been suggested that the degree of rugosity is not so much an indicator for the length, but more of the use of the horns (Loose 1975). This may be partly true, but it should be remembered, that a force acting on a long horn has a much greater momentum than the same force acting on a short horn.

The parietal crests are not widely separated. In the parietal area, the dorsal surface of the skull is inclined upwards towards the occipitals, which are only moderately elevated above the rest of the dorsal surface of the skull. The occiput is narrow and its posterior edge forms an open V-shape. If seen from caudal, the occiput is slightly lowered in the middle. It overhangs the posterior surface of the skull a little, but does not extend more caudally than the posterior surface of the occipital condyles. Compared to the skull from Mosbach (Loose 1975, Pl. 5–8; 10), which is the oldest skull of this species in western Europe, the occiput is a little wider and the V-shape is more marked. In fact, there is only a very slight indication of this V-shape in the Mosbach skull. The skull from Daxlanden, which by many is considered to be an atypical *S. kirchbergensis*, has an occiput that resembles the Mosbach skull more than the skulls from Neumark-Nord (Loose 1975, Pl. 5–8; 10). Skulls from the Eemian of Gimbs-

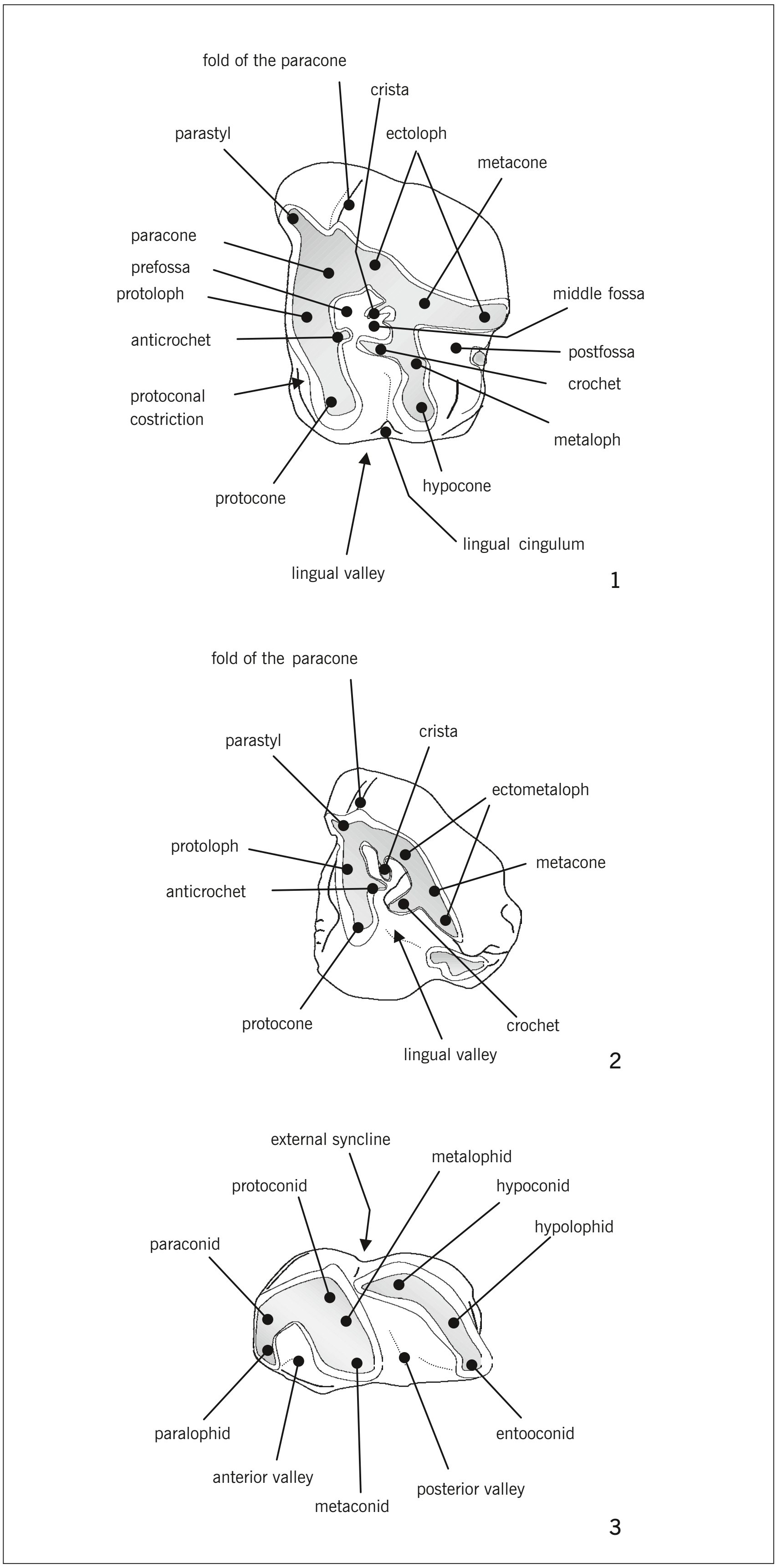


**Fig. 11** The nomenclature of the teeth after Guérin (1980), as examples: 1) P$^3$, 2) M$^3$, 3) M$_1$.

heim and from Krapina have a morphology that is very similar to that in Neumark-Nord (von Koenigswald 1988, Fig. K12–K13; Gorjanovic-Kramberger 1913, Pl. 1; 2,2). While the earlier occiputs are more similar to other species of *Stephanorhinus,* like *S. etruscus* and *S. hundsheimensis,* the younger samples, like Neumark-Nord, seem to have an occiput with a more pronounced V-shape.

The zygomatic archs project slightly laterally and the skull appears narrow if seen from above. The anterior edge of the orbits is situated more or less in the middle of the skull and above the posterior half of the $M^2$. There are two lacrymal foramina within the orbit.

The anterior part of the palate formed by the maxillary and the premaxillary is narrow and pointed and protrudes moderately anterior of the dentition. The posterior edge of the palate is U-shaped and extends forward till between the anterior lobes of the $M^3$. The dentition is large compared to the skull.

Loose (1975) gave great importance to the morphology of the postglenoid, posttympanic and paroccipital (=jugular) processes. As he indicated, the post tympanic process is well developed in *Diceros bicornis* and in lateral view can be seen as a third downward pointing process between the divergent postglendoid and paroccipital processes, whereas in other species it tends to be more reduced (in lateral view) and the other two processes are less divergent and placed more together. In the skull of *S. kirchbergensis* the posttympanic process is not really seen as a separate process from the paroccipital process and the paroccipital and postglenoid processes are placed very close together and even converge (Pl. 1; 2). The postglenoid process is particularly massive. The paroccipital process is laterally expanded near its tip, which is situated more laterally relative to the postglenoid process than in *S. hemitoechus* (Pl. 5). The morphology of this area and in particular the small space between the postglenoid and paroccipital process is very similar to the skull of *S. kirchbergensis* from Mosbach (Loose 1975, Pl. 13,2). In *S. hundsheimensis* and *S. etruscus* the space between these processes is much wider (Loose 1975, Pl. 13,4; Mazza 1988, Pl. 2–4). The skull from Steinheim assigned to »*D. merckii*« by Staesche (1941, Pl. 11) has a wide space between the postglenoid and paroccipital processes and in this it resembles *S. hemitoechus* rather than *S. kirchbergensis*. Its V-shaped occiput seems to consist entirely of gypsum, and there are no teeth left to confirm that the skull belonged really to *S. kirchbergensis*. The skull from Daxlanden (Loose 1975, Pl. 13,1), which is also believed to be *S. kirchbergensis*, has the paroccipital well separated from the postglenoid process. The feature of a short distance between these two processes seems to be constant in Neumark-Nord (see below), but if the skulls from Daxlanden and Steinheim really belong to *S. kirchbergensis*, the feature seems to be more variable in the older samples, where a morphology may occur, that seems to be primitive for the genus. The glenoids are wide. The hypoglossal foramen is placed relatively close to the median plane.

A second **skull** (Pl. 2,1) preserves most of the dorsal and right sides, while the left and lower sides are more damaged. Little is left of the basicranium.

The dorsal surface of the nasals largely faces upwards, but the anterior part slopes slightly. A very extensive area is covered with bone with a cauliflower texture that marks the origin of the anterior horn. Behind this cauliflower bone, the nasals are waisted. The nasals overhang the nasal aperture a little. The remains of a bony nasal septum suggest a modest development. There is an area with a modestly developed cauliflower texture on the frontals that marks the origin of the second horn. The dorsal profile of the skull is largely horizontal, but slopes upward in the parietal and occipital areas. Like in the skull described before, the occiput is narrow and has an open V-shape if seen from above and a depression in the middle if seen from behind. It overhangs the posterior side of the skull only a little and would not have reached more caudally than the occipital condyles, when they were still present.

The zygomatic arch is thin and its section just behind the orbit is 62.7 x 25.0 (mm). The anterior rim of the orbit is situated above the middle of the $M^2$ and more or less in the middle of the skull.

There is very little space between the retroarticular and jugular process. The post tympanic process is not recognised as a separate process in lateral view.

A **third** skull (Pl. 2,2) is represented by a number of fragments that fit together, constituting a large part of the skull, but also with many intermediate fragments missing. Whatever can be observed on the morphology is similar to what has been described above. The zygomatic arch is thin and its section just behind the orbit measures 63.5 x 14.9 (mm). The mandibular fossa has a cylindrical shape with transverse axis to slight saddle shape. As in the other two skulls, the retroarticular and jugular process are placed very close together and in lateral view the post-tympanic process is not recognised as a separate process.

The **mandible** is represented by two small fragments (E 24, 243 and E 24, 249). One having the roots of the left $P_2$ in the alveoles and the empty alveoles for the $P_3$. The length of the $P_2$ at the roots is 28.9; the crown must have been longer. This is a size that fits *S. kirchbergensis*, rather than *S. hemitoechus* or *C. antiquitatis*. A tiny fragment bearing half a $P_4$ derives probably from the same specimen.

The nomenclature of the **dentition** is indicated in Fig. 11 and the measurements in Tab. 2 and 3. There are various upper tooth rows and some isolated specimens as well as a complete and a fragmentary lower tooth.

The $\mathbf{P^2}$ is variable in its morphology. The antero-lingual cusp may be large and connected with a well developed crest to the ectoloph (Pl. 3,1), or it may be much smaller and connected to the postero-lingual cusp, while it is not connected to the ectoloph (Pl. 4,1). In all cases, the first lobe is relatively narrow, unlike in the $P^{3-4}$. The same tooth is not represented in the samples of the other species from Neumark-Nord. It is larger than its homologue in *S. hemitoechus* (Fig. 12).

The $\mathbf{P^3}$ and $\mathbf{P^4}$ (Pl. 3,1; 4,1) are similar in overall morphology. However, they differ in average size, though there is some overlap (Fig. 13). A specimen that was found together with a molar (Pl. 4,2), is believed to be a third premolar on the basis of its relatively small size.

The $P^{3-4}$ of *S. kirchbergensis* differ from those of *Coelodonta antiquitatis* (Pl. 26,1) in having: thinner and more smooth enamel, less cementum, a lower crown, a less buccally projecting parastyle, a more lingually placed metacone, a less angular ectoloph, a less distally extending protocone, a larger hypocone and a smaller prefossa that is less separated from the middle fossa. They are also clearly larger (Fig. 12; 13).

The $P^{3-4}$ of *S. kirchbergensis* differ from those of *Stephanorhinus hemitoechus* (Pl. 3,2) in having: thinner and more smooth enamel, slightly less developed metacones, slightly more anglular ectolophs, less developed anterior cingula, proto and hypocones placed further from the lingual sides

**Tab. 2** Measurements of the teeth of the rhinos from Neumark-Nord.

| | | *Stephanorhinus kirchbergensis* | | | | | | | *S. hemitoechus* | | | | *C. antiquitatis* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | NN 32 | | E 24 | near E24 | | 198 | | E24, 246 + 247? | | HK88: 14 | | 1996, 47 | | HK:300/17 |
| | | S | d | d | s | d | s | d | s | d | s | d | s | d | d |
| $M^3$ | DAP | 61.2 | 62.4 | 65.9 | | | 53.8 | 54.6 | 56.3 | | 64.5 | 60.4 | 44.9 | 46.1 | |
| $M^3$ | DAPb | 70.0 | 72.5 | 77.6 | | | 63.2 | 64.0 | 69.8 | | 69.5 | 68.1 | 48.2 | 51.0 | |
| $M^3$ | DTa | 70.2 | 70.0 | 75.2 | | 72.6 | 64.1 | 65.7 | 63.1 | | 61.4 | 62.1 | 57.3 | 56.8 | |
| $M^2$ | DAP | | 69.9 | 74.1 | | | 63.9 | 65.6 | 55.1 | 55.3 | 59.9 | 59.0 | 56.4 | | 51.2 |
| $M^2$ | DAPb | >59.7 | 64.9 | 68.9 | | | 60.4 | 58.0 | 53.8 | 54.0 | 52.1 | 52.1 | 53.1 | | >51.2 |
| $M^2$ | DTa | | 76.7 | 79.5 | | | 70.0 | 70.7 | 66.0 | >63.8 | 63.8 | 63.1 | 60.3 | | 58.5 |
| $M^2$ | DTp | 67.2 | 67.3 | 73.3 | | | 59.6 | ~ 58.6 | 58.9 | 60.6 | 53.0 | 54.9 | 55.1 | | 52.6 |
| $M^1$ | DAP | 65.3 | 66.7 | 64.8 | 61.1 | | 59.0 | | | | 43.6 | >49.2 | 43.8 | | |
| $M^1$ | DAPb | 61.4 | 54.5 | 62.9 | 61.4 | | 52.5 | 52.7 | | | >36.9 | 42.2 | >43.8 | | |
| $M^1$ | DTa | 70.9 | 73.7 | 76.4 | 69.1 | | >67.4 | 68.0 | | | 59.1 | 59.1 | 59.2 | | |
| $M^1$ | DTp | 64.3 | >68.4 | 69.3 | 59.1 | | >61.3 | 62.1 | | | 54.9 | 54.0 | 56.7 | | |
| $P^4$ | DAP | | 54.8 | | | | 48.9 | 49.5 | | | 43.8 | >41.6 | 38.1 | | |
| $P^4$ | DAPb | | 50.5 | | | | 46.1 | 47.3 | | | 40.8 | 42.6 | >38.1 | | |
| $P^4$ | DTa | | 77.4 | | | | 66.3 | 68.7 | | | 56.4 | 57.2 | 52.7 | | |
| $P^4$ | DTp | | 68.2 | | | | >59.3 | 59.9 | | | 52.6 | 50.5 | 47.8 | | |
| $P^4$ | Hli | | | | | | | | | | 25.2 | 21.2 | | | |
| $P^3$ | DAP | 48.3 | 50.9 | | 42.1 | | | | | | 37.2 | >37.2 | 29.0 | | |
| $P^3$ | DAPb | 42.3 | 43.3 | | 45.7 | | 40.3 | 39.4 | | | 36.2 | 36.7 | >29 | | |
| $P^3$ | DTa | 63.7 | 66.2 | | 60.7 | | 60.7 | 61.2 | | | 50.2 | 48.6 | >43.9 | | |
| $P^3$ | DTp | 56.6 | 61.4 | | 53.8 | | 54.8 | 56.9 | | | 48.5 | 45.6 | 41.0 | | |
| $P^3$ | Hli | | | | ~25.9 | | | | | | 18.2 | 17.0 | | | |
| $P^3$ | Hci | | | | ~15.9 | | | | | | | | | | |
| $P^2$ | DAP | 41.2 | 40.0 | | | | | | | | | | | | |
| $P^2$ | DAPb | 36.8 | 36.6 | | | | 31.9 | ~32.2 | | | | | | | |
| $P^2$ | DTa | 43.2 | 37.8 | | | | 43.5 | | | | | | | | |
| $P^2$ | DTp | 46.6 | 46.8 | | | | >42.8 | 42.4 | | | | | | | |

of the crowns, wider valleys between the proto and hypocones. The $P^3$ of *S. kirchbergensis* may overlap with the $P^4$ of *S. hemitoechus* (Fig. 12), but both $P^{3-4}$ of the former species tend to be relatively wider than the same teeth in the latter species.

The $P^{3-4}$ of *S. kirchbergensis* differ from those of the same species from Bilzingsleben in having the lingual cingula less pronounced. As in other teeth, the $P^{3-4}$ from Neumark-Nord tend to be very large compared to those from Bilzingsleben.

The **$M^1$** and **$M^2$** (Pl. 3,1; 4,1) have similar overall shapes and sizes, but differ in some minor morphological details. The lingual valley is narrower and has steeper walls in the $M^1$, and the base of the hypocone is more inflated in the $M^2$. Although there is much overlap, the $M^2$ tend to have greater lengths for a given width and occasionally may have relatively wide first lobes, compared to the second lobe (Fig. 13). A specimen that was found together with a premolar (Pl. 4,5), is believed to be a first molar on the basis of the narrow valley with steep walls, even though it is relatively long and with a relatively large DTa.

The $M^{1-2}$ of *S. kirchbergensis* differ from those of *Coelodonta antiquitatis* (Pl. 26,1) in having: thinner and more smooth enamel, less cementum, lower crowns, less pronounced metacone styles, parastyles that stick out more

**Tab. 3** Measurements of the lower teeth of the rhinos from Neumark-Nord.

| | | *Stephanorhinus hemitoechus* | | | | *Stephanorhinus kirchbergensis* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | HK88:14 | | | | E 24 | | | | |
| | | DAP | DAPb | DTa | DTp | DAP | DAPb | DTa | DTp | H |
| $P_2$ | d | 28.1 | 25.5 | 15.3 | 17.0 | | | | | |
| $P_3$ | s | 30.2 | 30.2 | 21.5 | 23.6 | | | | | |
| | d | 30.9 | 31.2 | 21.3 | 23.5 | | | | | |
| $P_4$ | s | 38.4 | 35.9 | 25.6 | 28.1 | | | | | |
| | d | 37.6 | 35.7 | 25.8 | 27.5 | -- | -- | -- | 31.9 | -- |
| $M_1$ | s | 37.1 | >37.1 | 28.2 | 29.7 | | | | | |
| | d | 39.6 | >39.6 | 28.7 | 29.6 | 56.7 | 55.1 | 37.3 | 35.7 | 32.9 |
| $M_2$ | s | 47.9 | >47.9 | 31.2 | 30.6 | | | | | |
| | d | 48.7 | 48.7 | 30.2 | 30.0 | | | | | |
| $M_3$ | s | 53.6 | 56.8 | 32.8 | 29.9 | | | | | |
| | d | 52.0 | 56.7 | 32.9 | 29.9 | | | | | |

anteriorly and less buccally, ectolophs that are oriented more obliquely to the length of the tooth row, more anteriorly placed protocones, less pronounced protoconal constrictions, lower anterior cingula, wider lingual valleys, lingual valleys with the bottom closer to the base of the crown, smaller postfossas, prefossas that reach less forward, lesser cristas and crochets which remain far from fusing and isolating a middle fossa or medifossette. Metrically they differ from the *Coelodonta* molars, in being much larger (Fig. 12).

The molars of *Stephanorhinus kirchbergensis* are more similar to those of *S. hemitoechus* (Pl. 3,2) than to those of *Coelodonta*. They differ, however, from the molars of *S. hemitoechus* in: slightly thinner and smoother enamel, slightly less pronounced protoconal constrictions, lower anterior cingula, and clearly wider lingual valleys. Metrically they differ in being larger (Fig. 12), but they group very well with an upper molar, probably a $M^2$, from Kirchberg, which is the lectotype of *S. kirchbergensis*.

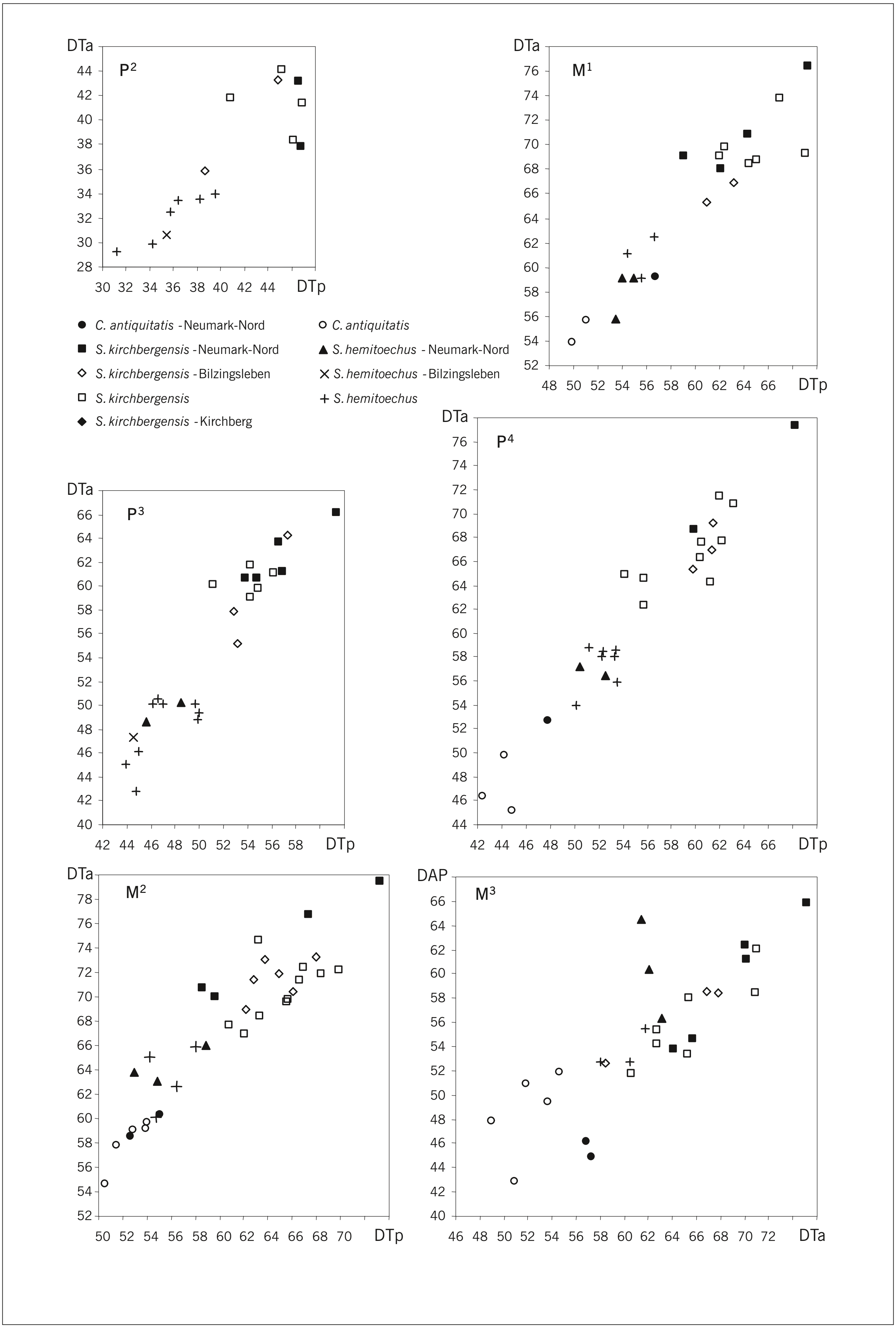
The **$M^3$** (Pl. 3,1; 4,1) differs from the $M^{1-2}$ in having a curved ecto-metaloph instead of an ectoloph and a metaloph. The differences with the $M^3$ of *Coelodonta antiquitatis* and *Stephanorhinus hemitoechus* are similar to those described above for the $M^{1-2}$. In addition, the $M^3$ of these species tend to be more elongate (with larger DAP, Fig. 12). This greater elongation is noted in *S. hemitoechus* in a more posteriorly placed metacone, leading to a curved ectometaloph, and in *Coelodonta* in a more posteriorly placed metacone and the presence of a both an ecto and a metaloph.

The **$P_4$** (Pl. 4,3) is represented by a posterior fragment in a mandible fragment. Its posterior interstitial wear facet seems to fit a corresponding facet on a molar which, for this reason, is probably a $M_1$. The enamel is relatively thin and smooth. When seen from lingual view, the posterior valley is V-shaped. With a DTp of 31.9, the specimen is metrically in the overlap of *S. hemitoechus* and *S. kirchbergensis*.

The anterior wear facet on the **$M_1$** (Pl. 4,2) appears to fit the corresponding facet on the $P_4$ described above. The hypolophid is oriented obliquely to the long axis of the tooth. The enamel is relatively thin and smooth. The anterior valley is U-shaped and the posterior valley is wide and U-shaped. This morphology fits *S. kirchbergensis* better than *S. hemitoechus*. Metrically the tooth is beyond the ranges of *S. hemitoechus* and is as large as in *S. kirchbergensis* (Fig. 14). Even if the tooth were a second molar, it would be too large for *S. hemitoechus*. The anterior lobe is peculiarly wide, as is also the case in *Coelodonta*, however, the specimen is much too large for that species and differs in its thinner and smoother enamel and in its morphology. The crown height can still be measured and is low. The hypsodonty index has one of the lowest values for any $M_1$ in Fig. 15, but is still in the lower end of the range of *S. kirchbergensis*. In general the $M_2$ tend to have lower crowns, and, if an $M_2$, the specimen would be well within the ranges of *S. kirchbergensis*.

The **vertebral column** is represented by four black specimens from one individual (E I) and a fifth white specimen from the same place (E I). One is an axis and another is also a cervical vertebra, while the others are thoracic vertebrae. The tentative positions of the thoracic and second cervical vertebrae are suggested by a comparison with the vertebrae of individual HK88:14 of *S. hemitoechus*, which are more fully described under that species, and specimens described and figured by K. D. Gorjanovic-Kramberger (1913) and J. J. A. Bernsen (1927). Though Bernsen assigned the specimens to »*Rhinoceros mercki*«, they probably do not represent that species, but another species of the genus *Stephanorhinus*. The nomenclature of the vertebrae is indicated in Fig. 16 and the measurements in Tab. 4,17 indicates the vertebrae present in Neumark-Nord and a selection of the morphological features observed in them and Fig. 18 gives a comparison of the metrical values of the different vertebrae.

The **axis or $C_2$** (Pl. 8,2) has a morphology that cannot be confused with any other vertebra. In comparison with the axis of *Stephanorhinus hemitoechus* (Pl. 8,1), the following differences are noted. It is higher and much less massive.


P²
DTa
44
42
40
38
36
34
32
30
28
30 32 34 36 38 40 42 44
DTp
M¹
DTa
76
74
72
70
68
66
64
62
60
58
56
54
52
48 50 52 54 56 58 60 62 64 66
DTp
● C. antiquitatis - Neumark-Nord
■ S. kirchbergensis - Neumark-Nord
◇ S. kirchbergensis - Bilzingsleben
□ S. kirchbergensis
◆ S. kirchbergensis - Kirchberg
○ C. antiquitatis
▲ S. hemitoechus - Neumark-Nord
✕ S. hemitoechus - Bilzingsleben
+ S. hemitoechus
P³
DTa
66
64
62
60
58
56
54
52
50
48
46
44
42
40
42 44 46 48 50 52 54 56 58
DTp
P⁴
DTa
76
74
72
70
68
66
64
62
60
58
56
54
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50
48
46
44
42 44 46 48 50 52 54 56 58 60 62 64 66
DTp
M²
DTa
78
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50 52 54 56 58 60 62 64 66 68 70
DTp
M³
DAP
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42
40
46 48 50 52 54 56 58 60 62 64 66 68 70 72
DTa

**Fig. 12 (opposite)** Bivariate diagrams of the upper cheek teeth. DTa (= width of the anterior lobe) versus DTp (= width of the posterior lobe). *Stephanorhinus kirchbergensis* from Bilzingsleben (FBFSUJB), Neumark-Nord (LVH) and other localities, including: Mosbach (NMM, SMNS), Steinheim (SMNS), Ehringsdorf (IQW), Taubach (IQW), Gimbsheim (NMM), Eich (NMM) and other »Rheinebene localities« (NMM). *Stephanorhinus hemitoechus* from Bilzingsleben (FBFSUJB), Neumark-Nord (LVH), and other localities, including: Las Majolicas (MNCN), Murr (SMNS), Ehringsdorf (IQW), Gimbsheim (NMM), Eich (NMM) and other »Rheinebene localities« (NMM). *Coelodonta antiquitatis* from Bad Frankenhausen (IQW), Ehringsdorf (IQW), Ariendorf (SMN), Gimbsheim (NMM) and Eich (NMM). No isolated specimens, but only teeth in mandibles or tooth rows have been used (save for Kirchberg), in order to minimise errors in assignation to position or to species.

The dorsal spine is narrow cranially, but increases gradually in width in caudal direction, though always narrower than in *S. hemitoechus* from Neumark-Nord. In lateral view, the dorsal spine is more extensive especially cranially. The anterior articulation facet is narrower. The width at the caudal articulation facets is less and the facets are more vertically inclined. The vertebral foramen is larger and the arch is less massive. The transverse process sticks out less laterally. The ventral crest is less marked.

Specimens from Taubach and Krapina that were assigned to *S. kirchbergensis* (Kahlke 1977, Fig. 41; Gorjanovic-Kramberger 1913, Pl. 7,3) have wide dorsal spines unlike the axis assigned here to *S. kirchbergensis*, but similar to that assigned here to *S. hemitoechus*. This is peculiar, but the specimen assigned here to *S. hemitoechus* belongs to a skeleton and there seems thus little doubt on its belonging to that species.

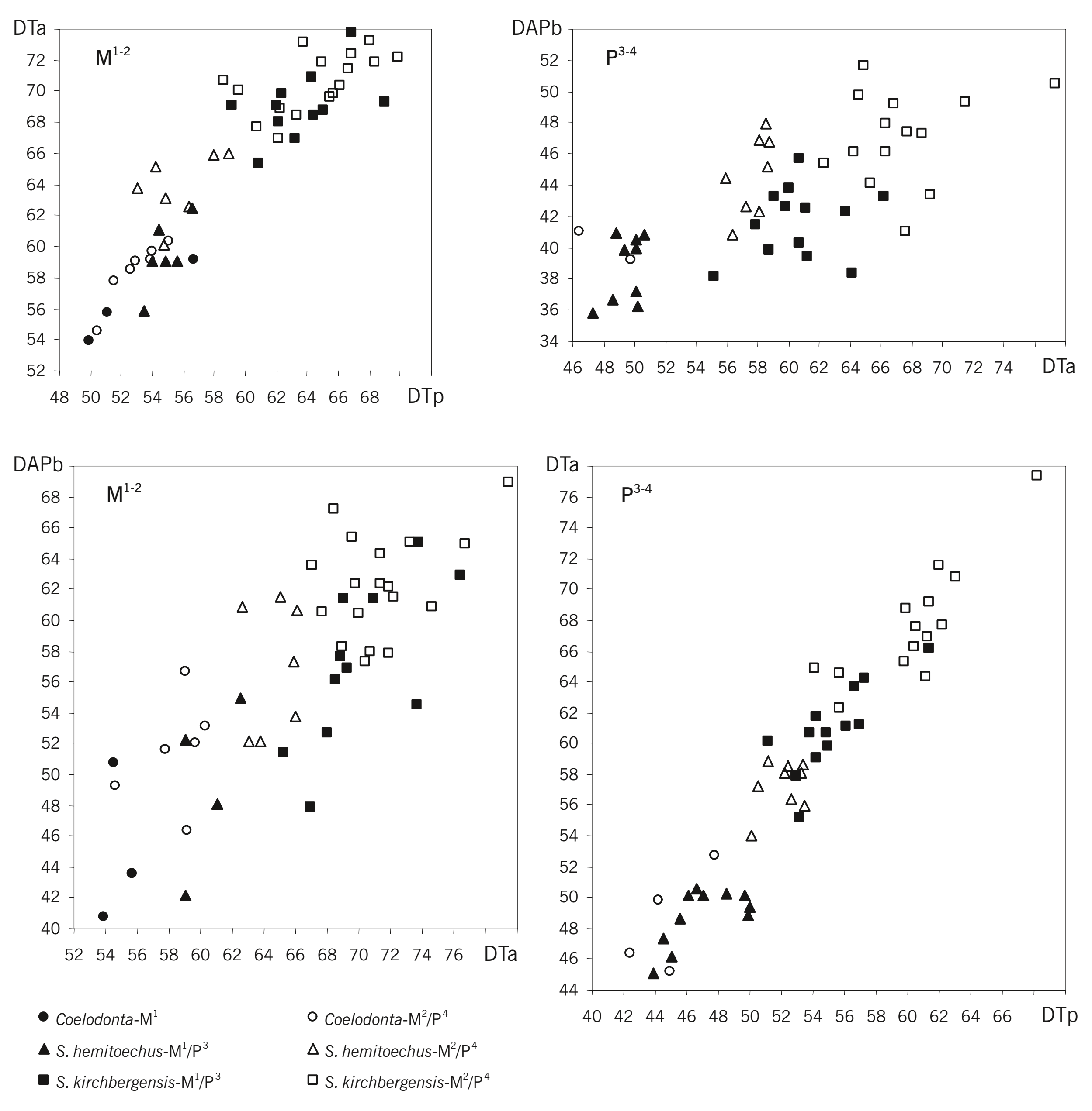

**Fig. 13** Bivariate diagrams of the P3/4 and M1/2. DTa (= width of the anterior lobe), DTp (= width of the posterior lobe) and DAPb (= basal length). Provenance of data as in Fig. 13. No isolated specimens, but only teeth in mandibles or tooth rows have been used (save for Kirchberg).

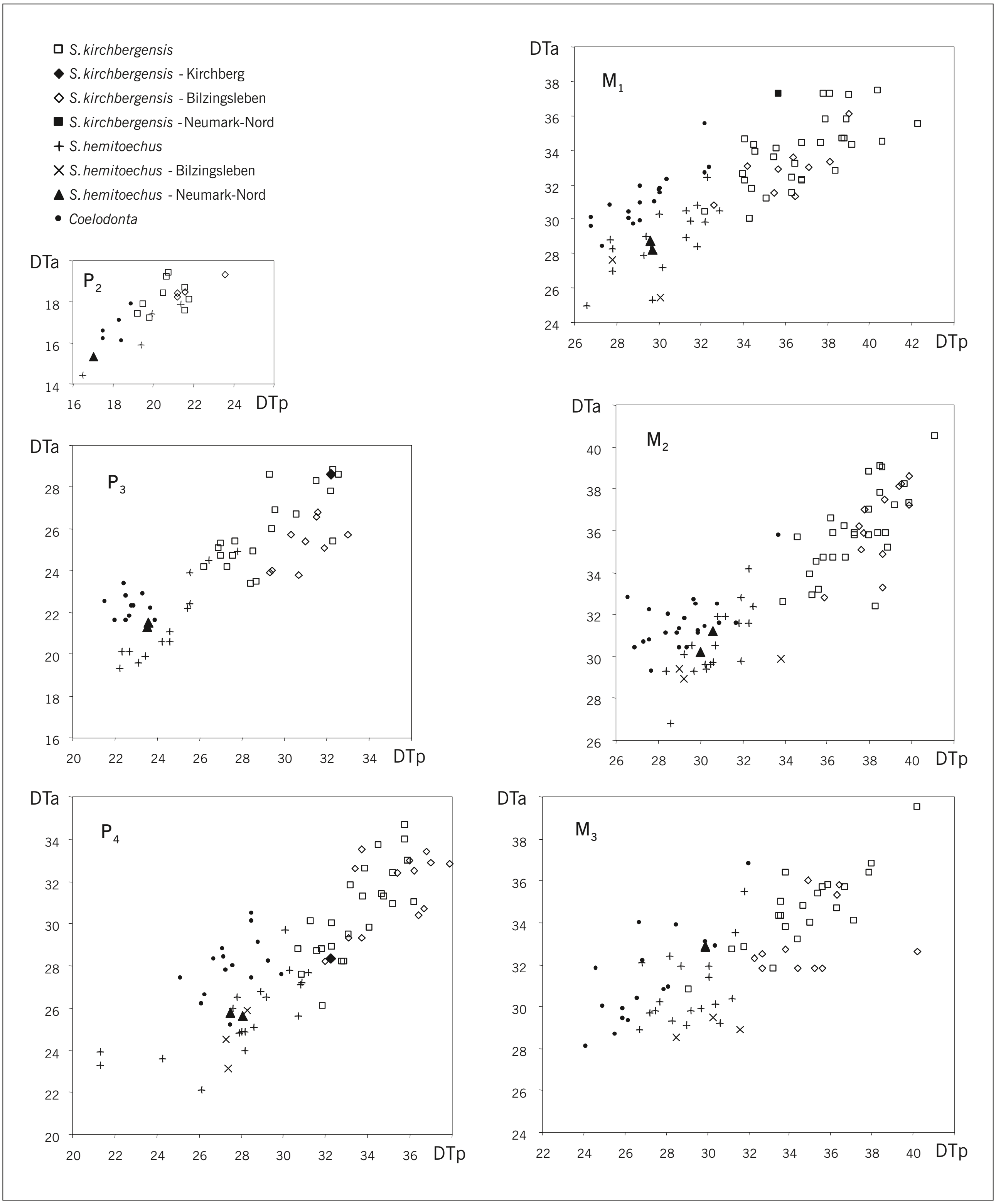

**Fig. 14** Bivariate diagrams of the lower cheek teeth: DTa (= width of the anterior lobe) versus DTp (= width of the posterior lobe). *Stephanorhinus kirchbergensis* from Kirchberg (SMNS, the specimen is probably a $P_3$, but is indicated also in the figure for the $P_4$), Bilzingsleben (FBFSUJB), Neumark-Nord (LVH) and other localities, including: Mosbach (NMM, SMNS), Steinheim (SMNS), Ehringsdorf (IQW), Taubach (IQW), Gimbsheim (NMM), Eich (NMM) and other »Rheinebene localities« (NMM). *Stephanorhinus hemitoechus* from Bilzingsleben (FBFSUJB), Neumark-Nord (LVH), and other localities, including: Steinheim (SMNS), Ehringsdorf (IQW), Taubach (IQW), Gimbsheim (NMM), Eich (NMM) and other »Rheinebene localities« (NMM). *Coelodonta antiquitatis* from Chlum (NMP), Steinheim (SMNS), Ehringsdorf (IQW), Belvedère (NMMa), Ariendorf (SMN), Backleben (IQW), Heldrungen (IQW), Kahla (IQW), Gimbsheim (NMM), Eich (NMM) and other »Rheinebene localities« (NMM). No isolated specimens, but only teeth in mandibles or tooth rows have been used.

In *Stephanorhinus hundsheimensis* (Toula 1902, Pl. 5,2) and *Diceros bicornis* (NNML 5738) the dorsal spine is narrower, and in the latter species especially at its caudal end. In *Coelodonta*, the transverse process seems to be more massive and directed more laterally and less distally and the dorsal spine seems to be more narrow (Bosuk-Bialynicka 1973, Pl. 7,2; 8,3).

The $C_5$ (Pl. 10,1) is intermediate in morphology between the vertebrae of *S. hemitoechus* that are interpreted to be $C_4$

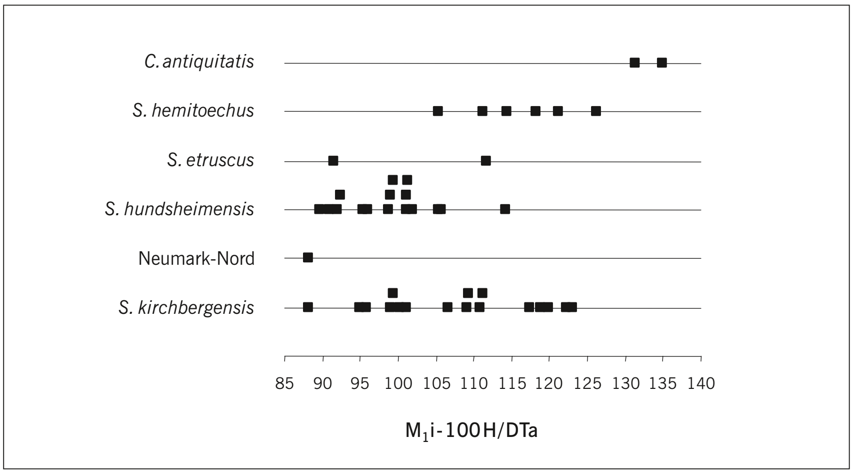

**Fig. 15** The hypsodonty index 100 H/DTa in the M1. Comparison of specimen E-24 of *Stephanorhinus kirchbergensis* from Neumark-Nord with *S. kirchbergensis* from Mosbach (NMM), Bilzingsleben (FSBFSUJ), Ehringsdorf (IQW), Taubach (IQW) and Gimbsheim (NMM), *S. hundsheimensis* from Untermassfeld (IQW), West Runton (NHM), Voigtstedt (IQW), Süssenborn (IQW), Mosbach (NMM) and Mauer (SMNK), *S. etruscus* from Olivola (IGF) and Upper Valdarno (IGF), *S. hemitoechus* from Ehringsdorf (IQW) and Eich (NMM), and *Coelodonta antiquitatis* from Chlum (NMP) and Gimbsheim (NMM).

and $C_6$ (Pl. 9,2; 10,2). It is not easy to interpret the differences in morphology with those vertebrae, because they can be due to a different position in the vertebral column or specific or individual differences. The caudal articular processes extend more distally than in those two vertebrae. This is also the case with the caudal part of the transverse process. In lateral view, the »bridge« over the transverse foramen seems to be more directed in a vertical direction and less dorso-cranial to ventro-caudal. The cranial articular processes are less developed and do not stick out anteriorly over the vertebral body. The anterior articulation (with the $C_4$) is narrower than in the $C_4$ and $C_6$ of *S. hemitoechus* and *S. etruscus* (Ambrosetti 1972, Pl. 3,7.8). The vertebral canal and transverse foramina are relatively large. The facets on the caudal articular processes are oriented more horizontally than in the specimens assigned to *S. hemitoechus*. This and the narrower anterior facet on the vertebral body suggest a greater mobility in the horizontal plane and less in the vertical plane.

A **$T_1$** (Pl. 12,2) is white, but was found together with various other vertebrae, that are black. It has very well developed cranial articular processes with articular facets that are steeply medially inclined, much in the style of the cervical vertebrae, but it has anterior costal facets. This combination of features is typical of the $T_1$. The specimen differs from the $T_1$ of *S. hemitoechus* in that the posterior costal facets are much smaller, the notch is less open and the vertebral canal is wider. The latter feature suggests the specimen belonged to a large species.

What seems to be the **$T_3$** (Pl. 12,3) is fragmentary and resembles the next vertebra that is represented in Neumark-Nord, but differs in reaching its greatest width at a level just ventral of the vertebral canal and in having the lateral costal facet in a slightly more ventral position. This suggests that it precedes the other vertebra, which is interpreted as a $T_5$. Gorjanovic-Kramberger (1913, Pl. 2,5) figured a vertebra of *S. kirchbergensis* from Krapina as $T_3$. The specimen is badly rolled, but it can be seen that it has the posterior costal facets below the middle of the vertebral body and its widest point is at the same level. The specimen from Krapina resembles a $T_2$ more than a $T_3$ from Tegelen figured by Bernsen (1927, Pl. 10,1.2) and probably is a $T_2$. Another specimen from Krapina was supposed to be a $T_5$, but might be a $T_4$ and has the greatest width more dorsally than the specimen from Neumark-Nord, which should precede this vertebra and might be a $T_3$. These slightly more anterior postitions for the Krapina specimens are assumed because of the number of types of vertebras that follow.

What seems to be the **$T_5$** (Pl. 12,1) has a long dorsal spine (which was not yet fully grown when the individual died), the anterior and posterior costal facets are situated dorsally of the middle of the vertebral body, but barely surpass the dorsal border of this body. The anterior and posterior main articular facets of the vertebra are widest in their ventral halves, the facets on the cranial and caudal articular processes are inclined medially, the greatest width of the transverse process is at the level of the dorsal border of the vertebral canal, the mammillary process is elevated just a little and the lateral costal facets are not fully vertical and are a little inclined ventrally. The specimen lacks two features that are present in a specimen from Krapina described and figured as a $T_5$ (Gorjanovic-Kramberger 1913, Pl. 7,4), but which might be a $T_4$. It has three features that are not present in the specimen from Krapina, but which are common in some of the more caudal vertebrae (Fig. 17). A specimen from Tegelen figured as a $T_4$ is probably also a $T_5$, because it has features that suggest a more caudal position than for the four thoracic vertebrae discussed above, this specimen is, however, atypical in having the anterior costal facet at the level of the middle of the vertebral body and not reaching its upper surface (symbol marked »T« in Fig. 17), which is a feature that suggests a more cranial position.

A **scapula** fragment is morphologically and metrically similar to the specimen described under *S. hemitoechus* and, like that specimen, is larger than *S. hemitoechus* and *S. kirchbergensis* from Bilzingsleben and *Coelodonta* (Fig. 19, Tab. 5). Its large size suggests that it belongs to one of the two species of *Stephanorhinus*. In this find complex, *S. kirchbergensis* is represented by the humerus and vertebrae; therefore the specimen is tentatively assigned to that species.

The **humerus** is represented by two specimens, which are here only compared to the more complete specimens which are fully described under *S. hemitoechus*. E I, 39 is the more complete specimen and lacks the proximal epiphysis because it is a juvenile. It is more gracile than the specimens assigned to *S. hemitoechus*, but then juvenile specimens tend to be less robust. However, the deltoid tuberosity is placed at a greater absolute distance from the distal articulation than in

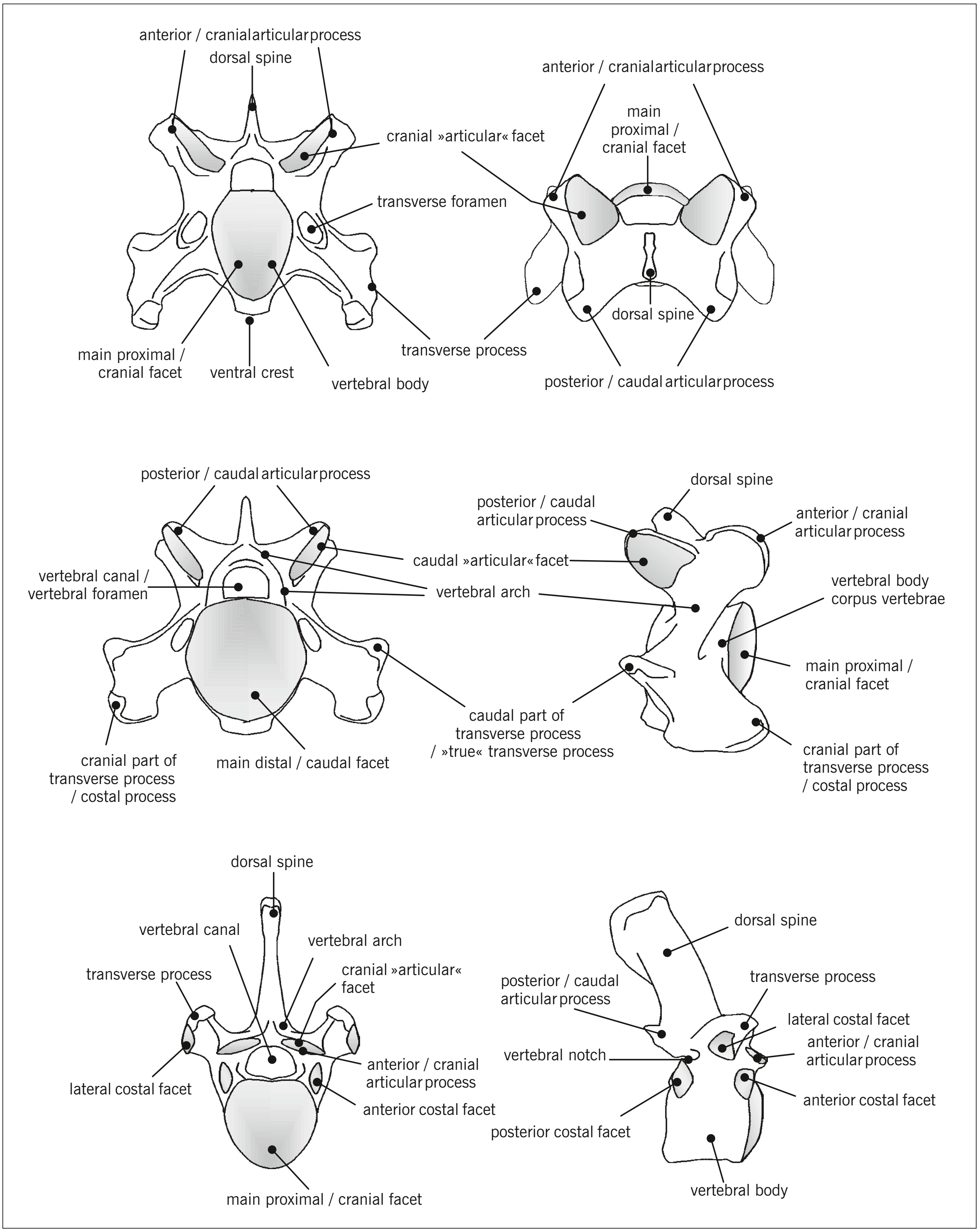

**Fig. 16** Nomenclature of the vertebrae, largely after Koch (1960), Getty (1975) and Evans/deLahunta (1980).

*S. hemitoechus.* This either suggests a very tall individual (still being a juvenile) or that this tuberosity is placed much more distant from the distal articulation, as is the case in *S. kirchbergensis* from Bilzingsleben. *Coelodonta* is morphologically more similar to *S. hemitoechus.* EI,39 belonged thus most probably to *S. kirchbergensis* for morphological reasons, but it also fits this species metrically (Fig. 20, Tab. 6). The other specimen is also large and might belong to a juvenile, but is less complete. Its assignation to *S. kirchbergensis* is less secure.

A distal third metapodial is probably a **Mc III** (Tab. 7), because the shaft is very flat and very wide just above the distal articulation. The distal articular surface is very large and even larger than in the specimens of *S. kirchbergensis*

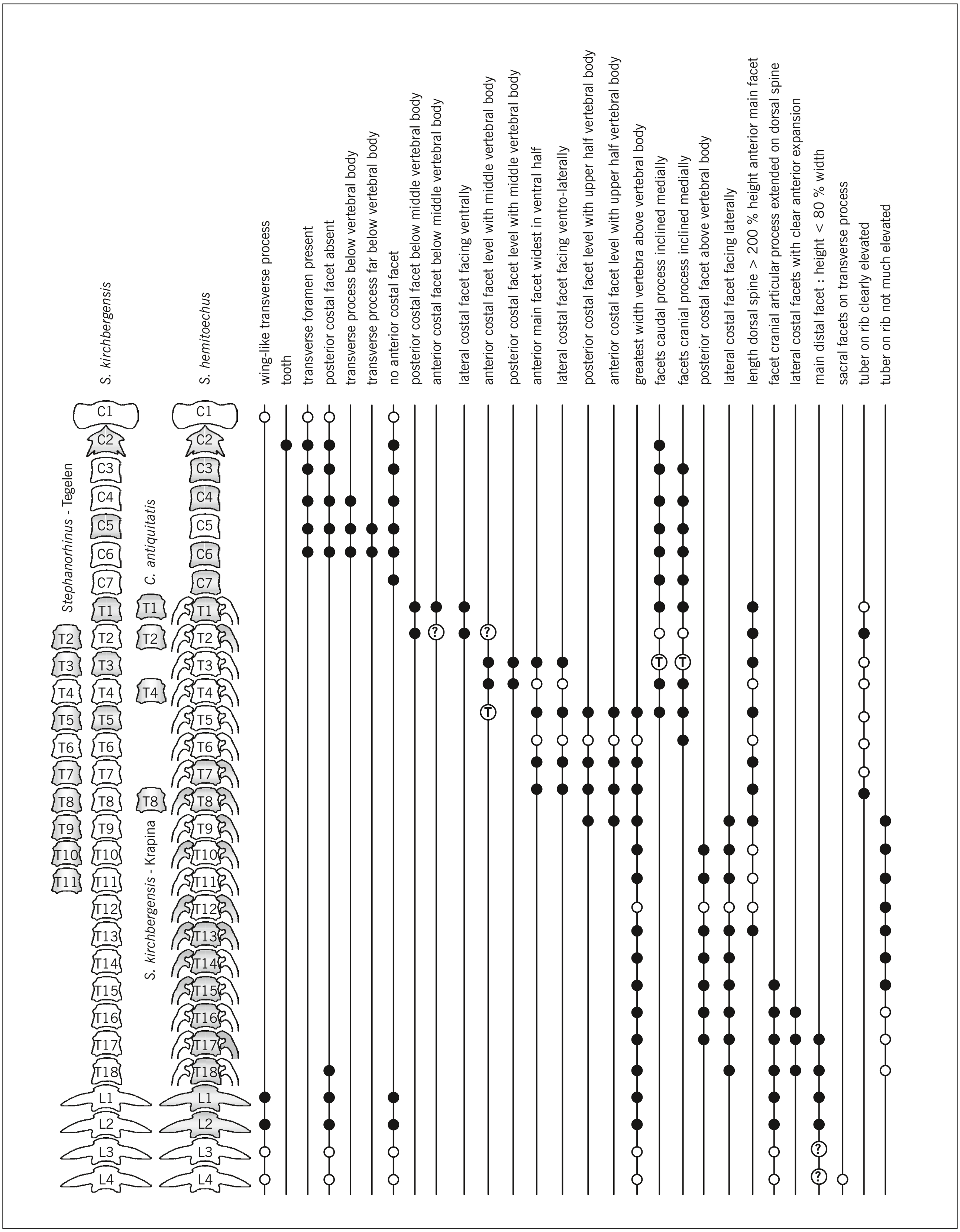

**Fig. 17** Representation of vertebrae and ribs (grey means present) and a selection of the features observed (black dots), probably present (circles) or possibly present (circles and question marks). Of some of the ribs only the approximate position is known (see text). In three cases the Tegelen specimens have different character states than expected, these are indicated as »T« and are discussed in the text.

from Bilzingsleben. Probably the specimen represents *S. kirchbergensis*, but it cannot be ruled out that it belongs to *S. hemitoechus*, which in Neumark-Nord has very massive limb bones.

### *Discussion*

The species *Stephanorhinus kirchbergensis* was based by Jäger (1839) on three teeth that are kept in the SMNS. These teeth indicate a very large species with a particular morphol-

**Tab. 4** Measurements of the vertebrae of the rhinos from Neumark-Nord. Note that the length (7) in the axis ($C_2$) is measured in a different way (see section on measurements).

| | measurement | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *S. hemitoechus* | | | | | | | | | | | | | | | | | | | | | |
| C2 | HK88:14/61 | l | 172.4 | 73.7 | 67.5 | | 68.8 | 32.7 | 121.77 | 157 | 87.7 | 79.2 | 157.1 | 83.7 | 39.5 | 104.8 | 157.1 | 61.5 | | | 10.7 | |
| | | r | | | | | | | | | 73.7 | | | | | 52.4 | | | | | 18.0 | |
| C2 | HK88:14/34 | l | 185.1 | 85.9 | 66.9 | ~ 51.0 | 80.0 | 29.7 | 136.3 | 88.2 | 105.6 | 70.4 | 220.2 | 76.8 | 42.9 | 107.8 | 161.3 | 68.9 | | | 17.7 | 14.3 |
| | | r | | | | | | | | | 108.2 | 70.2 | | | | | | | | | 20.2 | 18.6 |
| C3 | HK88:14/35 | l | 164.4 | 90.2 | 49.5 | 75.1 | 82.6 | 26.0 | 69.9 | 48.6 | 96.8 | | 209.6 | 96.8 | 34.3 | 107.4 | 57.3 | 72.4 | 106.8 | | 20.8 | 13.0 |
| | | r | | | | | | | | | 97.2 | 104.0 | 104.8 | | | | | | | | 21.5 | 15.5 |
| C4 | HK88:14/30 | l | | 90.7 | | 75.8 | 81.7 | 25.0 | 72.8 | 38.4 | 96.3 | | 191.8 | 96.4 | 33.4 | 107.5 | 66.1 | 72.0 | 107.8 | | 23.5 | 15.1 |
| | | r | | | | | | | | | 96.7 | 102.6 | 95.9 | | | | | | | | 24.1 | 14.7 |
| C6 | HK88:14/31 | l | 214.6 | 78.7 | 102.5 | 72.4 | 76.1 | 32.3 | 73.6 | 39.4 | 91.9 | | 165.6 | 95.6 | 34.6 | 117.1 | 63.1 | 78.2 | 106.9 | | 25.9 | 16.1 |
| | | r | | | | | | | | | 95.5 | 85.4 | | | | | | | | | 26.4 | 17.6 |
| C7 | HK88:14/36 | l | >240.3 | 75.7 | >134.2 | 66.2 | 68.9 | 33.9 | 76.3 | 54.6 | 101.4 | 37.8 | 162.3 | 97.9 | 43.3 | 112.1 | 67.4 | 76.5 | 117.6 | 103.4 | | |
| | | r | | | | | | | | | 95.5 | 39.7 | | | | | | | | | | |
| T1 | HK88:14/33 | l | >429.8 | 65.6 | >339.5 | 65.9 | 65.6 | 28.6 | 72.3 | 63.8 | 91.2 | 48.4 | 168.0 | 108.9 | 37.5 | 99.6 | 70.8 | 67.7 | 111.2 | 108.9 | | |
| | | r | | | | | | | | | >93.5 | 51.3 | | | | 49.8 | | | | | | |
| T7 | HK88:14/26 | l | 374.8 | 63.8 | 287.6 | 59.4 | 63.8 | 25.5 | 64.5 | 58.8 | 84.2 | 43.3 | 114.3 | 121.1 | 32.4 | 66.3 | 62.1 | 65.5 | 86.9 | 148.8 | | |
| | | r | | | | | | | | | 82.9 | 43.8 | | | | | | | | | | |
| T8 | HK88:14/32 | l | 330.5 | 62.4 | 228.2 | 60.9 | 62.4 | 24.6 | 64.3 | 61.3 | 80.2 | 42.2 | 109.7 | | 34.8 | 69.8 | 62.1 | 67.0 | 70.2 | 108.7 | | |
| | | r | | | | | | | | | 79.1 | 43.7 | | | | | | | | | | |
| T13 | HK88:14/27 | l | 201.6 | 60.3 | 117.5 | 58.3 | 59.2 | 24.0 | 68.5 | 70.9 | 85.7 | 43.6 | 123.5 | | 33.1 | 52.3 | 60.1 | 70.0 | 56.8 | 91.0 | | |
| | | r | | | | | | | | | 83.0 | 42.7 | | | | | | | | | | |
| T14 | HK88:14/29 | l | 168.5 | 58.8 | 86.0 | 59.2 | 58.8 | 22.4 | 68.9 | 78.9 | 88.2 | 45.7 | 118.7 | | 30.1 | 49.8 | 60 | 66.9 | 55.2 | 90.2 | | |
| | | r | | | | | | | | | 89.6 | 45.5 | | | | | | | | | | |
| T15 | HK88:14/ | l | 156.6 | ~58.4 | | ~54.8 | ~58.4 | | | | | | | | 29.2 | 54.6 | 63.6 | 66.4 | 54.8 | 85.0 | | |
| | | r | | | | | | | | | | | | | | 27.3 | 31.8 | | 27.4 | | | |
| T16 | HK88:14/37 | l | 154.0 | 53.3 | 74.1 | 57.6 | 56.7 | 21.6 | 68.4 | 72.7 | 100.9 | 44.1 | 109.8 | | 27.9 | 53.1 | 60.8 | 66.5 | 54.9 | 80.3 | | |
| | | r | | | | | | | | | >93.3 | 41.9 | | | | | | | | | | |
| T17 | HK88:14/ | l | | 55.1 | | | 55.1 | 21.5 | 69.3 | 75.7 | 98.5 | 47.4 | 107.6 | | 27.8 | 49.1 | 62.0 | 72.7 | 59.4 | 80.1 | | |
| | | r | | | | | | | | | 98.7 | 48.3 | | | | | | | | | | |
| T18 | HK88:14/25 | l | 150.8 | 57.4 | 76.3 | 54.9 | 54.9 | 23.2 | 69.3 | 64.3 | 92.3 | 47.4 | 100.7 | | 26.9 | 51.1 | 62.2 | 72.4 | 53.1 | | | |
| | | r | | | | | | | | | 93.9 | ~47.4 | | | | | | | | | | |
| L1 | HK88:14/24 | l | 157.8 | 54.3 | 76.8 | 56.3 | 52.0 | 27.1 | 70.3 | 65.7 | 96.0 | 49.8 | >315.4 | | 29.7 | 48.4 | 63.2 | 77.4 | 48.8 | | | |
| | | r | | | | | | | | | 97.7 | 52.3 | >157.7 | | | | | | | | | |
| L2 | HK88:14/28 | l | 158.8 | 52.9 | 79.2 | 54.7 | 52.9 | 26.2 | 69.4 | 60.4 | >92.8 | 42.4 | >252.8 | | 37.1 | 58 | 63.9 | 79.1 | 58.6 | | | |
| | | r | | | | | | | | | >90.7 | 43.9 | >126.4 | | | 29.0 | | | 29.3 | | | |

**Tab. 4** (Continuation).

| | measurement | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *S. kirchbergensis* | | | | | | | | | | | | | | | | | | | | | |
| C2 | EI | l | 197.6 | 79.7 | 79.8 | ~50.0 | 71.7 | 42.9 | 138.1 | 104.0 | 158.1 | 79.6 | 170.2 | 62.9 | 44.7 | 98.5 | 150.0 | 64.2 | | | 17.9 | 13.4 |
| | | r | | | | | | | | | 153.2 | 78.3 | | | | | | | | | 18.3 | 13.5 |
| C5 | EI | l | | 85.3 | | 75.2 | 85.3 | 31.4 | 76.3 | 42.5 | | | 179.0 | 94 | 37.6 | 114.2 | 49.9 | 62.6 | 91.2 | | 26.2 | 17.8 |
| | | r | | | | | | | | | 104.0 | >130.2 | 89.5 | | | | | | 45.6 | | 24.5 | 17.2 |
| T1 | EI | l | | 69.0 | | 66.0 | 64.7 | 20.2 | 81.2 | | | | >164.6 | 101.8 | 46.9 | | 69.3 | 67.6 | | 115.9 | | |
| | | r | | | | | | | | | | | | | | | | | | | | |
| T3 | EI | l | | | >>290 | | | | | >54.0 | >106.3 | 59.7 | 165.4 | 113.2 | ~38 | 84.1 | | | 90.0 | | | |
| | | r | | | | | | | | | | | 82.7 | 56.6 | ~19 | | | | 45.0 | | | |
| T5 | EI | l | >367 | 67.6 | >267 | 60.1 | 65.2 | 20.2 | 72.1 | 73.0 | >98.7 | >56.2 | 153.2 | 104.9 | 42.9 | 63.2 | 62.6 | 74.1 | 66.5 | 117.7 | | |
| | | r | | | | | | | | | | >52.7 | | | | 31.6 | | | | | | |
| | *C. antiquitatis* | | | | | | | | | | | | | | | | | | | | | |
| T1 | 95,3 | l | | | | >62.0 | 64.2 | | 78.0 | | | | 201.0 | 126.2 | ~36.7 | | 69.7 | 63.6 | | | | |
| | | r | | | | | | | | | | | 100.5 | 63.1 | | | | | | | | |

ogy of the teeth and coincide with the large species of rhino that is currently recognised in the Middle and Upper Pleistocene of western and central Europe under that name. This large rhino is known by skulls and postcranial material. The material of the large rhino from Neumark-Nord shares the morphological and metrical features of this species, as indicated by the type material and other material assigned to it, including the low occiput that does not overhang the occipital condyles and the thin smooth enamel and wide valleys of the teeth. Therefore the material of the large rhino from Neumark-Nord is assigned to *Stephanorhinus kirchbergensis*.

The material from Neumark-Nord includes exceptionally good cranial material, which helps to characterise the species. The morphology of the occiput appears to be rather constant in Neumark-Nord. It is low, narrow and barely overhangs the posterior side of the skull, all as in the early or primitive species of the genus, such as *S. hundsheimensis* and *S. etruscus* but unlike a more recent species like *S. hemitoechus*. These features seem thus to be primitive. The marked V-shaped posterior edge, when seen from above, is unique and should thus be a derived character within the genus. The feature is less pronounced in the geologically older skulls from Mosbach and Daxlanden. The paroccipital process reaches nearly as low as the postglenoid process; the posttympanic process is fused to the postglenoid process, closing the pseudo-auditory meatus. This is common in the genus. The paroccipital and postglenoid process are closer together than in any other species of the genus. But again, this feature is less well developed in the skull from Daxlanden.

The skulls from Mosbach and Steinheim that are assigned to *S. kirchbergensis* served as a reference for the species (Loose 1975, Pl. 3; 4; 8; 10; 13; Staesche 1941, Pl. 11). However, both skulls have very narrow nasals with a poorly developed cauliflower structure, which might give the impression that this is typical for the species. The skull from Mosbach has little or no wear on the $M^3$, suggesting that it is a very young adult. The skulls from Neumark-Nord, have worn $M^3$ and are thus ontogenetically older, and have wide nasals with clear, but not very extensive, nasal septa and well developed cauliflower texture on the nasals and to a lesser extent on the frontals.

F. Zeuner (1934) used an index of the width of the area of origin of the horn divided by the length of the skull. These values could be taken as some indication of the relative size of the horns. Zeuner gave the values 0.13, 0.18 and 0.22 for *S. kirchbergensis*, 0.22 being the value of the disputed skull from Daxlanden, which according to some belongs to *S. etruscus* or *S. hundsheimensis*. For Neumark-Nord the value is 0.23, confirming a large sized horn for *S. kirchbergensis*.

### *Stephanorhinus hemitoechus* (Falconer 1859)

**Types:** the specimens from the caves of Glamorganshire known by H. Falconer are the syntypes. Various specimens are figured by Falconer (1868). Number 48953 in the NHM, the posterior half of a skull from Minchin Cave is taken as the lectotype. It was was figured by Falconer (1868, Pl. 24,2.3).

**Type locality:** »Caves of Glamorganshire« as originally indicated, of these, Minchin Hole or Minchin Cave is the locality of the lectotype.

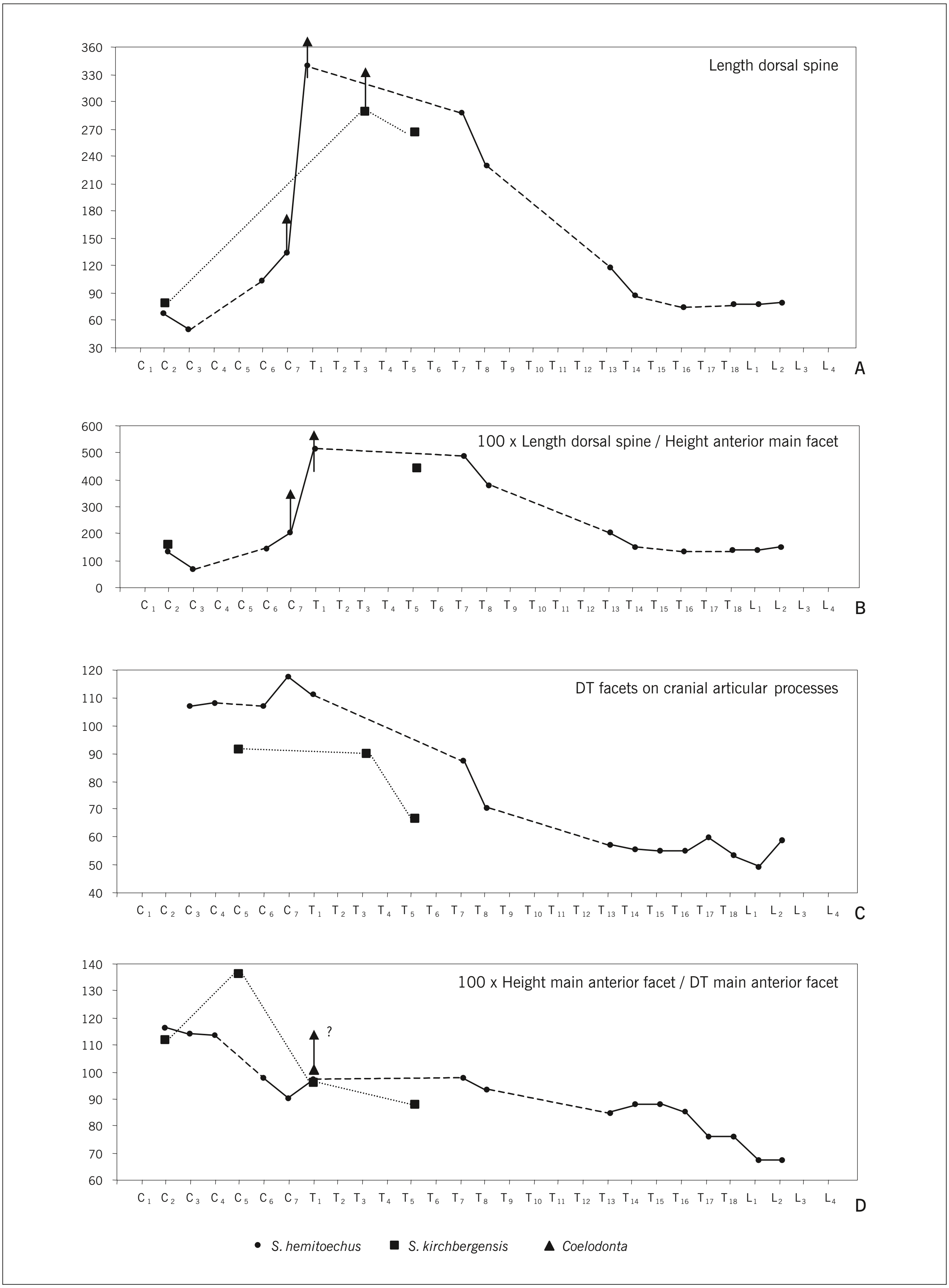

**Fig. 18** Variation of measurements and indices along the vertebral column. *S. hemitoechus* is represented by one individual (connected dots) and an axis of a second individual (isolated dot). Some of the values indicated are minimum or approximate measurements or indices calculated on them (consult Tab. 4). Data on *Stephanorhinus etruscus* from Capitone (E) from Ambrosetti (1972). Note that the latter species has eighteen thoracic and four lumbar vertebrae.

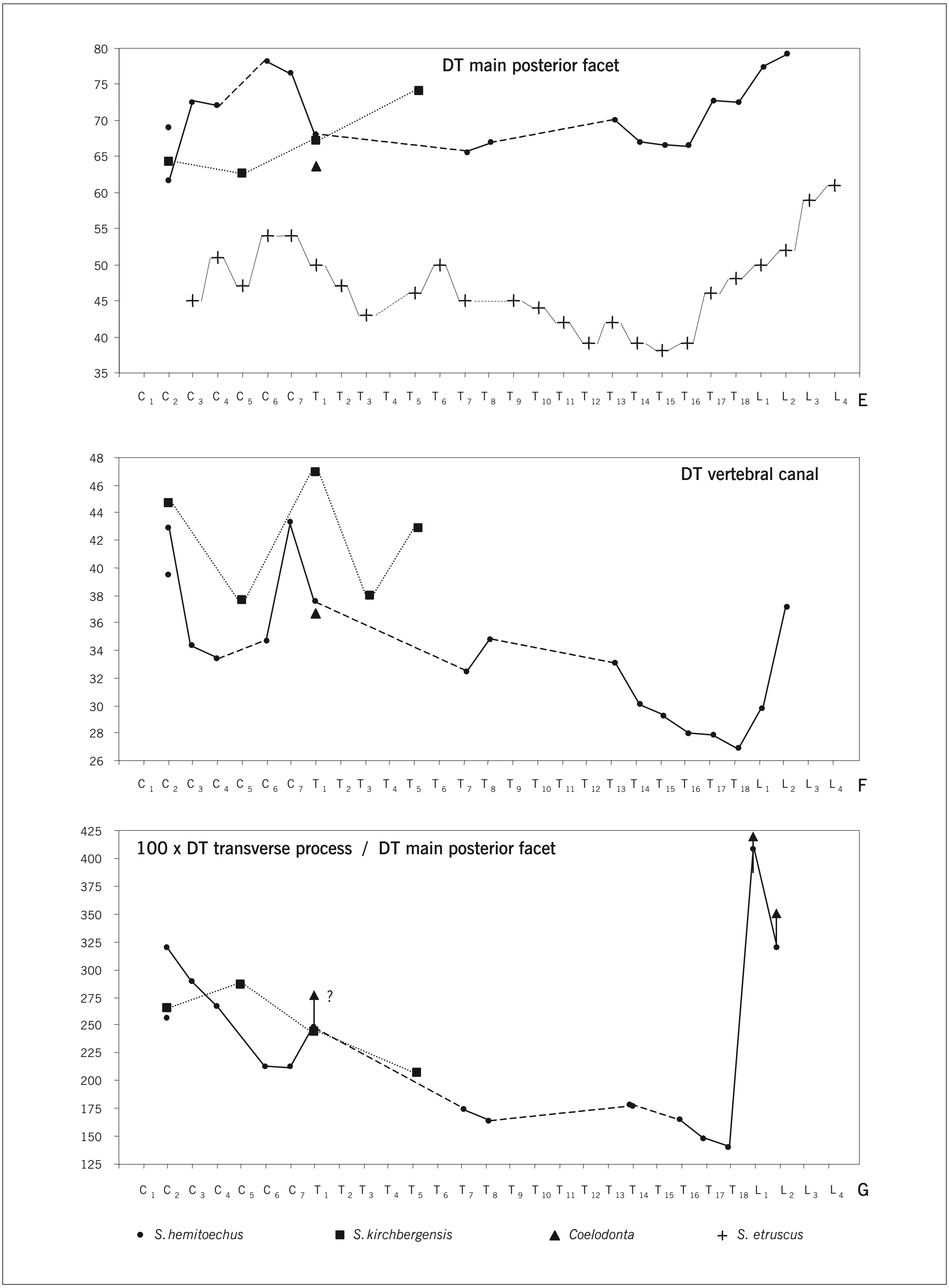

**Fig. 18** (Continuation).

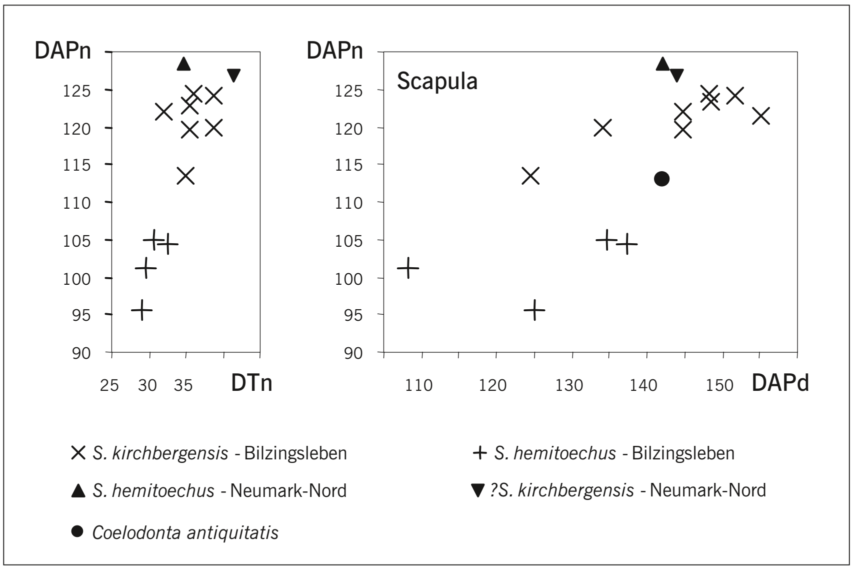

**Fig. 19** Bivariate diagram of the scapula. *Stephanorhinus hemitoechus* and *Stephanorhinus kirchbergensis* from Bilzingsleben (FBFSUJB), *S. hemitoechus* and ? *S. kirchbergensis* from Neumark-Nord (LVH) and *Coelodonta antiquitatis* (data from Borsuk-Bialynicka 1973).

**Tab. 5** Measurements of the scapula of the rhinos from Neumark-Nord.

|  | HK88: 14, 4 right | E I, 36 right |
|---|---|---|
| DAPd | 142.1 | 144.0 |
| DAPdf | 94.1 | 101.7 |
| DTd | 80.5 | >83.5 |
| DAPn | 128.3 | 126.8 |
| DTn | 34.6 | 41.6 |
| L | 523 | -- |

**Age of type locality:** Eemian/Ipswichian or zone 25 of Guérin (1980) for Minchin Hole.

**Material:**

189. HK 88: 14. Elements of a single individual, found disarticulated but in close proximity. A description, map and photographs of the find situation were given by Mania (1990, 45–46, Fig. 19, Pl. 26–29). Some silex implements were found together with the skeleton.

HK 88:14, 1 = skull
HK 88:14, 2 = right mandible
HK 88:14, 3 = left mandible
HK 88:14, 4 = right scapula
HK 88:14, 5 = right rib, possibly $R_2$
HK 88:14, 6 = left rib, possibly $R_{13}$
HK 88:14, 7 = right rib, probably $R_{11/12}$
HK 88:14, 8a + 8b = right rib (in two parts), probably $R_{11/12}$
HK 88:14, 9 = left rib, possibly $R_{15}$
HK 88:14, 10 = right rib, $R_{13}$
HK 88:14, 11 = left rib, probably $R_{10/11}$
HK 88:14, 12 = shaft of right rib, probably $R_{16/17/18}$
HK 88:14, 13 = left rib, probably $R_8$
HK 88:14, 14 = right rib, probably $R_{9/10}$
HK 88:14, 15 = right rib, probably $R_{10/11}$
HK 88:14, 16 = fragment of right rib, probably R8, same specimen as HK 88:14, 47
HK 88:14, 17 = right radius
HK 88:14, 18 = right femur
HK 88:14, 19 = right ulna
HK 88:14, 21 = left metatarsus IV
HK 88:14, 22 = right metatarsus IV
HK 88:14, 23 = right scaphoid
HK 88:14, 24 = vertebra $L_1$
HK 88:14, 25 = vertebra $T_{18}$
HK 88:14, 26 = vertebra $T_7$
HK 88:14, 27 = vertebra $T_{13}$
HK 88:14, 28 = vertebra $L_2$
HK 88:14, 29 = vertebra $T_{14}$
HK 88:14, 30 = vertebra $C_4$
HK 88:14, 31 = vertebra $C_6$
HK 88:14, 32 = vertebra $T_8$
HK 88:14, 33 = vertebra $T_1$
HK 88:14, 34 = axis (vertebra $C_2$)
HK 88:14, 35 = vertebra $C_3$
HK 88:14, 36 = vertebra $C_7$
HK 88:14, 37 = vertebra $T_{16}$
HK 88:14, 38 = rib fragment
HK 88:14, 39–44 = rib fragments
HK 88:14, 45 = rib fragment, belongs to HK 88: 14, 13
HK 88:14, 46 = rib fragment
HK 88:14, 47 = fragment of right rib, probably R8, same specimen as HK 88:14, 16
HK 88:14, 48–49 = rib fragments
HK 88:14, 50 = left navicular
HK 88:14, 51 = right navicular
HK 88:14, 53 = left patella
HK 88:14, 54 = first lateral phalanx, right of axis of foot
HK 88:14, 55 = left metatarsus II
HK 88:14, 56 = right metatarsus III
HK 88:14, 57 = right metatarsus II
HK 88:14, 58 = third lateral phalanx left of axis of foot
HK 88:14, 60 = right humerus
HK 88:14,-- = vertebra $T_{15}$ (=? HK 88:14, 61)
HK 88:14,-- = vertebra $T_{17}$ (=? HK 88:14, 61)
HK 88:14,-- = right cuneiforme III

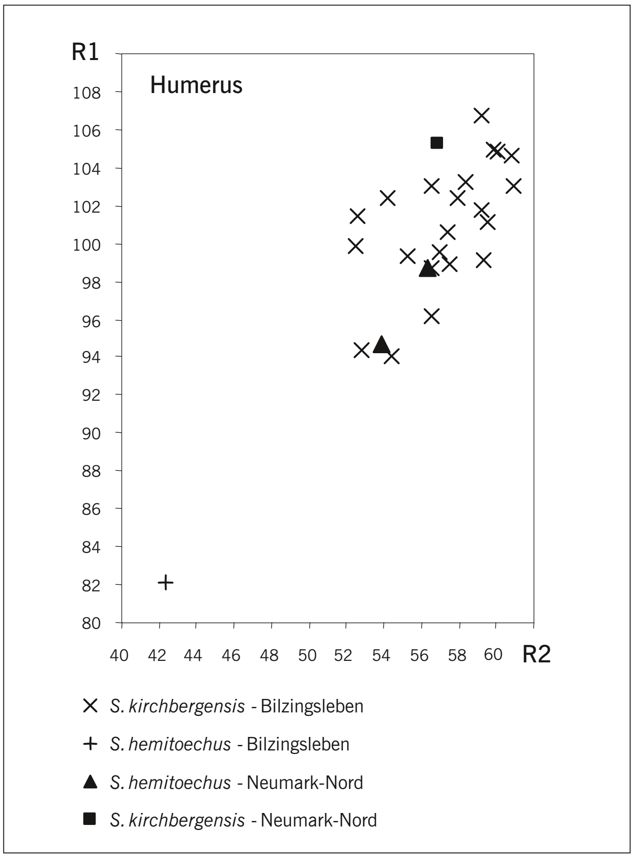

**Fig. 20** Bivariate diagram of the humeri of *Stephanorhinus kirchbergensis* from Neumark-Nord and Bilzingsleben (FSBFSUJ) and *S. hemitoechus* from Neumark-Nord and Bilzingsleben (FSBFSUJ).

**Tab. 6** Measurements of the humerus of the rhinos from Neumark-Nord.

| | *S. hemitoechus* | | *S. kirchbergensis* | |
|---|---|---|---|---|
| Humerus | HK88: 14, 60 | E24, 244+245 | E I, 39 | EI, 41 |
| | right | right | left | right |
| DAPp | 199.2 | 196.9 | juv. | juv.? |
| DAPp’ | 144.8 | 156.4 | juv. | -- |
| DTp | 165.6 | 170.0 | juv. | -- |
| DTpf | 115.8 | 104.2 | juv. | -- |
| L | 435 | ~459.2 | >>359 | -- |
| l | 387 | ~400.2 | juv. | -- |
| DAPd | 120.8 | -- | 130.8 | 117.1 |
| DTd | 154.3 | -- | -- | -- |
| DTdf | 105.3 | 106.4 | 109.8 | -- |
| R1 | 98.7 | 94.7 | 105.2 | 94.4 |
| R2 | 56.3 | 53.9 | 56.9 | -- |
| R3 | 77.5 | 70.3 | 71.1 | -- |

189. HK 88:14, 61 = axis found near the individual of HK 88:14, but not belonging to this individual

E 21 »Uferzone« (found near elephant »E 21«) = dorsal fragment of a skull from nasals to occiput

4-5-1994. = left lateral first phalanx found together with remains of cervids

204a. Found together with elephant skeleton no. »E II« and collected 3/9/1996:
E II, 27 = nasals
E II, 29 = occipital
E II, 28 = upper molar

200. Found near elephant skeleton no. E 24, remains of rhinos:
E 24, 244 = distal fragment of right humerus
E 24, 245 = proximal fragment of right humerus; 244 and 245 form a complete humerus
E 24, 246 = (=?) left $M^{2-3}$
E 24, 247 = right $M^2$

? 1996, 45 Ulna

*Description and comparison*

The **skull** (Pl. 5,1; 6,1; 7,3 Tab. 1) is excellently preserved, nothing is broken and nothing is deformed.

The dorsal surface of the nasals faces forward and upward in the anterior part and in the remaining part upward, producing an angle that can be seen in profile. The dorsal surface is covered by rugose bone with a cauliflower texture. At its major extension this cauliflower bone extends beyond the margins of the nasals. Behind this there is a slight waisting of the nasals. The cauliflower texture is very extensive

**Tab. 7** Measurements of the metapodials of the rhinos from Neumark-Nord.

| | | | DAPp | DTp | L | l | DAPd | DTd. |
|---|---|---|---|---|---|---|---|---|
| *S hemitoechus* | | | | | | | | |
| Mt II | HK88: 14, 55 | l | 46.6 | 33.3 | 153.2 | 151.5 | 41.3 | 39.8 |
| Mt II | HK88: 14, 57 | r | 48.0 | 34.8 | 163.6 | 152.4 | 40.9 | 40.0 |
| Mt III | HK88: 14, 56 | r | 58.1 | 56.1 | 183.9 | 176.9 | 46.9 | 52.6 |
| Mt IV | HK88: 14, 21 | l | 52.1 | 51.6 | 163.8 | 151.6 | 43.0 | 39.4 |
| Mt IV | HK88: 14, 22 | r | 51.8 | 51.2 | 162.9 | 153.2 | 43.6 | 39.1 |
| *S. kirchbergensis* | | | | | | | | |
| Mc III | NN50 | r | -- | -- | -- | -- | 56.3 | 63.5 |

**Tab. 8** Measurements (in mm) of the mandible of *Stephanorhinus hemitoechus* and the mandible fragment of *Coelodonta antiquitatis* from Neumark-Nord. Numbers 1, 3–11 and 13–16 refer to measurements of Guérin (1980). Way of measuring indicated in Figure 3.

| | HK88: 14, 3 left | HK88: 14, 2 right | E I, 42 right |
|---|---|---|---|
| 1) length | 558 | | |
| 3) height mandible below P2-3 | 91.1 | 97.3 | |
| 4) height mandible below P3-4 | 90.0 | 99.2 | |
| 5) height mandible below P4-M1 | 106.3 | 107.4 | |
| 6) height mandible below M1-2 | 108.5 | 106.3 | |
| 7) height mandible below M2-3 | 104.5 | 104.6 | |
| 8) height mandible behind M3 | 108.9 | 108.5 | |
| 9) width mandible below P4-M1 | | | |
| 10) width mandible below M2-3 | | | |
| 11) length symphysis | 138.4 | | |
| 13) DAP ramus | 177.8 | 179.0 | |
| 14) DT condyle | 114.3 | 114.3 | 88.7 |
| 15) height condyle | 293.3 | 297.9 | |
| 16) height coronoid | -- | -- | |
| 17) maximal anterior width | | | |
| 18) minimal anterior width | | | |
| 19) height symphysis | 55.9 | | |
| 20) DAP ramus at level of condyle | 152.7 | | 153.3 |
| 21) DAP facet condyle | 30.9 | 30.8 | 18.3 |
| 22) DAP mini ramus | 140.7 | 137.5 | 136.4 |
| 23) condyle above occlusal surface | 142 | 133 | |
| 24) condyle behind front M1 | 384/399 | 381/392 | |
| 25) depth mandible below P2 | 84.5 | -- | |
| 26) depth mandible below P3 | 93.5 | -- | |
| 27) depth mandible below P4 | 97.7 | 100.0 | |
| 28) depth mandible below M1 | 111.0 | 112.4 | |
| 29) depth mandible below M2 | 108.5 | 109.6 | |
| 30) depth mandible below M3 | 105.4 | 107.5 | |
| 31) width mandible below P2 | 60.3 | -- | |
| 32) width mandible below P3 | 60.4 | 61.1 | |
| 33) width mandible below P4 | 60.9 | 63.0 | |
| 34) width mandible below M1 | 65.7 | 67.6 | |
| 35) width mandible below M2 | 69.9 | 69.2 | |
| 36) width mandible below M3 | 69.0 | 70.5 | |

and indicates the origin of the anterior horn, which must have been large, long and directed anterior and upward. Below the nasals, there is the bony nasal septum, which is more developed as in *S. kirchbergensis* and has had at least a minimal antero-posterior extension of some 13 cm, and which served as a support of the large horn. The nasals overhang the nasal cavity more than in *S. kirchbergensis*.

The frontals have a second area with cauliflower texture, which is more developed than in *S. kirchbergensis*, and which marks the origin of the second, posterior, horn. The parietal crests are well separated. In the parietal and occipital area the dorsal surface of the skull is inclined upwards towards the occiput. The occiput is moderately wide (more than in *S. kirchbergensis*, less than in *Coelodonta*). If seen from above or from behind the occiput is more or less straight and does not have a V-shape or depression in the middle, as in *S. kirchbergensis*. The occiput is not only elevated, but also overhangs the posterior surface of the skull and reaches far more caudally than the caudal edge of the occipital condyles. The dorsal side of the skull, just above the occipital condyles is overhanging the condyles, whereas this surface in *S. kirchbergensis* has the opposite inclination.

Like in *S. kirchbergensis*, the zygomatic archs do not extend much laterally. The anterior edge of the orbit is positioned above the posterior half of the $M^3$. The premaxillary is more pointed than in *S. kirchbergensis*. In ruminants, narrow premaxillaries are considered to indicate browsing habits (Solounias et. al. 1988), which does not coincide with the assumed habits of this rhino. The posterior edge of the palate is U-shaped, with a U that is slightly wider than in *S. kirchbergensis*, but similarly extending forward till the first lobe of the $M^3$.

The glenoid is wide, but not as wide as in *S. kirchbergensis*. The postglenoid and paroccipital processes are close together, but not as close as in *S. kirchbergensis*. Below the pseudo-auditory meatus, a thin line marks the anterior extension of the posttympanic process, which is fused to the postglenoid process. If seen laterally, the posttympanic does not show up as a separate downward directed process. The morphology of this area is intermediate between that of *S. kirchbergensis* on the one hand and *S. hundsheimensis* and *S. etruscus* on the other. When seen from below, the posttympanic process is seen as a massive area posterior to the postglenoid process and lateral to the paroccipital process and is more extensive than in *S. kirchbergensis*. The hypoglossal and jugular foramina are separated only by a very thin bar of bone.

Remains of a second **skull** (Pl. 7,3) include the dorsal part, from the nasals to the occiput, and the posterior surface, from the occiput to one of the occipital condyles. The measurements that could be taken are indicated in Tab. 1. Behind the rugosities of the posterior horn, the dorsal surface rises markedly. The occiput overhangs the occiptal condyle and projects far more posteriorly than the condyle. The occiput is convex when seen from above and from behind and does not have a »V-shape« and depression in the middle as in *S. kirchbergensis*. Both features are typical for *Stephanorhinus hemitoechus*. The skull is broken along a nearly anteroposterior directed plane. The section shows a small cranial cavity, large sinusses in the occipital area, and a thick posterior wall of the skull that has a fine spongious structure. The dorsal wall of the skull is composed of much thinner, but compact bone.

A third **skull** (Pl. 7,1.2) is represented by a fragment of the nasals and a second fragment that includes the occiput and parietal region. The occiput is narrower than in *Coelodonta* and overhangs a little and thus approaches the common state in *S. hemitoechus*. Seen from above, the posterior edge of the occiput is convex and does not have the V-shape as described under *S. kirchbergensis*. Seen from the back, similarly the occiput is convex, and does not have a little depression in the middle. The morphology of the occiput is very much like in *S. hemitoechus*. The nasals have a well developed cauliflower texture that is clearly limited at the front, while the nasals extend more anteriorly with a lower and flat surface. The part of the bony nasal septum that is preserved has a minimum thickness of 16.9 mm. The specimen was broken along a transverse fracture, exposing a T-shaped section, in which the vertical part is the septum. The centre of this T-shape has spongious bone and the walls of the septum and lower surfaces of the nasals are formed by compact bone. This compact bone is covered (both on its vertical and horizontal surfaces) by additional layers of bone with a very fine spongious texture. The nasals turn slightly downwards at their lateral borders.

The **mandible** (Pl. 7,1.2 Tab. 8) does not bear any incisors or canines, but still widens a little in this area. It is waisted just behind the anterior part. This is unlike the state in the recent African rhinos, where, in addition, the anterior part of the mandible is much shorter. The posterior part of the symphysis is close to the anterior part of the $P_3$. The horizontal branch is relatively high. This differs from a toothless specimen from Bilzingsleben, where it is very low. Guérin (1980, 639) noted already that the variation in size is large in this species. When seen from the side, the mandible is elongate and the lower border is convex; the angle is not well developed. The ascending ramus is situated well behind the $M_3$. The condyle is situated well behind the posterior edge of the angle. The coronoid process is small and narrow, but reaches well above the condyle. The vertical facet behind the condyle, that articulates with the retroarticular process is saddle shaped (concavo-convex), unlike in the specimen, which is assigned to *Coelodonta*, where it is basin shaped (all concave). Its height is 47.3 (left) to 48.4 mm (right), while it is much lower in the other specimen (31.5 mm); similarly it is wider (38.4 and 38.9 mm respectively) than in the specimen assigned to *Coelodonta* (26.5 mm).

The upper **dentition** of *S. hemitoechus* (Pl. 3,2 Tab. 2) has been compared with that of *S. kirchbergensis* in the description of that species and this will not be repeated here.

Both **$P^2$** are lacking. The alveoles of the left $P^2$ were clearly in the process of being closed by growth of the maxillary. The left $P^2$ must have been lost during life and the right one possibly as well.

The **$P^3$** and **$P^4$** (Pl. 3,2) are similar in morphology, but differ very clearly in size. They differ from those of *Coelodonta* (Pl. 26,1) in having: thinner and less rugose enamel, less cementum, a lower crown, a parastyle that projects less buccally, metacone that is more lingually placed, an ectoloph that is oriented more obliquely to the length of the tooth row, a protocone that extends less distally, a larger hypocone, a smaller prefossa and the middle fossa is not isolated from the prefossa by the crista and crochet. They are also larger (Fig. 12) and tend to have a relatively wider posterior lobe (Fig. 13), which, no doubt is because the hypocone is larger. Neither the $P^3$, nor the $P^4$, have a lingual cingulum, which is different in the specimens of the same species from Bilzingsleben. However, there are only two $P^3$ and two $P^4$ belonging to a single individual, which maybe is just a peculiarity of this individual.

The **$M^1$** and **$M^2$** (Pl. 3,2) have a similar morphology, but the $M^2$ tend to be larger on average than the $M^1$ and tend to have a relatively wide first lobe (Fig. 13). The $M^{1-2}$ differ from those of *Coelodonta antiquitatis* (Pl. 26,1) in having: thinner and less rugose enamel, less cementum, lower crowns, not so pronounced metacone styles on the buccal wall, parastyles that are directed more anteriorly and less buccally, ectolophs that are oriented more obliquely to the length of the tooth row, protocones that are placed more anteriorly, deeper lingual valleys, smaller postfossas, prefossas that extend less forward, lesser cristas and crochets that do not fuse and so isolate a middle fossa. On average, the molars of *S. hemitoechus* are larger (Fig. 12).

The **$M^3$** (Pl. 3,2) differs from the anterior molars in having a curved ectometaloph. There is a particularly well developed crochet that is directed towards the protocone. The $M^3$ differs from its homologue in *Coelodonta* (Pl. 26,1), in much the same way as the anterior molars differ, but in addition it is different in having an ectometaloph, whereas the $M^3$ in *Coelodonta* is more similar to the $M^{1/2}$.

A **supernumerary upper molar** (Pl. 3,2) is present on the right side behind the $M^3$. It was about to appear at the age of death of this individual and is not worn. In overall shape it is similar to the $M^3$, but no details of its morphology can be seen.

The **$P_2$** (Pl 3,3) is a small and simple tooth, with a narrow anterior lobe. Both valleys are V-shaped with a sharp line at the bottom. At the occlusal surface, the tooth reaches much further anteriorly than at the base. This is common in *S. hemitoechus* and *Coelodonta*, but not in *S. kirchbergensis* (Van der Made 2000, Pl. 8,1; 2,1 versus Pl.1,2). The specimen is very small and is far outside the ranges for *S. kirchbergensis*, but is also small compared to the $P_2$ of *Coelodonta* (Fig. 14).

The **$P_3$** (Pl. 3,3) are much worn, and not much of their morphology is left. The posterior valley is V-shaped (when seen lingually) and very narrow near the bottom. The specimen is much smaller than the $P_3$ of *S. kirchbergensis*, but is in the ranges for *S. hemitoechus* from other localities (Fig. 14). The anterior lobe is narrow, unlike in most $P_3$ of *Coelodonta*, where the anterior lobes of the cheek teeth tend to be wide. The enamel is more or less thick and rugose.

The **$P_4$** (Pl. 3,3) are only slightly less worn than the $P_3$. The posterior valley is V-shaped and narrow and is directed antero-buccally. At the buccal side, the separation between the trigonid and talonid is marked with a furrow. There is some cementum deposited on the tooth. Metrically, the tooth behaves like the $P_3$: it is too small for *S. kirchbergensis*, but in the ranges for *S. hemitoechus* from other localities and the anterior lobe is narrow (Fig. 14; Tab. 3).

The **$M_1$** (Pl. 3,3) are totally worn off. They are too small for *S. kirchbergensis*, but fit *S. hemitoechus*, and the anterior lobe is narrow, unlike in most *Coelodonta* (Fig. 14).

The **$M_2$** (Pl. 3,3) is much worn. The posterior valley is V-shaped and deep. The anterior wall of the valley is not exactly transverse, but is directed antero-buccally. The enamel is rugose and there is quite some cementum. Metrically the tooth behaves like the previously described lower cheek teeth (Fig. 14).

The **$M_3$** (Pl. 3,3) has a V-shaped and narrow anterior valley. The posterior valley is slightly wider, but is also V-shaped with a very sharp line at the bottom. When seen from above, the lingual side of the talonid in *S. hemitoechus* is straight or bulges even lingually at the place of contact with the trigonid, whereas in *S. kirchbergensis* the lingual side of the talonid is directed slightly buccally before reaching the trigonid. The specimens from Neumark-Nord have the typical morphology of *S. hemitoechus*. The enamel is rugose and partially covered by cementum. The tooth is large, but is still in the ranges for *S. hemitoechus* from other localities (Fig. 14).

The **vertebral column** consists of cervical, thoracic, lumbar, sacral and caudal vertebrae, and is conventionally indicated by C, T, L, S and Ca and a number that indicates their position, e. g. $C_2$ for the axis. The number of vertebrae in a species is more or less constant and is indicated with a formula, for instance $C_7T_{18}L_6S_5Ca_{15-21}$ for the horse. General descriptions of the vertebrae are to be found in common treatises on anatomy (e. g. Koch 1960; Getty 1975; Evans/deLahunta 1980). The nomenclature is indicated in Fig. 16.

Descriptions of the vertebral column of the rhinos of the European Pleistocene, or of any age and provenance, are not common. A treatise as by Guérin (1980) does not describe the vertebrae and the same is the case with many other major papers on fossil rhinos (e. g. Schroeder 1903; Staesche 1941; Loose 1975; Fortelius et. al. 1983). Only the atlas is used for an extensive study of the phylogeny of a group of rhinos (Antoine 2002). Some descriptions are available however. F. Toula (1902) and P. Ambrosetti (1972) described and figured some of the vertebrae of the skeletons of *Stephanorhinus hundsheimensis* from Hundsheim and *Stephanorhinus etruscus* from Capitone. Bernsen (1927) described and figured a number of cervical and thoracic vertebrae (supposed to be $C^1$ to $T^9$) of *Stephanorhinus* from the latest Pliocene of Tegelen. Gorjanovic-Kramberger (1913) figured some vertebrae of *S. kirchbergensis* from Krapina. M. Borsuk-Bialynicka (1973) described the vertebral column of *Coelodonta antiquitatis*, but did not illustrate individual vertebrae. Schroeder (1906) described, but did not figure, the $T_{3-9}$ of *S. kirchbergensis*. A detailed description of the vertebrae of *Stephanorhinus hemitoechus* from Neumark-Nord seems thus worthwhile, even though morphological variation remains unknown.

A total of sixteen cervical, thoracic and lumbar vertebrae of the *Stephanorhinus hemitoechus* skeleton were recovered. Morphology and the articulation of the specimens with each other and with the ribs suggest that, these sixteen vertebrae represent at least four sections of the column, separated by hiatuses. The vertebrae give a fairly good impression of the morphology of the vertebral column of *S. hemitoechus*. The metrical values are indicated in Tab. 4.

The vertebrae and ribs of *S. hemitoechus* from Neumark-Nord and a selection of their morphological features are indicated in Fig. 17. This figure also gives the vertebrae from Neumark-Nord that are assigned to *S. kirchbergensis* and *Coelodonta* (which are described under those species), and the vertebrae from Tegelen and Krapina, which were described and figured by Bernsen (1927) and Gorjanovic-Kramberger (1913) and assigned to *R. mercki* (= *S. kirchbergensis*). The specimens from Tegelen do probably not belong to that species. Together, these vertebrae represent probably all cervical and thoracic vertebrae and thus a complete »synthetic« column can be reconstructed. The different features change along the column at different places in such a way, that apparently each position is characterised by a unique combination of features. Though, the features need not change in the same position in the column in each species (and there are three cases which hint that this indeed was the case), Fig. 17 represents probably a more or less typical vertebral column for *Stephanorhinus*.

Rhinos, like nearly all mammals, have seven *cervical vertebrae*, the first two being the atlas and axis. These vertebrae have very characteristic morphologies, while the following vertebrae are more uniform. The $C_{1-6}$ have large transverse processes, perforated by a transverse foramen. The last cervical vertebra, $C_7$, has a reduced transverse process and articulates posteriorly with the first rib. The cervical vertebrae tend to have small dorsal spines, which increase in length from $C_3$ to $C_7$. The cranial and caudal facets tend to be very convex and concave, respectively, but become more flat in the more caudal vertebrae.

Five cervical vertebrae of this individual were recovered, including the axis and $C_7$, but not the atlas. Three vertebrae have a morphology that corresponds to the $C_{3-6}$, which implies that one of these cervical vertebrae is missing. A morphological cline allows these three vertebrae to be arranged in a sequence. Among other changes, from $C_3$ to $C_6$ the cranial part of the transverse process extends more ventrally and the size of the transverse foramina increases (Tab. 4). A vertebra assigned to *S. kirchbergensis* (Pl. 10,1) fits at the position of the $C_5$ within this morphological sequence of *S. hemitoechus*. Tentatively, the vertebrae of *S. hemitoechus* are assigned to $C_3$, $C_4$ and $C_6$.

The **axis or $C_2$** (Pl. 8,1) is a very typical vertebra. The vertebral body is very small anteriorly, forming a »tooth«. There is a very wide anterior facet that passes below this »tooth«. The specimen from Neumark-Nord is particularly massive compared to the axis of other species. The dorsal spine is wide cranially, and increases gradually in width in caudal direction. In *Stephanorhinus hundsheimensis* this vertebra has a much narrower dorsal spine, which is even much more narrow at its caudal end; anteriorly it is much lower when seen in lateral view. The transverse process barely projects laterally, but extends slightly dorsally (Toula 1902, Pl. 5,2). In *Diceros bicornis* (NNML 5738) the dorsal spine is very narrow, and its caudal end is clearly even narrower than in *S. hundsheimensis*. The vertebral canal is large and the lateral walls of the arch are thin. The transverse processes project significantly, both laterally and dorsally. The tooth is wide and blunt. The ventral crest is well marked. The axis of *S. etruscus* (Ambrosetti 1972, Pl. 3,5.6.9) seems to be very similar to the one of *S. hunsheimensis* in most features, particularly in having a narrow dorsal spine.

The **$C_3$** (Pl. 9,1) has all the characteristics indicated above as typical for $C_{3-6}$. It differs from the following cervical vertebrae in that the caudal part of the transverse process extends more laterally. The cranial part of the transverse process does not extend ventrally below the vertebral body, though it is situated markedly below the caudal part. In lateral view, the lower border of the transverse process is angled; it is more or less horizontal in its cranial part, while distally it curves upwards toward the caudal end, which is situated at about the level of the posterior end of the vertebral body. In *S. hundsheimensis* (Toula 1902, Pl. 5,3) the lower border of the transverse process is almost straight and horizontal, or even lower at the caudal end, which is situated far behind the distal end of the vertebral body. The specimens figured by Bernsen (1927, Pl. 9,2.3) are in a bad state. They appear to have the vertebral canal, and transverse foramina that are relatively large, and the arch is certainly much higher. In *Diceros bicornis* (NMML 5738), the lower border of the transverse process is also angled, but turns markedly ventrally in its caudal part, which is situated well behind the vertebral body.

The **$C_4$** (Pl. 9,2) differs from $C_3$ in the following features. The cranial part of the transverse process has a convex, instead of a concave, lower border, is larger and projects more ventrally and less laterally and cranially. The dorsal spine seems to have a more massive base (it is broken off just above the base). No clear differences with *S. hundsheimensis* (Toula 1902, Pl. 5,4) can be seen. Again the specimen from Tegelen (Bernsen 1927, Pl. 9,4) has a relatively large vertebral canal. In *D. bicornis* (NNML 5738) the caudal part of the transverse process is more pronounced and extends more laterally and the lower border of the cranial part is straight. In addition, the cranial part has a second anterior process closer to the vertebral body (which is even more pronounced in $C_5$). In cranial view, the anterior articulation is squarer, particularly in the dorsal part.

The **$C_6$** (Pl. 10,2) has the same general shape as $C_{3-4}$, but is higher and its processes are directed less in cranio-caudal direction. The dorsal spine is directed vertically and is markedly longer than in the $C_3$. It ends in a point and not in a thickened »head«. The transverse process has a very extensive cranial part, that mostly is directed ventrally, but which extends at two places cranially beyond the vertebral body and at one place caudally. The anterior articulation is narrower than the posterior one, but becomes relatively wider from $C_3$ to $C_6$. There are no very striking differences with *S. hundsheimensis* (Toula 1902, Fig. 23). In *S. etruscus* (Ambrosetti 1972, Pl. 3,3.4) the transverse foramina are placed entirely dorsal of the middle of the main distal facet, instead of at the same level, the caudal part of the transverse process projects clearly more caudally than the main posterior facet, also the caudal articular process projects much caudally, and the dorsal spine is longer. In Tegelen (Bernsen 1927, Pl. 9,6) the vertebral canal seems to be larger, and the vertebral arch is much thicker in its dorsal part. In *D. bicornis* (NNML 5738) the lower anterior process of the cranial part of the transverse process is rounded and the caudal part extends more distally and more laterally.

The **$C_7$** (Pl. 11,1) is the last cervical vertebra and has a shape that clearly differs from the preceding vertebrae. It has well developed caudal costal facets (one on each side, right and left), which articulate with the anterior facets of the heads of the first ribs. The transverse processes are very small and are not perforated by a transverse foramen. The dorsal spine is much longer than in $C_6$ and its antero-posterior diameter is also much longer. The anterior facet is wider than in the preceding vertebrae. In *Stephanorhinus hundsheimensis* the transverse processes extend more ventrally (Toula 1902, Pl. 5,5). In the specimen from Tegelen (Bernsen 1927, Pl. 9,7), the cranial and caudal articular processes are oriented much more upward and the transverse process originates more dorsally and is not directed ventrally. The vertebral canal is large and, in particular, high. In *S. etruscus* (Ambrosetti 1972, Pl. 3,1.2), the posterior costal facets are placed slightly more dorsally and the dorsal spine may have been longer.

The **thoracic vertebrae** articulate with the ribs and tend to have three facets each: the anterior and posterior costal facets, which articulate with the head of the ribs, and the lateral costal facet, which articulates with the tubercle of the ribs. The last thoracic vertebra does not have a posterior costal facet, which may also be badly developed in other posterior thoracic vertebrae. Toula (1902), Ambrosetti (1972) and Borsuk-Bialynicka (1973) indicated eighteen thoracic vertebrae for *Stephanorhinus etruscus*, nineteen for *Stephanorhinus hundsheimensis*, eighteen for *Coelodonta antiquitatis*, eighteen for *Rhinoceros sondaicus*, nineteen for *Diceros bicornis*, and eighteen for *Ceratotherium simum. S. hemitoechus* may thus be expected to have eighteen or nineteen thoracic vertebrae. As we shall see with the description of the lumbar vertebrae, *S. etruscus* and *Coelodonta* have four lumbar vertebrae, and it seems that the sum of lumbar and thoracic vertebrae in a species is more constant than the number of each type. The lumbar vertebrae may hold the key for knowing how many thoracic vertebrae are present in *S. hemitoechus* (see below) and it seems that eighteen might be a likely number.

The posterior thoracic vertebrae and first lumbar vertebra were found in a row oriented towards the skull and the anterior thoracic vertebrae were found more dispersed, but closer to the skull (Mania 1990, Fig. 19). This and the smooth morphological and metrical gradient in these vertebrae and the fact that they articulate reasonably well, suggest that these posterior thoracic vertebrae represent a continuous series, $T_{13}$ to $T_{18}$, or alternatively $T_{14-19}$, depending on the number of thoracic vertebrae in this species or individual. The anterior thoracic vertebrae have not been found in a series that suggests their position, but they have a more variable morphology that facilitates their assignation to a certain position.

Certain features appear to be constant in all thoracic vertebrae, or also even in the cervical and lumbar vertebrae. Such features include the width of the anterior articular facet, and the length of the body. Others clearly separate anterior and posterior thoracic vertebrae, such as the length of the dorsal spine and the width at the facets on the cranial articular processes (Fig. 17; 18). They differ from the posterior thoracic vertebrae in having much longer dorsal spines.

The **$T_1$** (Pl. 11,2) differs from the following thoracic vertebrae represented in the collection in: 1) having the anterior costal facet in a very low position and facing ventrally, 2) the lateral costal facet facing ventrally and not ventro-laterally or laterally, 3) the transverse process projecting most at the level of the middle of the vertebral body and not above the vertebral canal, 4) the facets on the cranial articular process being inclined medially and not anteriorly, 5) the caudal costal facets being positioned ventrally of the middle of the vertebral body and not dorsally, 6) the dorsal spine being more slender and not having such a wide posterior surface, 7) the dorsal spine decreasing gradually in antero-posterior diameter and ending in just a small »head«, and 8) in having a relatively high vertebral canal. Moreover it differs from the vertebrae immediately following it in having the greatest width of the cranial and caudal articular facets (with the anterior and posterior vertebrae) having its greatest width in its dorsal half. This vertebra articulates posteriorly with, what is interpreted as, the second rib.

The vertebrae that are assumed to be the **$T_7$** (Pl. 12,1) and **$T_8$** (Pl. 12,2) are very similar. They have the upper borders of the anterior and posterior costal facets more or less level with the upper borders of the main articular facets of the vertebral body and have the transverse process reaching its maximum lateral extension at the level of the upper border or the vertebral canal. Metrically the $T_7$ differs from the $T_8$ in having a greater width at the facets on the cranial articular processes and in having a longer dorsal spine (though it is not fully grown in either of the specimens). Both specimens have facets on the cranial and caudal articular processes that dip forwards and maybe a little laterally. In this they differ from the vertebrae that are believed to be $T_3$ and $T_5$ of *S. kirchbergensis*, which have these facets dipping medially like in the $T_1$ and the cervical vertebrae. If both species are similar in this respect, there has to be a $T_6$ with the cranial facets dipping medially and with the caudal facets not dipping medially. Such a morphology is not present here and therefore the two vertebrae are believed to be posterior to the $T_6$. Morphologically the specimens resemble a vertebra which Gorjanovic-Kramberger (1913, Pl. 7,6) believed to be either $T_8$ or $T_9$, and which probably is a $T_8$. Vertebrae from Tegelen believed to be $T_{5-9}$ by Bernsen (1927), more probably are $T_{7-11}$ because they lack morphologies that are typical of the more cranial vertebrae and because they have morphologies that unite them with the more caudal vertebrae (Fig. 17). The $T_7$ articulates well with its anterior and lateral costal facets with, what should thus be, $R_7$ and both vertebrae articulate with a pair of ribs that should thus be $R_8$. In *S. hundsheimensis*, there is a break in morphology after the eighth rib (Toula, 1902; see description ribs). The lower tubercle in the ribs after $R_8$, is expected to be reflected in a different position or orientation of the lateral costal facet in the vertebrae after $T_8$, and indeed the lateral costal facet changes orientation and faces laterally, corroborating the position of vertebrae and ribs as interpreted here.

The remaining thoracic vertebrae from Neumark-Nord differ from the ones (immediately) preceding them in that: 1) the vertebral spine is much shorter and varies more along its length in its antero-posterior diameter, 2) the main cranial and caudal facets are widest in their dorsal half and not

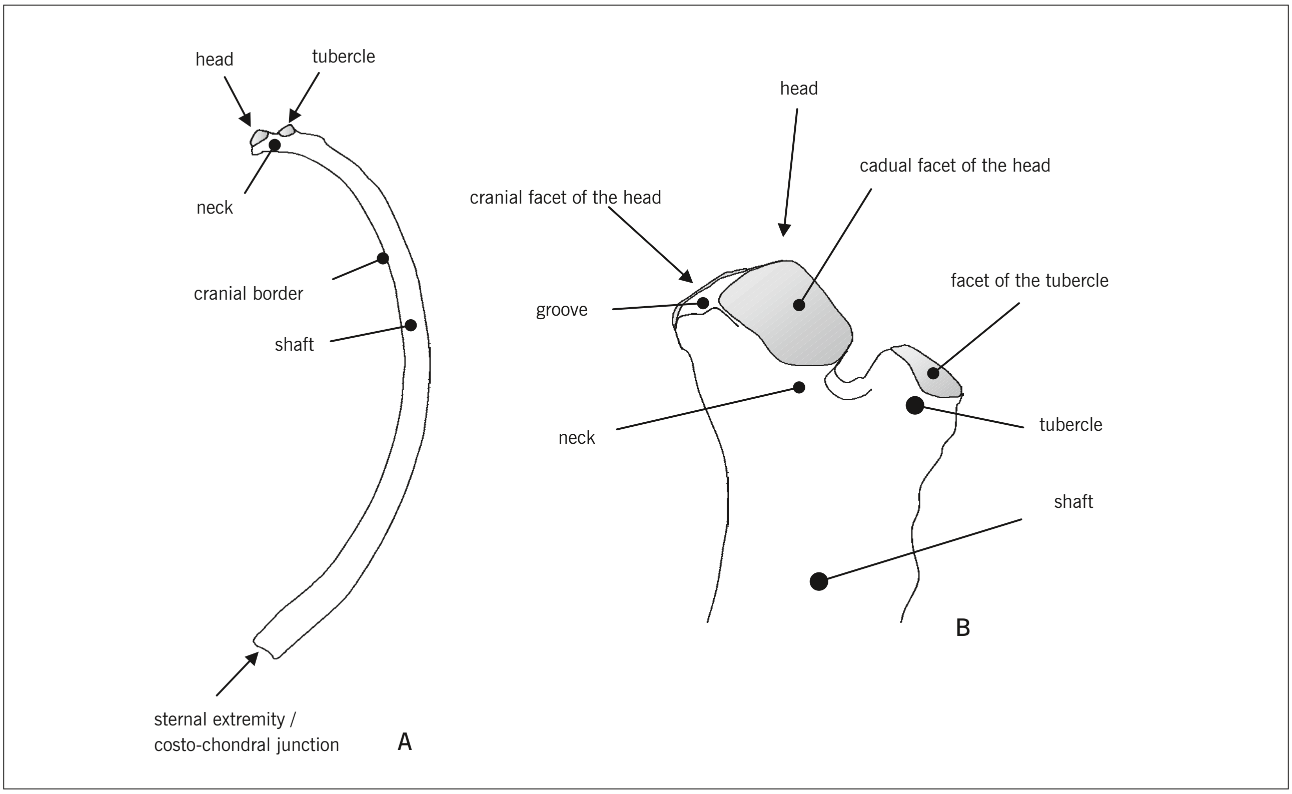

**Fig. 21** Nomenclature of the ribs, largely after Koch (1960), Getty (1975) and Evans/deLahunta (1980).

in their ventral half, 3) the anterior and posterior costal facets are placed largely dorsally of the main articular surfaces of the vertebral body and not at the level of the dorsal halves of these facets, 4) the mammillary process is directed more upward, 5) the lateral costal facets facing laterally instead of latero-ventrally.

The **$T_{13}$** (Pl. 14,1) (or $T_{14}$ if the total number of thoracic vertebrae is nineteen, instead of eighteen) is very similar to the next vertebra and differs mainly in its longer dorsal spine, which, however, is considerably shorter than in the more cranial thoracic vertebrae that are preserved.

The **$T_{14}$** (Pl. 14,2), **$T_{15}$** (Pl. 15,1) and **$T_{16}$** (Pl. 15,2) are similar, but differ in minor details. The facets on the cranial articular processes expand dorsally over the base of the dorsal spine in $T_{15}$ and do so even more on the following vertebrae. This is also reflected in the corresponding caudal facets. The lateral costal facets are more or less as long as high, but in the $T_{16}$, there is a small anterior extension of the facet. In the next two thoracic vertebrae this is still more pronounced and the lateral costal facet is a very elongate facet.

The **$T_{17}$** (Pl. 16,2) has very small anterior and posterior costal facets and in $T_{18}$ (Pl. 17,2) the anterior costal facet is barely visible, while the posterior one is entirely missing. These two vertebrae have posterior main articular facets that are clearly wider than in the previous vertebrae, but narrower than in the lumbar vertebrae.

The **lumbar vertebrae** do not bear ribs. There are two specimens which appear to articulate with each other and with the last thoracic vertebra. Toula (1902), Ambrosetti (1972) and Borsuk-Bialynicka (1973) indicated three lumbar vertebrae for *Stephanorhinus hundsheimensis* and four for *S. etruscus* and *Coelodonta antiquitatis*. Possibly, the total of thoracic and lumbar vertebrae is more constant than the number of each category, so that if we assume eighteen thoracic vertebrae, we also have to assume four lumbar vertebrae. Because the two lumbar vertebrae were found together with a series of posterior thoracic vertebrae, they most probably represent the first two lumbar vertebrae.

The **$L_1$** (Pl. 16,1) has very wide transverse processes, but they are much narrower than in the following vertebra. The facets of the cranial articular processes extend more in antero-posterior direction than in the thoracic vertebrae. The same is observed in the facets of the caudal articular processes. The specimen is asymmetrical in that its right transverse process is directed more anteriorly. In *S. etruscus* the dorsal spine of this vertebra and the next one, is longer (Ambrosetti 1972, Pl. 3,11).

The **$L_2$** (Pl. 17,1) has a still wider posterior main facet and wider transverse processes. It differs from the last lumbar vertebra, which has wide articular surfaces for the wing of the sacrum on the posterior side of the transverse processes. The $L_4$ of *S. etruscus* (Ambrosetti 1972, Fig. 2) has a vertically directed dorsal spine that has a very short cranio-caudal diameter. The $L_3$ of that species has also a vertically directed dorsal spine, but with greater cranio-caudal diameter. The $L_2$ of *S. etruscus* has a slightly caudally directed dorsal spine, like the second lumbar vertebra from Neumark-Nord. If *S. hemitoechus* would have three lumbar and nineteen thoracic vertebrae (instead of four and eighteen respectively), the morphology of the dorsal spine might be expected to be more similar to the $L_3$ of *S. etruscus*.

There are **ribs** of different types: true or sternal ribs, which are connected by cartilage to the sternum, and false or asternal ribs, which do not articulate with the sternum, instead most of these are connected to the costal arch which consists of cartilage, while the ends of the posteriormost

**Tab. 9** Measurements of the ribs of *Stephanorhinus hemitoechus* from Neumark-Nord.

| Rx | | | DAPh | DAPn | DTn | DAPft | DTft | DHF | L | DAPsma | DAPsmi | DTsma | DTsmi |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | HK88: 14, 5 | r | 40.8 | 30.4 | 22.2 | 28.5 | 15.5 | 13.8 | 690 | 52.2 | 34 | 40.2 | 17.1 |
| 7 | HK88: 14, 8 | r | 41.6 | 38.6 | 21.3 | | | 8 | 760 | 49.7 | 46.4 | 38.4 | 20.5 |
| 8 | HK88: 14, 13 | l | | | | | | | | | | | |
| 8 | HK88:14, 16+47 | r | 40.7 | 38.6 | 21.3 | 27.5 | 19.3 | 7.3 | 840 | 64.2 | 44.7 | 41.8 | 19.6 |
| 9-10 | HK88: 14, 14 | r | | 27.2 | 20.6 | 24.4 | 16.1 | 20 | 880 | 53.8 | 34.9 | 25.4 | 21.5 |
| 10-11 | HK88: 14, 11 | l | 42.3 | 24.6 | 20.1 | 25.3 | 15.8 | 18 | 960 | 46.6 | 33.7 | 33.7 | 22.2 |
| 10-11 | HK88: 14, 15 | r | 42.4 | 25.7 | 26.8 | 24.9 | 17.7 | 20.1 | 950 | 48.9 | 32.9 | 33.9 | 21.7 |
| 11-12 | HK88: 14, 8 | l | 40.3 | | 17.7 | 23.2 | 16.3 | | 980 | 42.3 | | 32.1 | 17.7 |
| 11-12 | HK88: 14, 7 | r | | | | | | | | | | | |
| 13 | HK88: 14, 6 | l | 35.4 | 27.2 | 17.9 | 23.2 | 15.8 | 15.2 | 980 | 44.3 | 31.2 | 31.9 | 19.6 |
| 13 | HK88: 14, 10 | r | 38.2 | 28 | 17.5 | 21.3 | 14.7 | 22.2 | >880 | >43.5 | 32.8 | 25.8 | 22.4 |
| 14 | HK88: 14, -- | l | | | | | | | | 42.8 | 28.8 | 18.7 | 16.8 |
| 15 | HK88: 14, 9 | l | 33.1 | 24.9 | 13.7 | 22.8 | 17.2 | 11.4 | 900 | 37.6 | 21.9 | 25.4 | 16 |
| 16-18 | HK88: 14, 12 | r | | | | | | | | 35.2 | 18 | 20.8 | 14.5 |

ribs are unattached at their distal ends and are called floating ribs (Fig. 21). Since the differences between these types are in the costal cartilage, which is not present in the fossils, there are no features that serve directly to recognise to which type of rib the fossils belong. The presence of eighteen–nineteen thoracic vertebrae indicates the presence of eighteen–nineteen pairs of ribs in different species of living rhinos, *Coelodonta* and *Stephanorhinus*. In analogy to the numbering of the thoracic vertebrae ($T_1$–$T_{18}$), the corresponding ribs are here indicated as $R_1$ to $R_{18}$ (or $R_{19}$, if there are nineteen pairs of ribs).

Eight right and six left ribs of the skeleton were recovered (Pl. 18; Tab. 9). By fitting these ribs to the vertebrae and by using morphologic and metric trends the ribs were arranged in a series and were tentatively related to the vertebrae and thus to a position. In this sequence metrical values either tend to increase distally towards a maximum before then decreasing again, or fluctuate and peak more than once. The ribs resemble a spiral with a small radius of curvature near the head and a much larger radius in the distal part. The more caudal the position of the rib, the larger radius of curvature near the head and the less the increase in radius in the distal part of the rib. This is not a tendency that peaks in a particular rib in the sequence, but seems to simply increase caudally. There is not much literature on the ribs of *Stephanorhinus* or any other rhino of this group. However, R. Getty (1975) indicated that in the horse, with a comparable number of ribs (eighteen pairs), the first and last one have different morphologies, that the length of the ribs reaches a maximum in the tenth and eleventh rib and that the width peaks in the sixth rib.

The **$R_1$** is the shortest and most massive rib and its width increases towards the sternal extremity. The $R_1$ in *Stephanorhinus hundsheimensis* has been figured by Toula (1902, Pl. 5,6.7). Such morphology is not present among the ribs from Neumark-Nord.

What might be the **$R_2$** (Pl. 18,8.16) is the smallest one of a group of relatively massive ribs with elevated tubercles and it is the least curved of them. In this latter respect it resembles the first rib. It has a cranial facet that articulates fairly well with the caudal facet for the rib on $T_1$, but does not articulate so well with the next vertebra that is preserved ($T_5$).

What is interpreted as the **$R_7$** (Pl. 18,7) is similar to the second rib, but is a little longer, wider and more curved. The facet that articulates with the lateral costal facet on the vertebra is placed on a high tubercle. This rib articulates with vertebra $T_7$, but not with $T_8$. Toula (1902, Pl. 5,8) figured a fifth rib, that is morphologically more or less similar to this specimen.

There are two specimens that are interpreted to be **$R_8$** (Pl. 18, 6.9). In one the proximal part is broken off, but what remains is symmetrical to the other rib. They are a little more massive and longer than the previous rib. The one that preserves the head articulates well with vertebrae $T_{7–8}$. The tubercle is only a little lower than in the $R_7$.

Toula (1902) indicated that in *S. hundsheimensis* from Hundsheim, $R_{1–8}$ have similar morphologies in head, neck and tubercle, but that in the more caudal specimens ($R_{9–19}$), the neck becomes longer, and thus the distance between head and tubercle as well. The following specimens from Neumark-Nord have clearly lower tubercles and longer distances between the head and facet of the tubercle.

A rib that is probably the **$R_{9–10}$** (Pl. 18,5) is a little bit longer and more curved than the previous ribs. Its head is broken. The tuber is clearly lower than in the previous specimens and resembles that of all following ribs. As a result of the tuber being lower, the facet of the tuber, which articulates with the lateral costal facet on the vertebra, is placed further away from the head (value DHF in Tab. 9).

There are two ribs of equal morphology (Pl. 18,4.10), which should be **$R_{10-11}$**. Morphologically they follow the previously described rib in being longer, more curved and with a lower tubercle. The vertebrae with which they should articulate are not preserved. The left rib has been broken, but grew together again. Broken ribs and traumatic skull damage does not seem to be rare in rhinos and results from fights between them (Garutt 1997).

Two **$R_{11-12}$** (Pl. 18,3.11) follow the previously described ribs morphologically and metrically and are longer, more curved and more slender (a trend starting with the fourth rib, which is the widest one). The length is identical to that of $R_{13}$, and other values are also close, suggesting that the position is rather posterior and possibly it is twelve. The morphology of the head and tubercle is very similar to a proximal eleventh rib of *S. hunsheimensis* from Hundsheim, figured by Toula (1902, Pl. 5,9), but then this morphology does not seem to change much in this range of the series. However, the specimen figured by Toula, differs from all vertebrae from Neumark-Nord in this approximate position in its cranial border being angled below the tubercle and rather straight in shaft. In the specimens from Neumark-Nord, there is not such a clear angle, and the cranial border is more evenly curved.

What is interpreted as the **$R_{13}$** (Pl. 18, 2.13.16) is represented by two specimens that follow the previous ribs in the morphological and metrical tendencies. Both articulate well with vertebra $T_{13}$. Whereas in horses the length of the ribs reaches its maximum in the $R_{10}$ and $R_{11}$ (Getty 1975), this seems to be a little more posteriorly in this individual of a rhino.

What is interpreted as the **$R_{14}$** (Pl. 18,13) is represented by a fragment of a shaft that is intermediate in diameter between the previous and following ribs.

What is interpreted as the **$R_{15}$** (Pl. 18,14) is shorter, thinner and more gracile than the previous ribs and articulates with vertebra $T_{16}$ (HK 88:14, 27) and seems to articulate with $T_{17}$, which is in a bad state.

A fragment of a still smaller rib (Pl. 18,1), should represent **$R_{16/17/18}$**. Toula (1902, Pl. 5,10.11) figured the eighteenth and nineteenth ribs of *S. hunsheimensis* from Hundsheim. These specimens seem to diverge from the more cranial ribs in their proximal morphology. The specimen from Neumark-Nord lacks the area of head and tubercle, but the curvature of the proximal part is such that the specimen seems to differ in a similar way as the eleventh ribs differ from the specimens from Hundsheim.

The **scapula** (Pl. 19,2; Tab. 5) has an oval glenoid cavity, without a glenoid notch. It is slightly elongate (Antoine 2002, 185). In *Coelodonta* the scapula is approximately as elongate, and in *Diceros bicornis* and *Ceratotherium simum* is more elongate. The posterior and proximal borders make an acute angle that projects posteriorly. The tuber of the spine is larger than in the living African rhinos and the woolly rhino, but less than in *Rhinoceros* (Walker 1985, 13; Borsuk-Bialynicka 1973, Pl. 8; 9). In overall shape, the scapula is like in *S. hundsheimensis*, maybe slightly more elongate (Toula 1902, Pl. 6,1). The specimen is larger than in *S. kirchbergensis* and *Coelodonta* and much larger than in *S. hemitoechus* from Bilzingsleben (Fig. 19).

The **humerus** (Pl. 19,1; Tab. 6) of the skeleton HK 88:14 is very massive. There is a second humerus, that is very similar, and which probably belongs to the same species. Both humeri differ from two other humeri that are assigned to *S. kirchbergensis* (see description under that species).

From above the greater tubercle can be seen to have both the posterior and the anterior parts well developed. In anterior view, the anterior part of the greater tubercle is not very high. A second tubercle, which is interpreted here as the lesser tubercle, is clearly higher. Between the two tubercles, there is a deep intertuberal groove (best seen in proximal view). In the living African rhinos, there is an intermediate tubercle (Walker 1985, 48; Guérin 1980, Fig. 10), but it is lacking here, as well as in the other Pleistocene species of *Stephanorhinus* (Fortelius et. al. 1993, Pl. 2) and *Coelodonta* (Borsuk-Bialynicka 1973, Pl. 10,2).

The deltoid tuberosity is very well developed and the bone here is very wide. Its lower border forms a point that is directed latero-distally. This tuberosity is not so well developed in the other Pleistocene species of *Stephanorhinus* (Fortelius et. al. 1993, Pl. 2), but is well developed in the African rhinos (Walker 1985, 48) and in *Coelodonta* (Borsuk-Bialynicka 1973, Pl. 10,2; 11,4).

The distal articular surface is cylindrical with a groove in the middle. The lateral side of this articular surface reaches much more distally than the medial side. As a result, the axis of the articular surface and the long axis of the bone make a sharp angle. In *S. kirchbergensis* from Bilzingsleben the medial and lateral parts of the facet extend as much distally and the angle is closer to 90 degrees. In other species of Pleistocene *Stephanorhinus*, the medial part does not extend so far distally (Fortelius et. al. 1993, Pl. 2), but the humeri in *Coelodonta* and the living African rhinos resemble the specimen from Neumark-Nord in this respect (Borsuk-Bialynicka 1973, Pl. 10,2; 11,4; Walker 1985, 59). This different angle in *S. hemitoechus* and *Coelodonta* suggests that in an articulated limb the long axis of the radius and humerus are not parallel, but form an angle. If this indeed was the case, the legs of the different species transferred in different ways the forces imposed by the weight of the animals.

The lateral epicondyle is not very strongly developed; this is noted in a small difference between the DTd and DTdf values. This condition is similar in the other Pleistocene species of *Stephanorhinus* and *Coelodonta* (Fortelius et. al. 1993, Pl. 2; Borsuk-Bialynicka 1973, Pl. 10,2; 11,4), while in the living African rhinos the lateral epicondyle is much more developed (Walker 1985, 59). These rhinos tend to have a much wider olecranon fossa.

Stephanorhinis *hemitoechus* and *S. kirchbergensis* from Bilzingsleben are metrically well separated. However, the two specimens from Neumark-Nord that are assigned *S. hemitoechus* are in the ranges of *S. kirchbergensis* from Bilzingsleben (Fig. 20).

The **ulna** (Pl. 20,1) has a marked angle between the olecranon and the shaft. The articular facet for the humerus is not as wide as in the living African rhinos (Walker 1985, 127). It is longer (515 mm) than a specimen of *S. hemitoechus* from

**Tab. 10** Measurements of the ulna of the rhinos from Neumark-Nord.

| | *Stephanorhinus hemitoechus* | | *Coelodonta antiquitatis* |
|---|---|---|---|
| | HK88:14, right | 1996, 45 left | 95, 3 right |
| DAPh | 115.0 | <112 | |
| DTh | 83.4 | ~74 | |
| DAPn | 101.6 | 92.4 | |
| DTn | 35.6 | <37.9 | |
| DAPm | 131.6 | 128.4 | |
| DTm | | 88.4 | >76.6 |
| DAPf | 85.7 | 91.3 | ~73 |
| L | 515 | | |
| Lu | 171.7 | 155.5 | |
| DAPd | 71.5 | | |
| DTd | 44.2 | | |

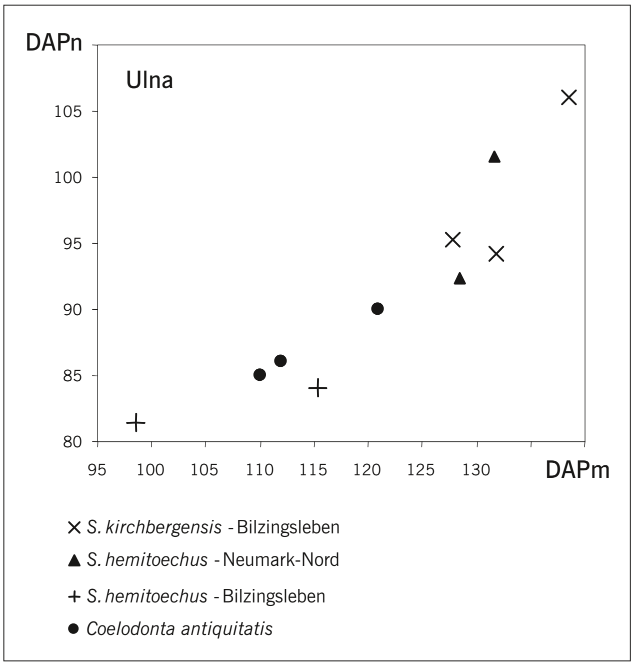

**Fig. 22** Bivariate diagram of the ulna. *Stephanorhinus hemitoechus* from Neumark-Nord (LVH) and Bilzingsleben (FBFSUJB), *Stephanorhinus kirchbergensis* from Bilzingsleben (FBFSUJB) and *Coelodonta antiquitatis* (data from Borsuk-Bialynicka 1973).

**Tab. 11** Measurements of the radius of the rhinos from Neumark-Nord.

| | HK88: 14, 17 Right | E I right |
|---|---|---|
| DAPp | 86.2 | 72.5 |
| DAPpf | 75.8 | 65.5 |
| DTp | 114.0 | 109.1 |
| DTpf | 103.7 | 107.8 |
| L | >402 | 361.6 |
| l | 360 | 324.4 |
| DAPd | 69.1 | >71 |
| DAPdf | 50.5 | 55.2 |
| DTd | 95.6 | 107.4 |
| DTdf | 84.4 | 97.9 |

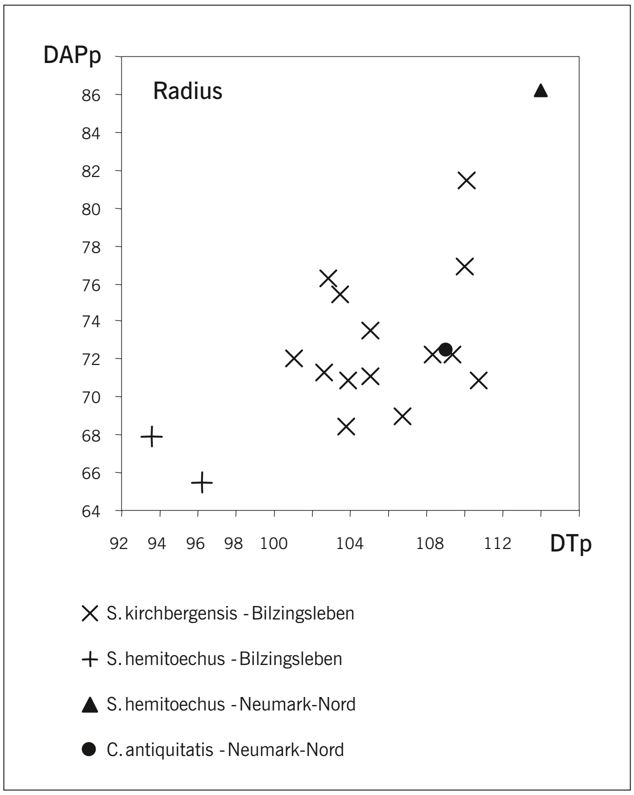

**Fig. 23** Bivariate diagram of the radius: DAPp (antero-posterior diameter of the proximal part) versus DTp (= transverse diameter of the proximal part). *Stephanorhinus kirchbergensis* and *S. hemitoechus* from Bilzingsleben (FBFSUJB) and *S. hemitoechus* and *Coelodonta antiquitatis* from Neumark-Nord.

Bilzingsleben (471 mm). It is interesting to note that the length of the olecranon (Lu = 171.7; Tab. 10) is considerably greater than in any of the *S. kirchbergensis* (142.3, 165.6, 169.6) and *S. hemitoechus* (≥122) from Bilzingsleben. The triceps brachii muscle inserts at the head of the olecranon and extends to the elbow joint. A relatively long olecranon augments the momentum of this muscle, but the muscle has to contract more to cause the same degree of extension, resulting in a more powerful, but slower action. Long olecraneii are common in relatively slow animals such as suids and powerful digging animals. There is another ulna, of about the same size. Both are in the metrical ranges of *S. kirchber-*

**Tab. 12** Measurements of the scaphoid, navicular, third cuneiform and patella of *Stephanorhinus hemitoechus* from Neumark-Nord.

| | | | DAP | DT | H | DTf | Hf |
|---|---|---|---|---|---|---|---|
| scaphoid | HK88: 14, 23 | d | 92.5 | 60.5 | 67.2 | | |
| navicular | HK88: 14, 50 | s | 71.9 | 53.9 | | | |
| navicular | HK88: 14, 51 | d | 68.4 | 59.3 | | | |
| cuneiform III | HK88: 14, -- | d | 56.6 | 51.5 | | | |
| patella | HK88: 14, 53 | | 72.9 | 103.9 | 97.7 | 87.4 | 80.2 |

*gensis* and larger than *S. hemitoechus* from Bilzingsleben and *Coelodonta* (Fig. 22). This second ulna might belong to either *S. hemitoechus* or *S. kirchbergensis*.

The **radius** (Pl. 20,2; Tab. 11) is again a massive bone. Its DAP and DT values are much greater than in *S. hemitoechus* from Bilzingsleben, and even *S. kirchbergensis* (Fig. 23), but its length is closer to that in the former species, whereas it is inferior to the length in the latter. Also *Coelodonta* has a robust, but smaller radius (Borsuk-Bialynicka 1973, Tab. 41). The anterior border of the proximal facet is not straight but curves inward in the middle (»M-shaped« sensu Antoine 2002, 190).

The **scaphoid** (Pl. 22,5; Tab. 12) is a large bone comparable in size to the scaphoid in *Stephanorhinus kirchbergensis* from Bilzingsleben. The facet for the trapezium (the third and posterior facet at the distal side) is relatively large. No postero-proximal facet for the semilunar is observed. This is peculiar, since P. O. Antoine (2002, 195) indicated such a facet for *Ceratotherium*, *Diceros*, *Rhinoceros* and *Coelodonta* and indicated that the presence is a primitive trait. In *S. kirchbergensis* from Bilzingsleben, this facet is also lacking. The facet for the magnum is concave, as is normal in all these rhinos.

The **femur** (Pl. 21,1; Tab. 13) is a very large bone. The greater trochanter is not well developed and is lower than the head, as is the case in *Stephanorhinus*, *Coelodonta*, *Ceratotherium* and *Diceros*, but less so in *Rhinoceros*. The lesser and third trochanters are well developed.

**Tab. 13** Measurements of the femur of *Stephanorhinus hemitoechus* from Neumark-Nord.

| | HK88: 14, 18 Right |
|---|---|
| DAPpf | 95.3 |
| DTp | 211.5 |
| L | 503 |
| DAPd | 181.9 |
| DTd | 150.9 |
| DTdf | 126.0 |

The bone, and the shaft in particular, is massive as in *Ceratotherium*, *Diceros* and *Coelodonta*, but unlike in *Rhinoceros* and *Stephanorhinus etruscus*, *S. hundsheimensis* and *S. kirchbergensis* (Walker 1985, 71; Borsuk-Bialynicka 1973, Pl. 21; Fortelius et. al. 1993; material from Bilzingsleben). The shaft is straight, as is the case in other species of *Stephanorhinus* and in *Coelodonta* and the living African rhinos, but unlike in *Rhinoceros* where it is curved in the vertical antero-posterior and transverse planes, where the head projects medially beyond the medial epicondyle.

In distal view, the medial ridge of the trochlea is much elevated, but the lateral ridge is nearly not elevated. This is also the case in *S. etruscus*, *S. hundsheimensis*, *S. kirchbergensis* and *Rhinoceros sondaicus*, but in *Ceratotherium* and *Diceros* the lateral ridge is more elevated (Fortelius et. al. 1993; Walker 1985, 84). The inter-condyloid fossa is very narow compared to most rhinos of this group.

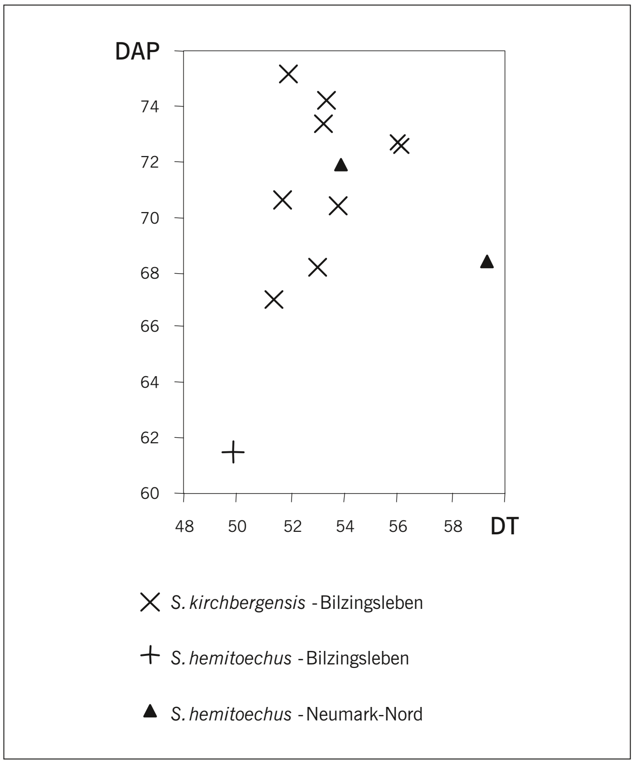

**Fig. 24** Bivariate diagram of the navicular. *Stephanorhinus hemitoechus* from Neumark-Nord (LVH) and Bilzingsleben (FBFSUJB) and *Stephanorhinus kirchbergensis* from Bilzingsleben (FBFSUJB).

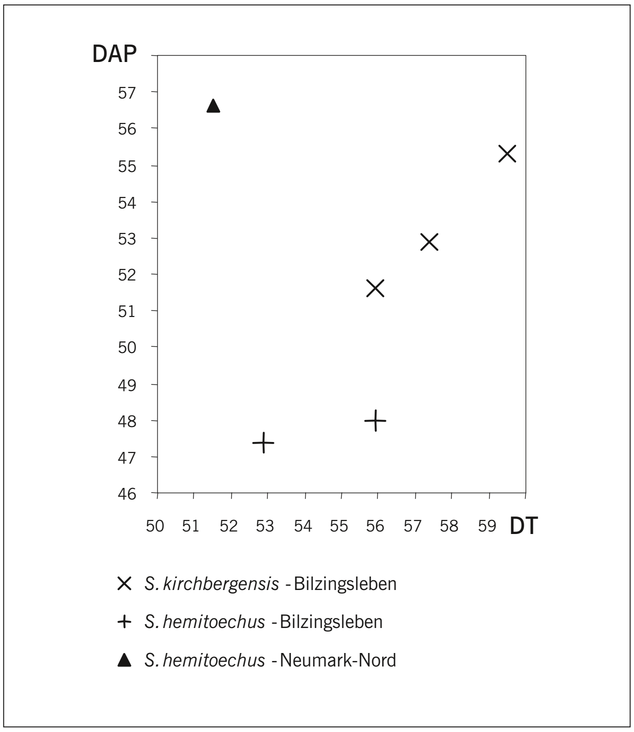

**Fig. 25** Bivariate diagram of the third cuneiform. *Stephanorhinus hemitoechus* from Neumark-Nord (LVH) and Bilzingsleben (FBFSUJB) and *Stephanorhinus kirchbergensis* from Bilzingsleben (FBFSUJB).

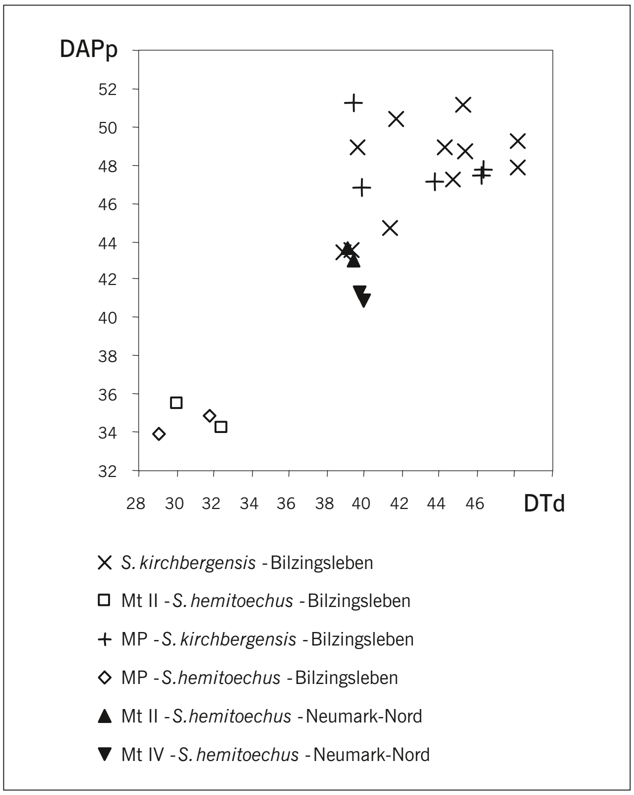

**Fig. 26** Bivariate diagrams of the distal articular surfaces of the lateral metapodials. Mc II, Mc IV, Mt II and Mt IV of *Stephanorhinus kirchbergensis* and Mt II of *S. hemitoechus* from Bilzingsleben (FBFSUJB), lateral MP of unknown exact position of *S. kirchbergensis* and *S. hemitoechus* from Bilzingsleben (FBFSUJB) and Mt II and Mt IV of *S. hemitoechus* from Neumark-Nord (LVH).

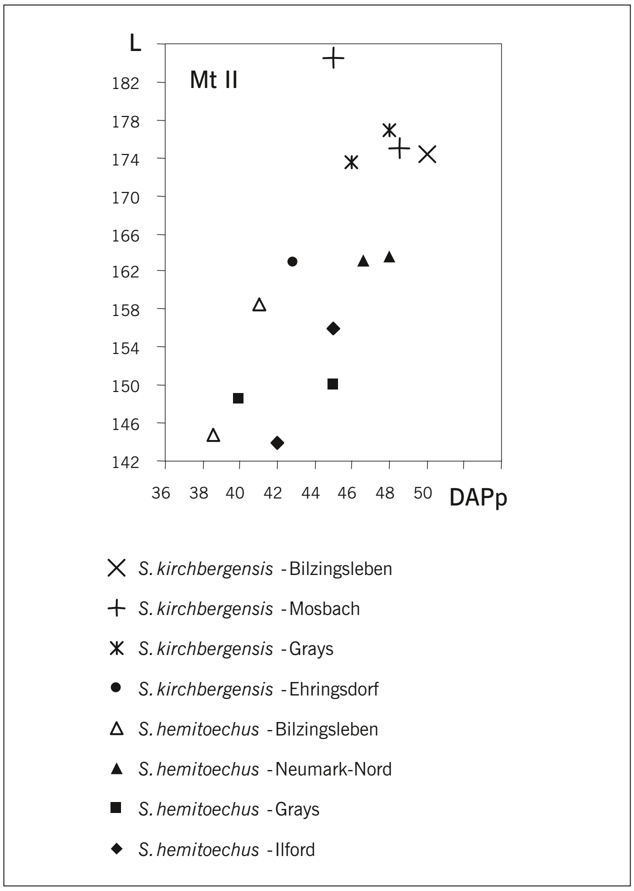

**Fig. 27** Bivariate diagram of the second metatarsal. *Stephanorhinus hemitoechus* from Neumark-Nord (LVH), Bilzingsleben (FBFSUJB), Grays (Fortelius et. al. 1993) and Ilford (Fortelius et. al. 1993) and *Stephanorhinus kirchbergensis* from Bilzingsleben (FBFSUJB), Ehringsdorf (IQW), Mosbach (Fortelius et. al. 1993) and Grays (Fortelius et. al. 1993). Two specimens from Mosbach that are listed by Fortelius et. al. (1993) are believed to be *S. hundsheimensis*.

Most of the femurs of the two species of rhinos from Bilzingsleben are broken and too few measurements can be taken for a useful metrical comparison.

The **patella** (Pl. 21,2; Tab. 12) is not a bone that is frequently described in great detail. A specimen of *S. hundsheimensis* from Hundsheim figured by Toula (1902, Pl. 10,3) seems to be flatter (with a smaller DAP) than the one from Neumark-Nord.

The **navicular** (Pl. 22,3; Tab. 12) is comparable in size to *S. kirchbergensis* from Bilzingsleben, and is clearly larger than *S. hemitoechus* from that locality (Fig. 24).

The **third cuneiform** (Pl. 22,2; Tab. 12) has the posterolateral process poorly developed, which is normal in the living rhinos and *Coelodonta* (Antoine 2002, 226). It has a long DAP as in *S. kirchbergensis* from Bilzingsleben, but is relatively narrow, also compared to *S. hemitoechus* from Bilzingsleben (Fig. 25).

The **second metatarsal** (Pl. 22,1; Tab. 7) has DAP and DT values that are much larger than in *S. hemitoechus* from Bilzingsleben but are comparable to those in *S. kirchbergensis* from Bilzingsleben (see Fig. 26 for the DAPd and DTd). The bone is shorter than in *S. kirchbergensis* and tends to be robust, like in *S. hemitoechus* from other localities that are of the same age or younger, while in Bilzingsleben the bone tends to be more slender (Fig. 27).

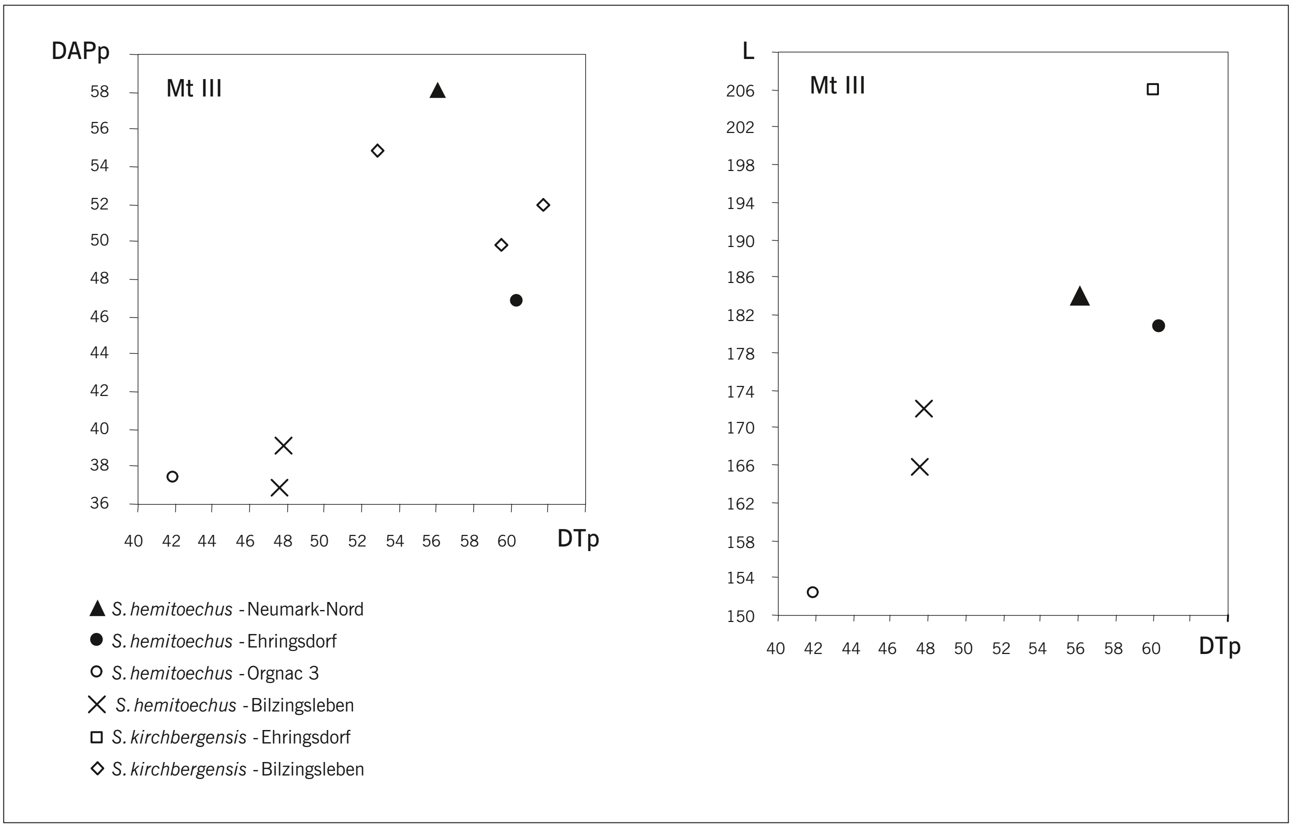

**Fig. 28** Bivariate diagrams of the third metatarsal: DAPp (antero-posterior diameter of the proximal part), DTp (=transverse diameter of the proximal part), L (=length). *Stephanorhinus hemitoechus* from Neumark-Nord (LVH), Ehringsdorf (IQW), Orgnac 3 (LPTUP), Belvedère (Fortelius et. al. 1993) and Bilzingsleben (FBFSUJB) and *Stephanorhinus kirchbergensis* from Bilzingsleben (FBFSUJB) and Ehringsdorf (IQW).

The **third metatarsal** (Pl. 23,1; Tab. 7) has the common morphology of this bone in rhinos, with its nearly symmetrical distal articulation and its relatively flat proximal articulation, but is relatively stout. Its DTd (maximal) is 59.4 mm. It is much bigger than the Mt III of *S. hemitoechus* from Bilzingsleben and Orgnac 3, but is comparable to a Mt III from Ehringsdorf attributed to *S. hemitoechus*. It has DAP and DT values comparable to those of the Mt III of *S. kirchbergensis*, but is shorter and thus stouter (Fig. 28).

The **fourth metatarsal** (Pl. 22,2; Tab. 7) has DAP and DT values that are larger than in *S. hemitoechus* and comparable to those in *S. kirchbergensis* from Bilzingsleben (Fig. 26), but the bone is shorter than in the latter species.

The **first lateral phalanx** (Pl. 22,4) cannot be assigned to a certain position (pes or manus, II or IV). The specimen that belongs to the skeleton is slightly larger than in *S. hemitoechus* from Bilzingsleben (Fig. 29; Tab. 14). Another, but morphologically very similar specimen that was found along with cervid bones, but not together with other rhino remains, is slightly smaller and well in the ranges of *S. hemitoechus* from Bilzingsleben.

The **third lateral phalanx** is a little larger than in *S. hemitoechus* from Bilzingsleben (Fig. 30; Tab. 14).

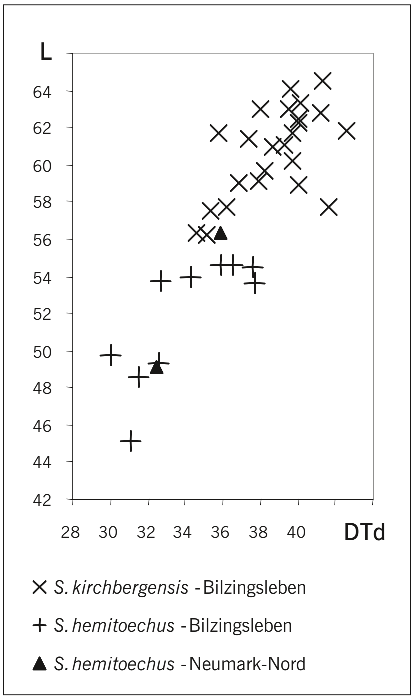

**Fig. 29** Bivariate diagrams of the lateral first phalanx of *Stephanorhinus hemitoechus* from Neumark-Nord and *Stephanorhinus kirchbergensis* and *S. hemitoechus* from Bilzingsleben (FBFSUJ).

### *Discussion*

Various names, that never became widely used, may refer to what at present is indicated as *Stephanorhinus hemitoechus*, among them *Rhinoceros lunellensis* Gervais 1848–1852, based on material from Lunel Viel. However, in a relatively recent publication on the rhinos from Lunel Viel Gervais's species was not even named (Bonifay 1973). This illustrates well that this name is now a forgotten name (in the sense of

**Tab. 14** Measurements of the lateral phalanges of *Stephanorhinus hemitoechus* from Neumark-Nord.

| | | | H | DAPpf | DTp | DTpf | L | DAPd | DTd |
|---|---|---|---|---|---|---|---|---|---|
| 4/5/ 94 | first | left | 34.9 | 29.8 | 36.6 | | 49.1 | 25.3 | 32.5 |
| HK88: 14, 54 | first | right | 39.7 | 34.8 | 43.7 | | 56.3 | 28.6 | 35.9 |
| HK88: 14, 58 | third | left | 33.7 | | 35.6 | 30.2 | 66.5 | | |

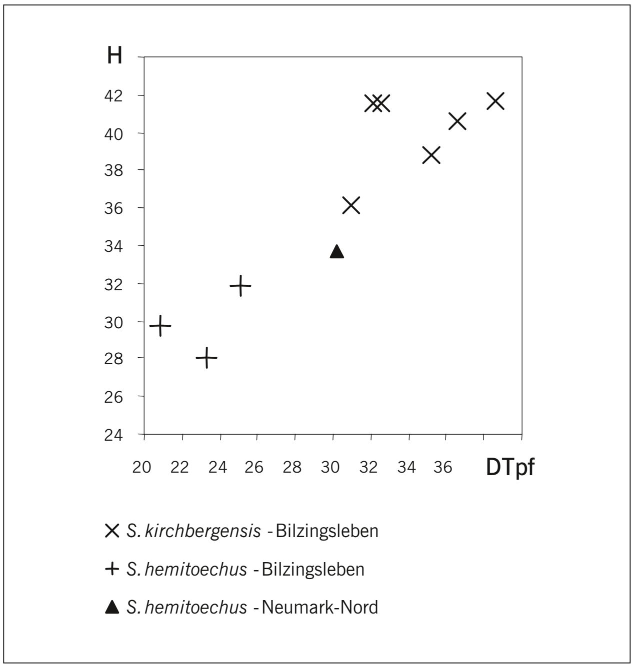

**Fig. 30** Bivariate diagrams of the lateral third phalanx of *Stephanorhinus hemitoechus* from Neumark-Nord and *Stephanorhinus kirchbergensis* and *S. hemitoechus* from Bilzingsleben (FBFSUJ).

the ICZN), and the same is the case with the other names. The name *Rhinoceros leptorhinus* Owen, 1846 was widely used, but, if R. Owen named this species (and not merely was mistaken in the assignation of the material), it is a homonym of *Rhinoceros leptorhinus* Cuvier, 1822.

Falconer proposed the name *Rhinoceros hemitoechus* and usually 1868 is taken as the year of publication, the posthumous publication of many of Falconers manuscripts, including one describing and figuring the rhino material from Minchin Hole. However, W. B. Dawkins (1867) mentioned *R. hemitoechus* already as a species named by Falconer. C. T. Gaudin (1859) published that Falconer recognized a species *Rhinoceros hemitoechus* in the deposits of the caves of Glamorganshire, because of its half complete bony nasal septum (A. Currant, pers. comm.). This seems to be a valid publication in the sense of the ICZN (1999): supplying a definition, indicating the type locality (»Glamorganshire«) and the author (which need not be the author of the publication, article 50.1.1), but not indicating a holotype or the syntypes. The author and year of publication thus is Falconer (1859).

The material from the caves of Glamorganshire known at the time by Falconer, should be considered as syntypes and all the different caves from which they come belong to the »type locality« (ICZN, 1999, article 76.1). Falconer (1860) described fossiliferous deposits from caves of Gower in Glamorganshire, indicated *R. hemitoechus* to be present in Bacon Hole and Minchin Hole and mentioned two skulls from from the latter cave, but did not give a description or figures of these specimens. One of these two specimens is lost and the second was broken during excavation (A. Currant, pers. comm.). Falconer (1868, Pl. 23,1; 24,2.3) figured specimens from Minchin Hole, including the posterior half of a skull that is now kept in the NHM under number 48953. This specimen probably is part of the second skull and is the best specimen to take as a lectotype (A. Currant, pers. comm.), which practically restricts the type locality to Minchin Hole. Some of the other specimens figured by Falconer, may have been of the same skull, but it is difficult to know which ones.

Owen's species was based on a skull from Clacton (no. 27836 in the NHM). A. Azzaroli (1962) indicated the skull from Clacton to be the lectotype of the species *»hemitoechus«* and this was accepted by some later students (e.g. Loose 1975). However, the specimen from Clacton was not a syntype and thus its designation as a lectotype is invalid (ICZN, 1999, article 74.2).

The lectotype skull from Minchin Hole has a wide occiput that overhangs the occipital condyles. These features are similar in the specimens from Neumark-Nord, described above, but are different in *S. etruscus*, *S. hundsheimensis*, *S. kirchbergensis* and *S. choukoutienensis*. The lectotype occiput does not have a V-shape as described for *S. kirchbergensis*, but is again like the specimens from Neumark-Nord. The upper dentition from Neumark-Nord resembles those from Minchin Hole figured by Falconer (1968, Pl. 16 etc.) in general aspect and in having narrow transverse valleys. The lower dentition from Neumark-Nord resembles the one from Minchin Hole figured by Falconer (1968, Pl. 19) in that the molars have narrow V-shaped fossids, the M$_3$ seems to be high crowned and the P$_2$ small. As described above, the dental remains from Neumark-Nord differ from those of other species of the genus *Stephanorhinus* and *Coelodonta*, but resemble the material from Minchin Hole. Therefore, it seems justified to assign the material to *Stephanorhinus hemitoechus.*

Azzaroli (1962), Guérin (1980) and Fortelius et. al. (1993) noted different stages of evolution in *S. hemitoechus* in either skull morphology, hypsodonty, and size and/or robusticity of the limb bones. Azzaroli (1962) introduced two names, *D. hemitoechus falconeri* for the subspecies present in Clacton, Bucine and Mosbach, and *D. hemitoechus aretinus* for the subspecies present in the Late Pleistocene of the Val di Chiana. While he indicated an (invalid) lectotype for the species *hemitoechus*, he ignored that one of the two subspecies he recognized should bear this name, and seems to have forgotten to indicate holotypes for the newly named subspecies. The inclusion of the material from Clacton in *D. h. falconeri* implies that a skull from Clacton is at the same time holotype of *R. leptorhinus* Owen, invalid lectotype of *R. hemitoechus* and syntype of *»falconeri«*. Notwithstanding all this, Azzaroli's names are available. I suggest here to take the skull from Clacton as a lectotype of the subspecies *S. hemitoechus falconeri*.

Guérin (1980, 1043) suggested that *D. h. hemitoechus* is the valid name for the Middle and *D. h. aretinus* for the Late Pleistocene form. However, Guérin (1980, 910; 1158) indicated that the typelocality of *»hemitoechus«* is Minchin Hole of Eemian and thus Late Pleistocene age. This seems to be correct and implies that not *»falconeri«* but *»aretinus«* is a synonym of *»hemitoechus«*. Here, it is considered that there are two subspecies: *Stephanorhinus hemitoechus hemitoechus* and *S. h. falconeri*.

*Stephanorhinus hemitoechus* is the species known from the late Middle and Late Pleistocene with the following features: it is the most hypsodont species of the genus, has a very small P2, it is not very large, and it has a skull with a marked concave dorsal profile and an overhanging occiput (Staesche 1941; Kahlke 1975, 1977; Loose 1975; Guérin 1980; Fortelius et. al. 1993). The skull and dentition from Neumark-Nord fit these morphological and metrical criteria and resembles the material assigned by these authors to *S. hemitoechus*.

As appears from the description above, an increase in size and robusticity seems to have occurred late in the Middle Pleistocene (anterior to OIS7) and the form from Neumark-Nord is robust. The valid subspecific name for the rhino from Neumark-Nord is thus *Stephanorhinus hemitoechus hemitoechus*.

*Coelodonta* Bronn, 1831

**Type species:** *Rhinoceros antiquitatis* Blumenbach, 1799
*Coelodonta antiquitatis* (Blumenbach, 1799)
**Type specimen:** present whereabouts unknown (Guérin 1980, 1155)
**Type locality:** not exactly known, but near Göttingen (Guérin 1980, 1155)
**Age of type specimen:** unknown (Guérin 1980, 1155)

**Material:**
187. - Excavation »Unterer Uferhorizont« 18-21/11/1986):
    HK 87: 300, 17 - right $M^2$
    HK 87: 300, 610 - posterior skull fragment
? 192. NN 33 - left astragalus, »Obere Uferzone«
? 195. Collected June 1995 from the »Untere Uferzone«:
    95, 3 - left ulna
    95, 4 - anterior thoracic vertebra (T1)
201. 1996, 47 - Complete skull, collected in the summer of 1996 from the »Untere Uferzone« (=1996, 36)
204b. Found together with a skeleton of Elephas numbered »E I« (=? E 20) and collected 2/9/1996:
    ?E I, 35 - hyoid
    ?E I, 38 - fragment of pelvis, including the articular facet with the femur
    ?E I, 40 - right radius
    E I, 42 - condyle and processus coronoideus of right mandible of *Coelodonta antiquitatis*
204b. collected 5/8/1996: - right M1/2 (M2?)

#### Description and comparison

The **skull** (Pl. 24,1; 25,2; Tab. 1) is in an excellent state; no deformation is visible and only some of the right teeth are missing, the left zygomatic arch is broken, but only a tiny piece of bone is missing, and the tip of the left postglenoid process is broken. The $P^2$ probably dropped out during the life of the individual.

The dorsal surface of the nasals is steeply inclined in its anterior part, much more than in *Stephanorhinus*. The cauliflower texture is very well developed and sticks out beyond, what otherwise would be the border of the nasals, behind it the nasals are narrower. This texture marks the origin of the anterior horn and its development and the shape of the nasals suggest a very large and partially anteriorly directed horn. The bony nasal septum has a maximum thickness of nearly 7 cm and extends far into the nasal cavity. The tip of the nasals extends far anteriorly beyond the premaxilla. The frontals have another area with cauliflower texture, that is very well developed, but less so than on the nasals. This area marks the origin of the second horn. The dorsal profile of the skull makes a clear angle, with nasals and frontals forming a horizontal line and the parietals and occipital an ascending line. The occiput overhangs the posterior face of the skull and extends as far caudal as the caudal surface of the occipital condyles. The occiput is wide and its posterior border is convex. When seen from the back, it is also wide and convex; there is no depression in the middle as in many other species. The occipital condyles are placed far apart and the width measured at these condyles is greater than in the other two species (Tab. 1). The wide occiput and wide condyles seem to have served to attach a more powerful neck musculature and to support greater forces, and their size is probably related to the very large horns, which, when used must have caused great forces on the neck. The fact that the occiput is moderately high, when compared to *S. hemitoechus*, but much wider, as well as the wide condyles, suggests that the forces were greater in transverse direction than in the vertical direction.

The zygomatic archs are thin and not very wide and as a result the skull is narrow. The anterior limit of the orbit is just anterior to the middle of the skull and above the anterior part of the $M^3$. The premaxillary is narrow and ends square, unlike in *Stephanorhinus* where it is pointed. There seem to be two alveoles for small incisors, probably the right and left deciduous incisors, but the alveoles are closed and the incisors must have dropped out during life. N. V. Garutt (1994) reported the presence of upper milk incisors in 4 % of 267 *Coelodonta* skulls. The posterior edge of palate has a very wide U-shape that reaches as far forward as the anterior part of the $M^3$.

The glenoid is much narrower than in *S. hemitoechus* and *S. kirchbergensis*. The postglenoid process is massive and placed far medially. The mandibular »fossa« is convex in all directions and articulates with a concave facet on the mandible that is described below. The paroccipital or jugular process is directed posteriorly and is placed far behind the postglenoid process with a large distance between them. Both processes reach about equally far downward. The posttympanic process is well developed, and extends far forward and fuses with the postglenoid process, closing the pseudo-auditory meatus from below. It does not show up as a separate downward directed process if seen from the side, but if seen from below it is very extensive and forms a wide bulge behind the glenoid, which protrudes laterally. The separation of the postglenoid and paroccipital processes is wider than in *Stephanorhinus* and approaches the state in the living species of rhinos, in particular *Dicerorhinus sumatrensis*. But then, in the living species, the posttympanic process does not touch the postglenoid process, and does not close the pseudo-auditory meatus from below. In the living African rhinos, the tip of the paroccipital process is much more dorsal than the tip of the postglenoid process, but in *Dicerorhinus sumatrensis* the tip of the paroccipital process is nearly as ventral, and in this respect it is similar to *Stephanorhinus* and approaches *Coelodonta*.

The anterior border of the foramen lacerum is formed by a deep carotid incisure. Next to this incisure there is no well developed oval incisure. Instead there is a wide foramen that is separated from the foramen lacerum by a thin bony plate (which is broken on the right side). This seems to occur frequently in *D. bicornis* (Guérin 1980), but the separation is not complete in the specimen figured by Loose (1975, Pl. 7,3 – note the right side). The retroglenoid foramen reaches to the middle of the postglenoid process, which is further than in *Stephanorhinus*. The hypoglossal foramen is large and measures 15.1 x 17.8 on the left and 17.4 x 18.2 (mm) on the right side. It is more widely separated from the jugular foramen than in *Stephanorhinus*.

The posterior part of a second **skull** (Pl. 25,1; Tab. 1) preserves the part behind the orbits. Probably it is slightly compressed in a more or less dorso-ventral direction.

The parietals must have been much inclined, since they make a sharp angle with the posterior side of the skull. However, this angle is probably a little exaggerated by deformation. The occiput clearly overhangs the posterior side of the skull and reaches far more caudal than the occipital condyles. The occipiut is very wide and convex both when seen from above and from behind, unlike in many species of *Stephanorhinus* (except *S. hemitoechus*) where there is a more or less pronounced V-shape when seen from above and a depression in the middle when seen from behind. Only one occiptal condyle remains, but it is placed clearly away from the foramen magnum and when complete, the condyles must have been very wide.

The postglenoid and paroccipital processes are widely separated. The posttympanic process is fused to the postglenoid process, closing the pseudo-auditory meatus from below, but cannot be seen as a separate downward directed process when seen from the side. It is very extensive when seen from below. The basicranium is still partially covered by sediment, but as far as could be seen the carotid incisure is deep, but the presence of a foramen instead of an oval incisure could not be confirmed. The hypoglossal foramen is large.

A fragment of a **mandible** (Pl. 25,3) consists of the upper part of the ramus, including the condyle, but the coronoid process is broken off. The few measurements that can be taken (Tab. 3) suggest a much smaller size than in *Stephanorhinus hemitoechus*. The width of the condylar facet is 88.7 mm in this specimen and 114.3 in *S. hemitoechus* and the width of the corresponding facet on the skull is 94.2–102.9 mm in *Coelodonta*, 112.4–113.7 in *S. hemitoechus*, and 127.1–132.4 in *S. kirchbergensis* (Tab. 8). The posterior facet which articulates with the retroarticular process is concave or »basin shaped«, while in *S. hemitoechus* it is concavo-convex or »saddle shaped«. The facet is also much smaller (31.5 mm high and 26.5 mm wide). These differences suggest that this mandible fragment belongs to a different and smaller species, *Coelodonta antiquitatis*. However, the DAP of the ramus at the level of the condyle and the minimum DAP at the middle of the height of the ramus are comparable to *S. hemitoechus* (Tab. 10) and the coronoid process is much less elevated. This suggests that the temporal muscle exerts its maximal force in a more vertically inclined direction and that it works with a relatively greater arm, resulting in a relatively greater momentum than in *S. hemitoechus*.

The **upper dentition** (Pl. 26,1) has been compared above with the dentitions of the species *S. kirchbergensis* and *S. hemitoechus*. In general the *Coelodonta* dentition differs from that of the genus *Stephanorhinus* in its smaller size, more rugose and thicker enamel, higher crowns, more square ectolophs that are directed more parallel to the long axis of the tooth row, more marked metacone ribs on the buccal wall, more posteriorly placed protocones, smaller hypocones, narrower and shallower lingual valleys, larger and deeper prefossas, larger crestas and crochets that tend to isolate a medifossette from the prefossa, lingual parts of the proto and metalophs that become more antero-posteriorly oriented, and prefossas that are also more antero-posteriorly directed. Whereas in the lower dentition, the anterior lobes are relatively wide (Fig. 14), the proportions of the upper teeth are more normal in this respect (Fig. 12; Tab. 2). The $M^3$ from Neumark-Nord are short for *Coelodonta*, but there does not seem to be a clear evolutionary tendency in increasing or reducing the length of this tooth. An isolated specimen (Pl. 26,2) is believed to be an $M^2$, because of its size, but might also be a large $M^1$. Another isolated specimen might also be second upper molar.

The **hyoid** (Pl. 26,3; Tab. 15) is described here, because it was found together with other remains that are believed to belong to *Coelodonta*. However, the bone is not frequently described, and at present there are no morphological arguments to assign it to one species or the other. The nomenclature (after Koch 1960 and Getty 1975) is indicated in Fig. 10,2. The lingual process is not well developed in *Canis* and *Sus*, short in *Bos* and equally long in *Equus*, but in that taxon it is laterally flattened (Koch 1960; Getty 1960). The resemblance to the hyoid of *Diceros bicornis* (NNML 5738) in general morphology and size, suggests that the specimen may well belong to a rhino. However, its width at the tubercles for articulation with the ceratohyoids is greater and the thyrohyoids are more slender and more divergent. Another difference is that, the shape formed by the medial surfaces of the thyrohyoids and the basihyoid is more or less parabole shaped, while in *D. bicornis*, there are two clear angles in this structure at the place where the thyrohyoids meet the basihyoid.

**Tab. 15** Measurements of the hyoid bone E I, 35 of ?*Coelodonta antiquitatis* from Neumark-Nord.

| | left/middle | right |
|---|---|---|
| L | -- | |
| DT | -- | |
| Llp | 71.3 | |
| Hlp | 18.0 | |
| DTlp | 17.6 | |
| DAPbh | 23.5 | 23.0 |
| DTbh | 73.0 | |
| DTthmi | 66.4 | |
| DAPtch | 18.6 | 16.6 |
| DTtch | 12.1 | 11.3 |
| Lth | -- | |

There are rugosities at the ventral side of the lingual process near the point of its greatest width and at the ventral side of the basihyoid near the tubercles for articulation with the ceratohyoids. The lateral sides of the lingual process are concave, forming a dorsal ridge and thus a triangular transverse section.

The vertebra **$T_1$** (Tab. 4) was not found in association with the other rhino specimens. It has large anterior and posterior costal facets that are at the level of the ventral half of the vertebral body, the large lateral costal facet is situated at the level of the dorsal half of the vertebral body and faces ventrally. The main articular facets of the vertebral body have their widest point in their dorsal half. The widest point of the vetebra is just ventral of the dorsal surface of the vertebral body. The resemblance with $T_1$ of the skeleton of *S. hemitoechus* is great, but its minimal width and width at the cranial articular processes are much greater, while the width and height of the main articular facets and vertebral foramen are less, suggesting a smaller, but more massive animal. The vertebrae of *S. kirchbergensis* tend to be of less massive construction. This $T_1$ differs from the one assigned to *S. kirchbergensis* in having much larger posterior costal facets. The specimen was found together with the ulna described below.

Few observations can be made on a fragment of an **ulna**, save for that it is small (Tab. 10). It might belong to *Coelodonta.*

A **radius** (Tab. 11) might belong to this species. It has great DAP and DT values as in *S. hemitoechus* from Neumark-Nord, and distally it is even wider, though its length is lesser. In robusticity it approaches *Coelodonta antiquitatis* (Borsuk-Bialynicka, 1973, Tab. 41) and might belong to this species.

A fragment of a **pelvis** including the articular facet of the acetabulum, but little more, might belong to this species. There is not much morphology to base a determination on. With a maximum diameter of 92.6 mm of the facet, the specimen is small in comparison to *S. kirchbergensis* from Bilzingsleben and is in the ranges of *S. hemitoechus* of that species (Fig. 31). However, as we have seen under the description of the latter species, this seems to have become more massive with time and its pelvis might be expected to be larger as well. *Coelodonta* seems to be smaller. In this place more remains were found that can be assigned to *C. antiquitatis*. For these reasons, the specimen is tentatively assigned to the latter species.

The **astragalus** (Tab. 16) was not found associated with other rhino remains. As a peculiarity it has a facet for the calcanaeum, which projects laterally more than normal. The recent publications that treat the astragalus, coincide in that the astragalus of *S. kirchbergensis* is particularly large, but give importance to different morphological features, or do not agree on a particular feature, and in any case do not take into account possible morphological evolution within the species[3]. The specimen from Neumark-Nord is of intermediate size (Tab. 9) and either close to or within the ranges of the large *S. kirchbergensis*, and it tends to be larger than the few specimens attributed to *S. hemitoechus*, while the few specimens that are attributed to *Coelodonta*, show a wide range in sizes (Fig. 32).

The astragalus of *S. kirchbergensis* is said to be enlarged latero-medially and to have a very wide trochlea (Fortelius et. al. 1993). The species should thus have low values for the

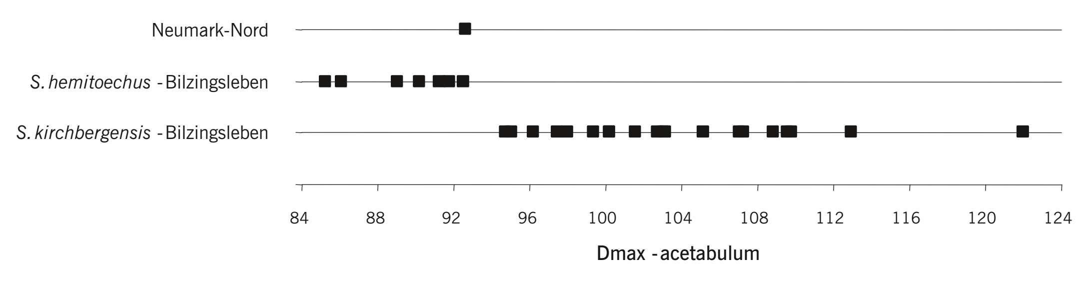

**Fig. 31** The size of the pelvis, as indicated by the maximum diameter of the articular facet of the acetabulum, from Neumark-Nord, compared to *Stephanorhinus kirchbergensis* and *S. hemitoechus* from Bilzingsleben (FBFSUJ).

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[3] The increase of the robusticity in time of many of the limb bones in *S. hemitoechus*, suggests that the astragalus of *S. hemitoechus* might also have become larger or more robust.

**Tab. 16** Measurements of the astragalus of ?*Stephanorhinus hemitoechus* from Neumark-Nord.

| | NN 33 |
|---|---|
| Lext | >81.6 |
| Lm | 69.7 |
| Lint | 86.8 |
| DT | 96.4 |
| DTpf | 86.3 |
| DTpf’ | 72.0 |
| DTdf | >72.3 |
| Rint | 73.1 |
| Rm | 46.6 |
| DAPdf | >50.4 |

index: 100 Lint/DTp. However, in the older sample of *S. kirchbergensis* from Bilzingsleben, the contrary seems to be true, while in the younger samples of Ehringsdorf and Taubach, the values are indeed much lower, suggesting an increase in robusticity over time (Fig. 33). The few specimens attributed to *S. hemitoechus* and *Coelodonta* do not show such a change and tend to be intermediate between the robust and gracile astragali of *S. kirchbergensis*. The value for Neumark-Nord is within the ranges of *S. hemitoechus* and of the Bilzingsleben sample of *S. kirchbergensis*, but is superior to that of the Ehringsdorf and Taubach samples of the latter species.

A wide trochlea (compared to its radius) should show up in low values for the index: 100 R/DTp. A decrease in values occurs in *S. kirchbergensis* from the older sample of Bilzingsleben to the younger samples of Ehringsdorf and Taubach (Fig. 34). The values for *S. hemitoechus* are not particularly high, nor low, and those for *Coelodonta* tend to be high. The specimen from Neumark-Nord has the highest value of all.

The raw values show a slight decrease in Lint, Lm and R of *S. kirchbergensis* from Bilzingsleben to Ehringsdorf and Taubach, whereas DTp remains more or less the same, suggesting that the changes in the values of the indices described above are mainly due to a decrease in the radius of the trochlea. The Neumark-Nord specimen does not fit well in the tendency in the *S. kirchbergensis* lineage, but is not unlike *Coelodonta*, in having a large R, but not very large Lint. This might be due to a smaller distance between the trochlea and the distal facet, at least at the medial side.

The distal facets for navicular and cuboid taken together tend to be relatively wide in *S. kirchbergensis* and this is noted in the index: 100 DTdf/DTp. The distal facets seem to become even wider in the younger samples of *S. kirchbergensis* (Fig. 35), while the values seem to remain low in

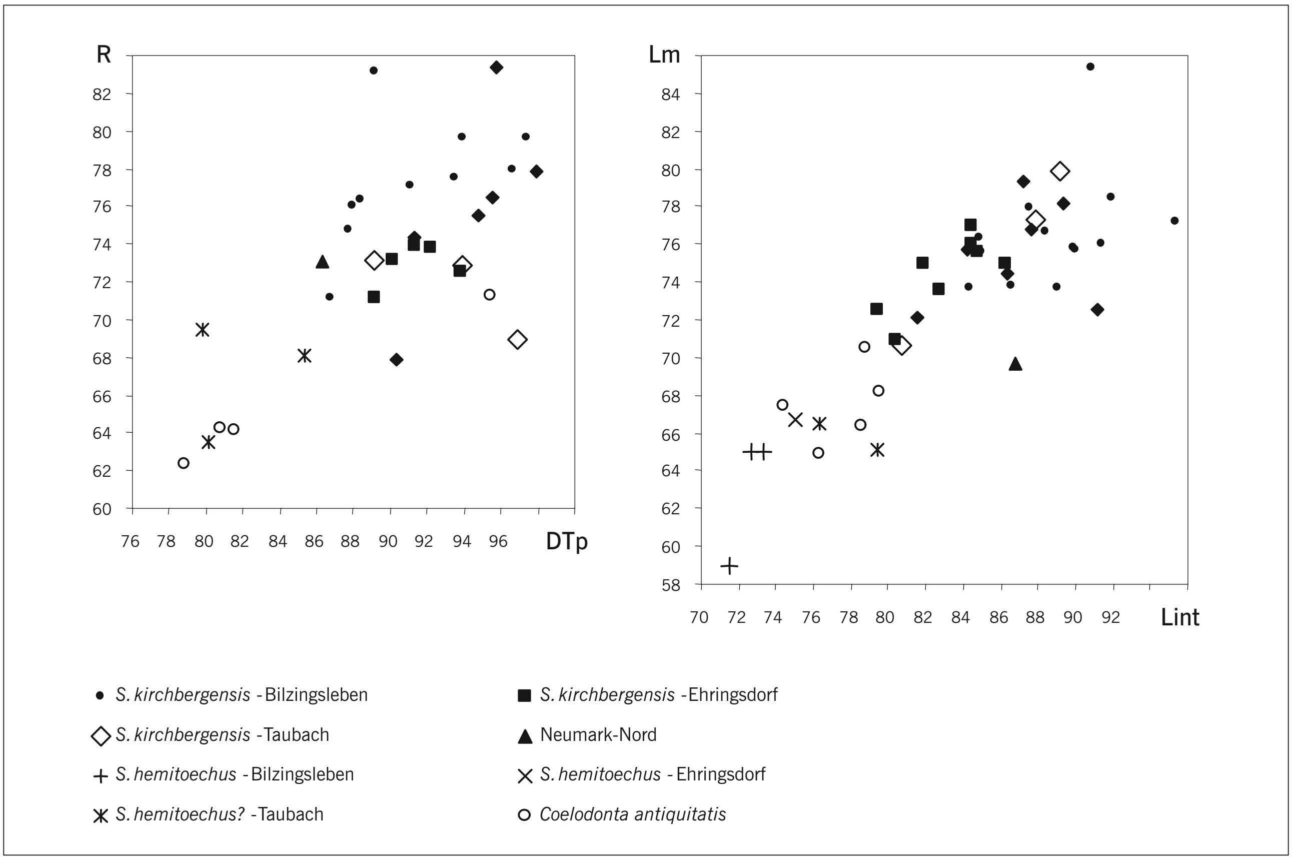


**Fig. 32** Bivariate diagrams of the astragalus; R (medial diameter of the trochlea) versus DTp (width of the trochlea) and Lm (length in the middle) versus Lint (medial length). *Stephanorhinus kirchbergensis* from Bilzingsleben (FBFSUJ), Ehringsdorf (IQW) and Taubach (IQW), *Stephanorhinus hemitoechus* from Bilzingsleben (FBFSUJ), Ehringsdorf (IQW) and Taubach (IQW), *Coelodonta antiquitatis* from Zasuhino (GIN), Chlum (NMP), Wannen (SMN) and Heringen (IQW).

**Fig. 33** The values for the index 100 Lint/DTp of the astragalus in the different samples of rhinos. Provenance of data as in Fig. 15.

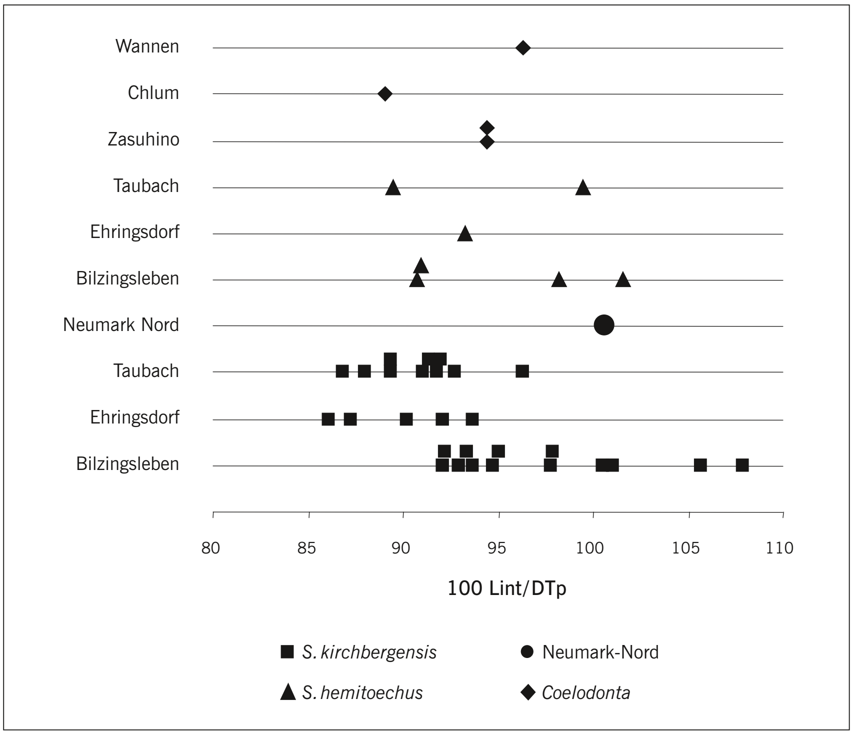
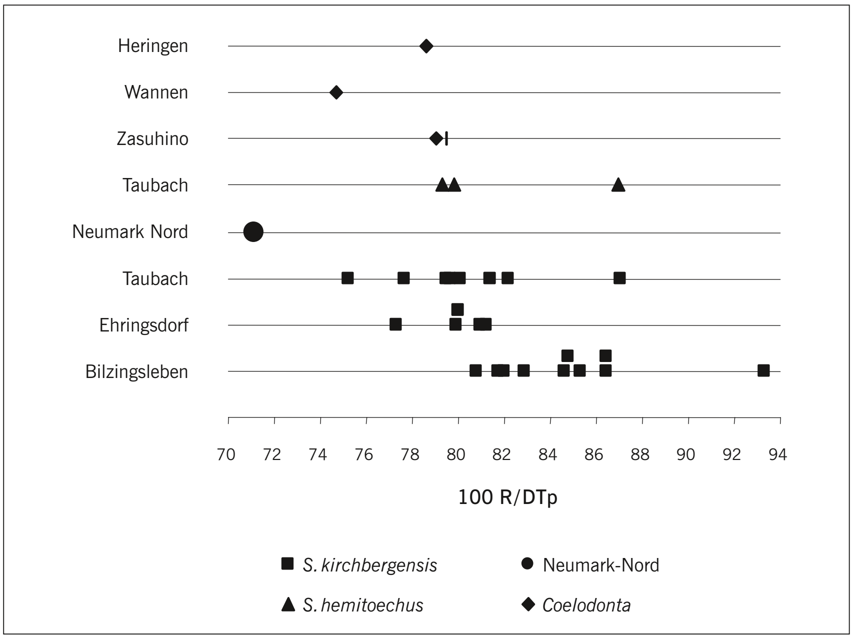


**Fig. 34** The values for the index 100 R/DTp of the astragalus in the different samples of rhinos. Provenance of data as in Fig. 15.



*S. hemitoechus* and possibly in *Coelodonta* as well. The specimen from Neumark-Nord seems to differ again from the samples of *S. kirchbergensis* from Ehringsdorf and Taubach.

The assignation of the astragalus from Neumark-Nord to a species is not satisfactory, but the features and data considered here, are not against an assignation to *Coelodonta*, while they do not fit in the evolutionary tendencies in *S. kirchbergensis*.

### *Discussion*

*Coelodonta antiquitatis* was the first of the European Pleistocene rhinos to receive a scientific name, and in fact it was named various times before any of the other species were named. The oldest name *Rhinoceros lenenensis* Pallas, 1773 is now considered to be a forgotten name and the specific name *Rhinoceros antiquitatis* Blumenbach, 1799 is used in combination with the generic name *Coelodonta* Bronn, 1831. Roger (1887; who placed the species in *Atelodus*) listed various other synonyms of the woolly rhino: *R. tichorhinus* Cuvier, *R. pallasi* Desmarest, *R. jourdani* Lortet & Chantre, *C. bojei* Bronn, *Hysterotherium Quetlinburense* Giebel and the generic name *Tichorhinus*. Nevertheless, for over a century there seems to have been a relative consensus about *Coelodonta antiquitatis* and there have been no major problems in its recognition, though occasionally the specific or generic names *tichorhinus* and *Tichorhinus* have been used. The species is easily recognised by its very extensive bony nasal septum, hypsodont teeth, upper molars with frequently a closed medifossette, etc. These and other character-

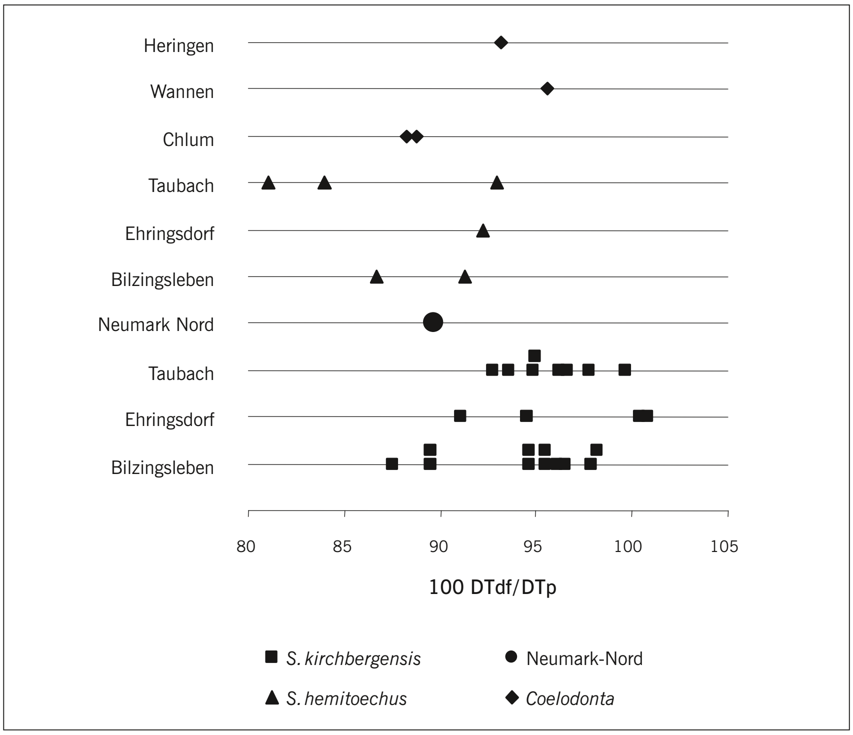


**Fig. 35** The values for the index 100 DTdf/DTp of the astragalus in the different samples of rhinos. Provenance of data as in Fig. 15.

istic features, mentioned in the description, indicate that the material from Neumark-Nord belongs to the species *Coelodonta antiquitatis*.

Guérin (1980) indicated that the holotype could not be found anymore in the collections and that the exact type locality is not known either. He recognised two evolutionary stages of woolly rhino and named the most primitive stage *C. antiquitatis precursor*. The type is from La Fage and the diagnosis was given as: »*C. antiquitatis* de grande taille à membres élancés; tous les os longs et les métapodes se distinguent de ceux de la forme type par leurs proportions plus graciles, tant au niveau des épiphyses qu'à celui des diaphyses«. This implies that the type of *C. antiquitatis* should belong to the second stage of evolution with more robust long bones. It is not clear, whether this is an observation or an assumption. The age of Neumark-Nord suggests, that the material should belong to *C. a. praecursor*, however, with the doubts that remain on the assignation of the scanty post cranial material, it is better to refrain from an attempt to assign the material from Neumark-Nord to a particular stage of evolution.

## 2.2. Functional morphology, ecology and stratigraphy

### *Size of the skull*

It has been argued that *S. kirchbergensis* is not a very large species, because its skull is not very large (Loose 1975). However, the teeth and postcranial remains at Bilzingsleben and other localities indicate a very large animal (Van der Made 2000). Yet it is noteworthy that the skull of such a large animal is relatively small and indeed absolutely shorter than the skull of the smaller *S. hemitoechus*. In fact, most Pleistocene rhinos from western Europe have skulls of roughly the same size.

The bones and teeth of *S. kirchbergensis* are large, which implies that its skull is relatively small, at least compared to the state in other species of the same genus and *Coelodonta*. This can easily be seen: the posterior edge of the M$^3$ is positioned about level with what should be the posterior rim of the orbit, if this were preserved as a bony structure, and the premolar row extends far forward. Though there is some individual variation, the tooth row tends to reach further backward in *S. kirchbergensis* than in the other species of the genus and in *Coelodonta*.

The functions of the skull include: 1) providing space and protection for the brain, eyes, ears and smell and taste organs, 2) taking food and mastication, and, in the case of the rhinos, 3) supporting the horns. It is difficult to see how a small skull in a large species improves most of these functions, unless it has something to do with mastication or the momentum of the forces generated by using the horn. Alternatively, the other species may have acquired a larger skull because of the mechanics of mastication or the horns. The placement of the teeth further away from the condyle-glenoid articulation tends produce a more even occlusion, whereas, when the distance to the articulation is smaller, the posterior teeth tend to occlude earlier than the anterior teeth. It is not the intention here to present an extensive interpretation of the masticatory mechanics of *Stephanorhinus* and *Coelodonta*, however, it is noted that the relatively small skull size in *S. kirchbergensis* compared to the other species may have something to do with dietary preferences.

### *Size of the horns*

The size of the base of the horns can be measured as the antero-posterior or transverse diameter of the area with cauliflower texture. Probably these measurements have a relationship with the length of the horn; the longer the horn, the greater the momentum of the forces acting on it, and the larger its base needs to be. This idea seems to be confirmed by the observation that the African rhinos tend to have longer or larger horns and have wider areas with cauliflower texture than the Asian rhinos.

As indicated above, Zeuner (1934) used an index (width of cauliflower area/length of skull) that suggests a relative size for the horn (Since in the species here, the cauliflower structure reaches the edge of the nasals, it corresponds to measurement 33.). *Dicerorhinus sumatrensis*, which is known to have a small horn, has a value of 0.20, while *Ceratotherium* and *Diceros*, with large horns, have values of 0.22–0.23 and 0.24 respectively. Zeuner (1934) gave the values, for what we call now *S. etruscus* 0.10–0.17, *S. hunsdsheimensis* 0.18–0.24 and *S. kirchbergensis* 0.13–0.22. For Neumark the values are 0.23 for *S. kirchbergensis*, 0.25 for *S. hemitoechus* and 0.26 for *Coelodonta*. The values suggest larger horns for the species present at Neumark-Nord than for *S. etruscus* and *S. hundsheimensis*. What is of interest here, is that *S. kirchbergensis* has lower values than *S. hemitoechus* and *Coelodonta* which seems to confirm a relatively smaller horn for the skull of *S. kirchbergensis*, which is already relatively small.

In a general sense, the values of this index tend to be higher in the species with wider and more elevated occiputs that overhang the posterior side of the skull. This suggests a relationship between horn size and occiput morphology. This is not surprising, since the neck musculature has to support the forces generated by the use of the horns and its momentum depends partially on the position of the origin of the muscles relative to the occipital condyles. However, Zeuner (1934) interpreted the shape of the occipital area in terms of dietary preferences of the species: grazers bear their head lower and browsers higher. Probably, the function of the neck musculature and the transmission of forces through the cervical vertebrae are very complex and cannot be understood by the study of the occipital area alone.

### *The vertebral column*

In the description of the vertebrae of the different species most attention was paid to features that show the position of the individual vertebrae within the column and only in certain vertebrae, such as the axis, comparisons with other species were made. For a functional or phylogenetic interpretation, the column should, if possible, best be studied as a whole and not as individual vertebrae. This was attempted in Fig. 18, where we can see the variation of a metrical feature through the column.

The size of the vertebral canal might be expected to be related to body size and is larger in the vertebrae assigned to *S. kirchbergensis* than in the vertebrae of *S. hemitoechus* (Tab. 4)[4]. Various processes and facets appear to be relatively well developed in *S. hemitoechus*, suggesting that it is a relatively robust, muscular or physically strong species.

The absolute and relative lengths of the dorsal spine can be seen to increase steeply towards the anterior thoracic vertebrae before dropping towards the lumbar vertebrae (Fig. 18a.b). The $T_{14}$ has still a clearly longer dorsal spine than $T_{15}$–$L_2$, suggesting that this marks the end of the »dorsal hump«. Even though the thoracic vertebrae of *S. kirchbergensis*, represented in fig. 18, are not in the same position as those of *S. hemitoechus*, it can be seen that they have relatively short dorsal spines. This feature seems to correspond to a different feature in the axis. In *S. hemitoechus*, the axis has a dorsal spine that is very massive and particularly wide at its caudal end. In *S. kirchbergensis* the dorsal spine of the axis is moderately widened at its caudal end, and to some extent this is also the case in *S. hundsheimensis*, whereas in *Dicerorhinus*, *Diceros* and *Coelodonta* the spine is not caudally widened. The feature of a caudally widened dorsal spine may thus characterise the genus, or at least some of its species. These observations suggest a particularly strong dorsal and neck musculature in *S. hemitoechus*. Some of these muscles serve to elevate the neck and/or cranium. A stronger neck musculature might be related with the larger horns as interpreted from the development of the areas with cauliflower structure that mark the origin of the horns.

The width measured at the facets of the cranial articular processes (Fig. 18c) is seen to be great in the cervical and anterior thoracic vertebrae and to decrease markedly after the $T_5$. In general, compressive forces are transmitted at the facets. The great distance between the right and left facets and their orientation, suggests major transverse stresses in this part of the column. This is a general feature in many (or all?) mammals. However, the width is smaller in the large species *S. kirchbergensis*, suggesting again that these stresses are lesser than in *S. hemitoechus*. Again this might be related to a major development or more intensive use of the horns in the latter species.

The antero-posterior and transverse diameters or the surface of the main anterior and posterior facets may be related to the transmission of forces in antero-posterior direction, body weight, or the degree of movement between the vertebrae. The width of the main posterior facets in the two species from Neumark-Nord shows a different pattern: *S. kirchbergensis* seems to have a very narrow facet in the $C_5$, but a relatively wide facet in the $T_5$ (Fig. 18e). A comparison with *S. etruscus* shows a more or less similar pattern in the variation in the width of the main posterior facets in *S. hemitoechus* and *S. etruscus*. This variation has probably a functional meaning; possibly there is more mobility between certain vertebrae, than between others. Differences and coincidences in the size of particular facets in these species probably indicate adaptations. The very low values for *S. etruscus* are striking, while *S. hemitoechus* has relatively high values compared to *S. kirchbergensis*. The first species is probably a small and relatively slender species, the second is larger and more robust, and the third one is much larger but of gracile proportions. The relatively large facets in *S. hemitoechus* might be related to its body weight, but also to compressional forces related to the size and use of its horns.

It has already been indicated that the number of thoracic vertebrae are either eighteen or nineteen in the Pleistocene Eurasian and living Asian and African rhinos. Reduction of the number of thoracic vertebrae is probably a derived fea-

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[4] However, this is not confirmed in the size of the foramen magnum – Tab. 1.

ture that occurred several times within these rhinos. Guérin (1980) derived *D. hemitoechus* from *D. etruscus etruscus*, but not from *D. etruscus brachycephalus* (= *S. hundsheimensis*). In the cladistic analysis of Fortelius et. al. (1993), *Stephanorhinus etruscus*, *S. hundsheimensis* and *S. hemitoechus* form an unresolved clade. If the number of thoracic vertebrae in *S. hemitoechus* turns out to be indeed eighteen, as supposed here, this would support a closer relationship between *S. etruscus* and *S. hemitoechus*.

The foregoing merely is suggestive of the potential information that the vertebral column contains. However, future work on more and more complete columns might yield more solid results on functional anatomy and phylogeny.

### *Some observations on the ecology of the rhinos from Neumark-Nord*

The assumption that the skull morphology of *Stephanorhinus kirchbergensis* suggests browsing on bushes (Zeuner 1934), that its teeth are relatively low crowned, and its predominant occurrence in »interglacial« fossil associations that include forest dwellers, lead to the view that the species is a browser that lived in warm wooded landscapes. In German it is called »Waldnashorn«, or forest rhino. Because *S. hemitoechus* and *C. antiquitatis* have the opposite character states, they are usually seen as adapted to steppe and tundra. Hence the name »Steppennashorn« or steppe/prairy rhino for *S. hemitoechus*.

Grazers tend to eat larger quantities of lower quality food. In general this food is also harder and more abrasive and tends to grow close to the ground, so that occasionally sand grains may be ingested, which further increases wear. Therefore grazers tend to have various adaptations including hypsodonty, cementum on the crowns, various mechanical adaptations that affect the mode and force of occlusion and frequently reduction of premolars and increase of size in the posterior molars. The latter two adaptations are very well known from suids and other artiodactyls, where it serves to bring the main masticatory surface more to the back, increasing thus the force when masticating, but they are not so common in perissodactyls, which tend to molarize the premolars (as in horses). In artiodactyls that increase the size, and in particular the length, of the posterior molars, there tends to be an increase in hypsodonty and/or relative enamel thickness from the anterior to the posterior molars.

*Stephanorhinus kirchbergensis* is often seen as a low crowned rhino. Its cheek teeth have indeed lower crowns than those of *S. hemitoechus* and *Coelodonta*, however, they are on average more high crowned than those of *S. etruscus* and *S. hundsheimensis*, especially the $M_3$ (Fig. 15; 42). For a late Middle or Late Pleistocene rhino, it is thus low crowned, but its earliest representatives lived together with *S. hundsheimensis* and in this period should thus be considered to be relatively high crowned.

*Stephanorhinus kirchbergensis* is also said to have relatively large premolars and indeed its $P_2$ is much higher than in *S. hemitoechus*, possibly also relatively higher. However, this is only one aspect of the size of the premolars. It is possible to express the size of the premolars as a percentage of the size of other teeth and thus compare the relative size of premolars in species of different absolute sizes. Van der Made (1999, etc.) expressed the size of the different teeth as a percentage of the length and width of the first molar, either using teeth in a mandible or by means of large samples. The first molar was believed to be the »most stable« tooth, since the sizes of all other teeth are very clearly affected by dietary adaptations. Also the length of the M1 seems to be affected by dietary adaptations and in Fig. 43 the width of the first lobe of the first molar is used as a standard. The $P_2$ in *S. hundsheimensis* is very large, while the other species of *Stephanorhinus* have $P_2$ with similar relative sizes and *Coelodonta* has still smaller premolars.

The rhinos with most cementum on their teeth are *Coelodonta* and *S. hemitoechus*. However, also *S. kirchbergensis* tends to have more cementum on its molars than *S. hundsheimensis* and *S. etruscus*. *Stephanorhinus kirchbergensis* tends to have relatively thin enamel. This is an interesting feature, but needs further study.

It is not the intention here to discuss biomechanics of the skull and details of molar morphology. However, it can easily be seen that there are many parallels in the molar morphology of *Coelodonta* and *Ceratotherium*, for example, the tendency in the proto and metalophs to become oriented in a more antero-posterior direction and the tendency to have a relatively wide anterior lobe in the lower cheek teeth. *Ceratotherium* is the rhino that is most adapted to grazing of all living rhinos. Though rhinos have M3 that tend to be small relative to the anterior molars, there is a tendency to increase $M_3$ length in *S. hemitoechus* and *C. antiquitatis* (see descriptions and Fig. 12).

In addition to dental features, the width of the snout may give information on the dietary preferences. Grazers tend to have wide snouts and browsers narrow and elongate snouts (Solounias et. al. 1988). Though there are differences between the species, all *Stephanorhinus* and *Coelodonta* have skulls with elongate and narrow snouts compared to the skulls of the living African rhinos, in particular the grazer *Ceratotherium*. However, specimens of *Coelodonta*, which preserve the soft parts have wide and flat upper lips, which resemble those of *Ceratotherium* (Wüst 1922).

The features discussed above show that these rhinos behave in a way similar to artiodactyls through increasing M3 size and hypsodonty and reducing premolar size. Various dental features suggest that *S. hundsheimensis* is the rhino that is most adapted to browsing, or least to grazing. This addition seems redundant, but we should bear in mind, that browsing is probably the primitive state in this type of rhinos. *Coelodonta* is the rhino that is most adapted to grazing, but probably not to the same extent as *Ceratotherium*. Within the remaining rhinos, *S. hemitoechus* seems to be most adapted to grazing and *S. etruscus* least. The picture that emerges is thus that in the latest Early Pleistocene (when *S. hundsheimensis* appeared or became more abundant), indicates that the rhino community became less adapted to grazing, while during the Middle Pleistocene there was a definite tendency towards more grazing (or at least the ingestion of more, harder, or more abrasive food). All this is in relative terms, since we do not know what they really ate and in what proportions. In this context, *S. kirchbergensis* does not appear as the most typical browsing or least grazing rhino.

The fossils from Neumark-Nord provide a possibility to test the hypotheses on the diet of these rhinos based on functional morphology. From the fossas of several upper dentitions, plant remains have been collected. The fossas were covered by the sediment in which the fossils were found (Pl. 27,1a.2a). When this sediment was removed, plant remains, without any sediment, appeared (Pl. 27,1b.2b); these remains were sampled (Pl. 27,1c.2c). In collections of recent herbivores, it is common to see plant remains in the fossas and fossids of the teeth, and on several occasions, these have been mentioned or described in bisons (Guthrie 1990, 176–177), *Coelodonta* (Garutt et. al. 1970, as cited by Kahlke 1999) as well as other animals. The case of Neumark-Nord may be among the oldest, described up to now. The plant remains are still under study.

Locomotory adaptations are the other main type of adaptations that can be studied in palaeontology. Most of these rhinos have relatively gracile limb bones. However, it appears that during the late Middle Pleistocene, *S. hemitoechus* became more robust (Guérin 1980; Fortelius et. al. 1993). The same occurred in *Coelodonta* (Guérin 1980). *Ceratotherium*, which lives predominantly in open landscapes, has also very robust limb bones compared to the Asian rhinos, which live in more closed environments. Possibly *S. hemitoechus* and *Coelodonta* adapted in a similar way to more open environments. This does not seem to have occurred in *S. kirchbergensis*.

The biogeography of the different species gives another indication as to their ecology. *S. kirchbergensis* dispersed into Europe during interglacial periods. During successive interglacials its westward expansion seems to have increased, but it does not seem to have entered into Spain, whereas *S. hemitoechus* is present in many localities (Cerdeño 1990; Alférez/Iñigo 1990). In all German localities with *S. kirchbergensis* it is more abundant than *S. hemitoechus*, which is a rather unusual phenomenon: in large mammals, the smaller of two similar species tends to be more common. Its absence in Spain might be due to a more open or dry landscape and its greater abundance in Germany might be due to more extensive closed or less dry environments. Similarly, *S. hundsheimensis* is a very common rhino in large parts of Europe, but is rare or absent in Spain, while true *S. etruscus* is relatively rare in mid-latitude Europe. In the period of overlapping temporal distribution of these species, *S. etruscus* is found in Huéscar, Atapuerca TD4–6, Atapuerca TD8 and Westerhoven, while *S. hundsheimensis* is found in Vallonnet, Untermassfeld and Dorn-Dürkheim[5].

### *The woolly rhino in interglacial environment*

The occurrence of three species of rhinos at the interglacial locality of Neumark-Nord is an interesting phenomenon. There are so not many localities in the Pleistocene of Europe with *Coelodonta antiqutiatis*, *Stephanorhinus hemitoechus* and *Stephanorhinus kirchbergensis*. Most authors see the presence of *C. antiqutiatis* and *S. kirchbergensis* in Europe as indicative of glacial and interglacial conditions, respectively (although Loose 1975 considered the presence of the woolly rhinos as continuous).

Guérin (1974) reported all three species from La Fage. However, *Coelodonta* is reported only from bed 5 and *S. kirchbergensis* from bed 3. The two beds were assumed to be close in age within the Saalian. In Ehringsdorf, *S. kirchbergensis* is indicated to be present, along with *Elephas*, in the Lower Travertine and *Coelodonta* in the Ilm gravels and the Upper Travertine, where it occurs together with Mammuthus, *Megaloceros giganteus* and *Alces* (von Koenigswald/Heinrich 1999). Both upper and lower Travertine are assumed to have been formed in a warm period in the Saalian (Mallik et. al. 2000; Mania et. al. 2003). Then there are some apparent or dubious associations. For instance, the gravel pits in the Rhine valley (e.g. Eich, Gimbsheim). W. von Koenigswald (1988) described the Eemian fauna from these localities, but did not include *Coelodonta*, although it is not known from which level each fossil comes. Von Koenigswald and W.-D. Heinrich (von Koenigswald/Heinrich 1999, Fig. 7) explicitly indicate that *Coelodonta* belongs to a group of taxa that did not occur during the Eemian in what they call middle Europe, even though they indicate its presence in »certain Eem-interglacial« in localities in the Rhine valley, such as Eich (von Koenigswald/Heinrich 1999, 99–100), and in the upper beds at Burgtonna (von Koenigswald/Heinrich 1999, 101). Steinheim has the three species of rhinos, but then it has also three levels: the famous interglacial fauna with *Elephas antiquus* is sandwiched between levels with *Mammuthus*. Von Koenigswald and Heinrich (von Koenigswald/Heinrich 1999) indicate the presence of *Coelodonta* only in the uppermost level, although the exact provenance of many of the specimens is not known. A. J. Stuart (1982) indicated the presence of *Coelodonta* and *S. hemitoechus* together with *Ovibos* and lemmings and more typical interglacial elements in the latest Eemian of Crayford, but interpreted this as the transition of the following cold stage. And at Stoke Tunnel, also of latest Eemian age, *Coelodonta* was found together with *Emys orbicularis*. C. Petronio and R. Sardella (Petronio/Sardella 1998) reported *Coelodonta*, *Stephanorhinus hemitoechus*, *Hippopotamus* and *Elephas antiquus* from layer b at Ingarano (Apulia, southern Italy), which they correlated to OIS 3. This seems thus to be a glacial situation where the »glacial taxa« extend into a refuge of the »interglacial taxa«.

In the case of Neumark-Nord, excellent material shows the presence of the three species *C. antiquitatis*, *S. hemitoechus* and *S. kirchbergensis*. And it does not seem very likely that complete skulls in very good condition have been reworked, nor does the sedimentary environment suggest such reworking. At various points fossils of the different species have been found in direct association (Fig. 36).

On 2/9/1996 the remains of an elephant, provisionally called E I, were excavated. Along with this *Elephas antiquus*, remains of *Equus*, *Megaloceros giganteus* and of rhinos were collected. Though the assignation of individual specimens

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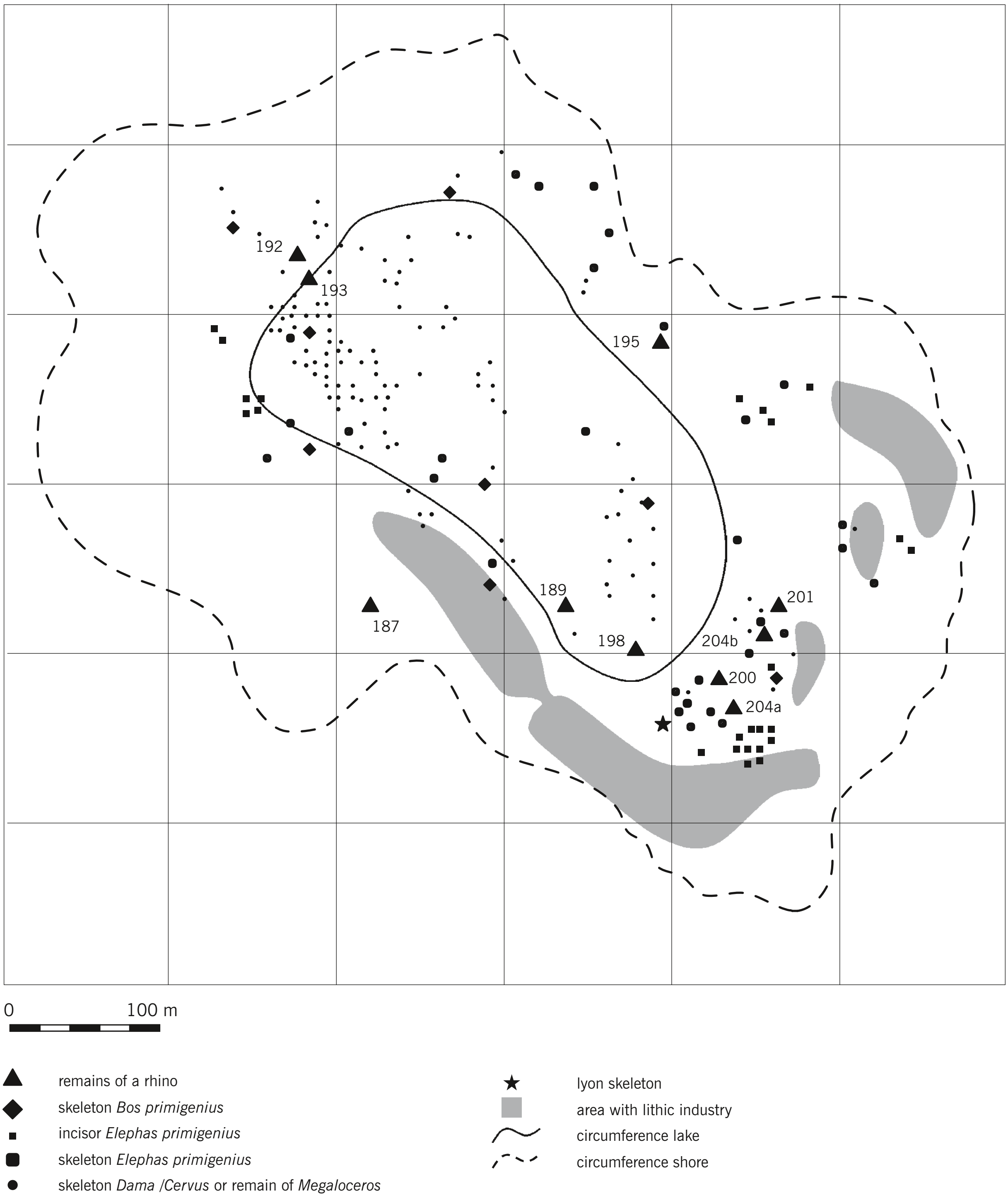
[5] Descriptions or citations by the following authors, but not necessarily with the taxonomy adopted here: Cerdeño 1987; Cerdeño 1993; Van der Made 1996; Van der Made 2001; Stromer von Reichenbach 1899; Van Kolfschoten 1989; Moullé 1998; Kahlke 2001; Franzen et. al. 2000.



| *S. kirchbergensis* | *S. hemitoechus* | *Coelodonta* |
|---|---|---|
| 193 = NN 32 - skull | 189 = HK 88: 14 - skull & skeleton | 187 = HK87: 300 - skull |
| 198 - skull | 189 = HK 88: 14, 61 - axis | 192 - NN 33 - astragalus |
| 200 = E 24 - skull & frags | 200 = E 24 - humerus, $M^X$ | 195 = 95, 3-4 - ulna & $T_1$ |
| 204b = E I - vertebrae & humerus | 204a = E II - nasals, occiput & $M^X$ | 201 = 1996, 47 - skull |
| NN50 - Mc III | E 21 - skull fragment | 204b = E I, 35-42 - hyoid, mandible, etc. |
|  | 1996, 45 - ulna |  |
|  | Frühling 94 - lateral phalanx |  |

**Fig. 36** The Neumark-Nord OIS 7 lake, the distribution of lithic artefacts, and the finds of remains of large mammals, in particular the rhinos.

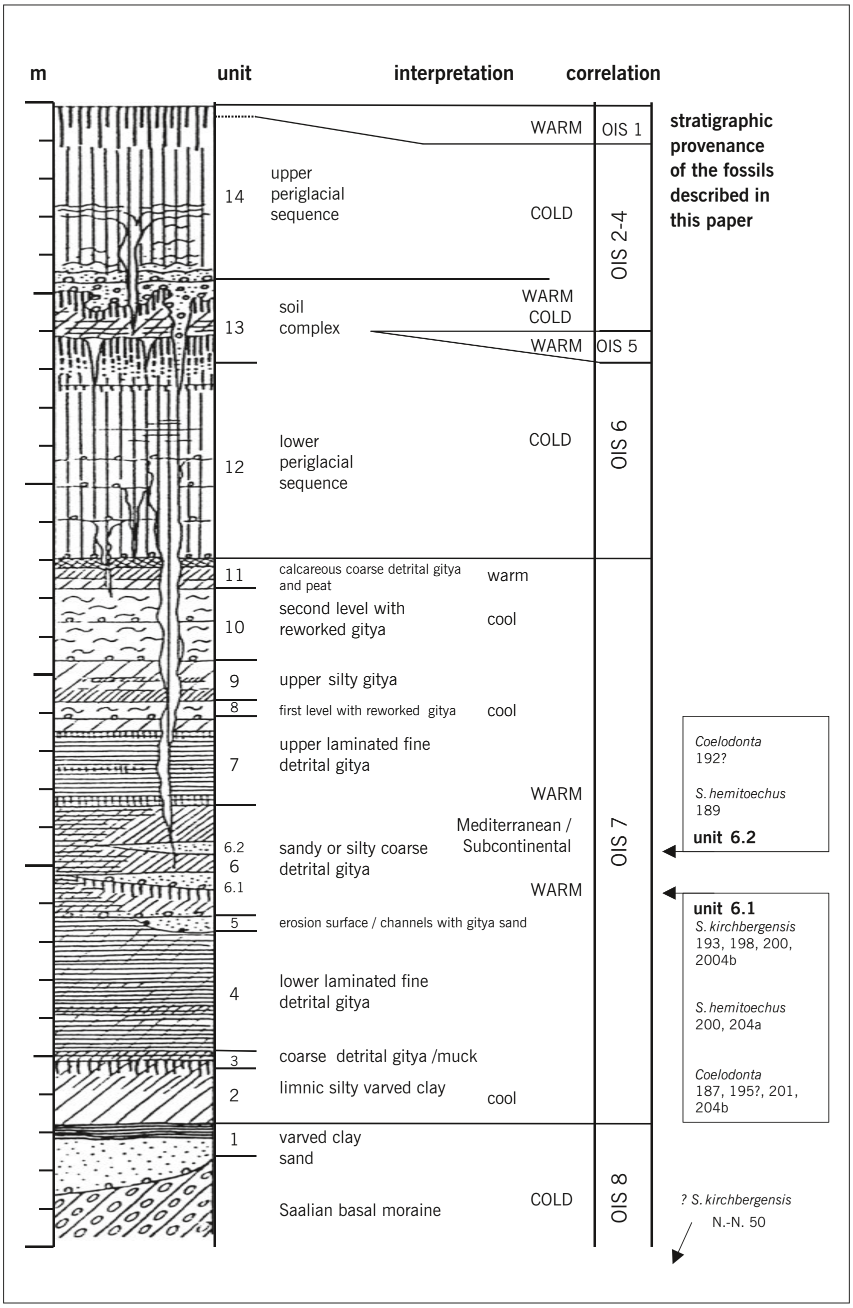


**Fig. 37** The stratigraphy of Neumark-Nord after Mania (in prep.), the proposed correlation to the OIS and the stratigraphic provenance of the fossil rhinocerotidae described in this paper.

to species of rhino is not always easy, the assignation of a fragment of a mandible (E I, 42) to *Coelodonta* seems secure and the assignation of a number of vertebrae and a large and gracile humerus to *Stephanorhinus kirchbergensis* also seems secure. This implies that both species lived at the same place at the same time, or at least within such a short time as to be fossilised together.

In the summer of 1996, various remains were collected from the »Untere Uferzone« (=lower shore), including remains of *Bos primigenius*, *Equus*, *Cervus elaphus*, and a skull of *Coelodonta* and an ulna of a different species, probably *S. hemitoechus*.

At a site close to the remains of an elephant, provisionally called E 24, remains were collected that belong to: *Elephas antiquus*, *Cervus elaphus* and *Bos primigenius*, as well as a skull of *S. kirchbergensis* and a humerus that is far too robust for that species and which is identical to the humerus of the skeleton of *S. hemitoechus*.

It thus appears that any one of the three species of rhinos has lived together at Neumark-Nord with any of the other species, and it seems very likely that all three were contemporaries. This does not necessarily mean that they lived most of the time together and shared or competed for resources, but it suggests that they at least shared the water of the lake. *Coelodonta* did not only occur with the other two species of rhinos and in particular with *S. kirchbergensis*, but also with *Bos primigenius*, *Cervus elaphus* and such a typical »interglacial« form as *Elephas antiquus*.

The different fossiliferous points that yielded rhinoceros remains are in two levels that are not wide apart: units 6.1 and 6.2 (Fig. 37). In unit 6.1 all three species are present and in unit 6.2 *S. hemitoechus* was found along with a possible *Coelodonta*. Pollen collected from the Neumark-Nord sequence, shows that unit 6 is within the interglacial sequence and that units 6.1and 6.2 are dominated by *Corylus* (hazel) (Seifert 1990, Fig. 6). Within this interglacial

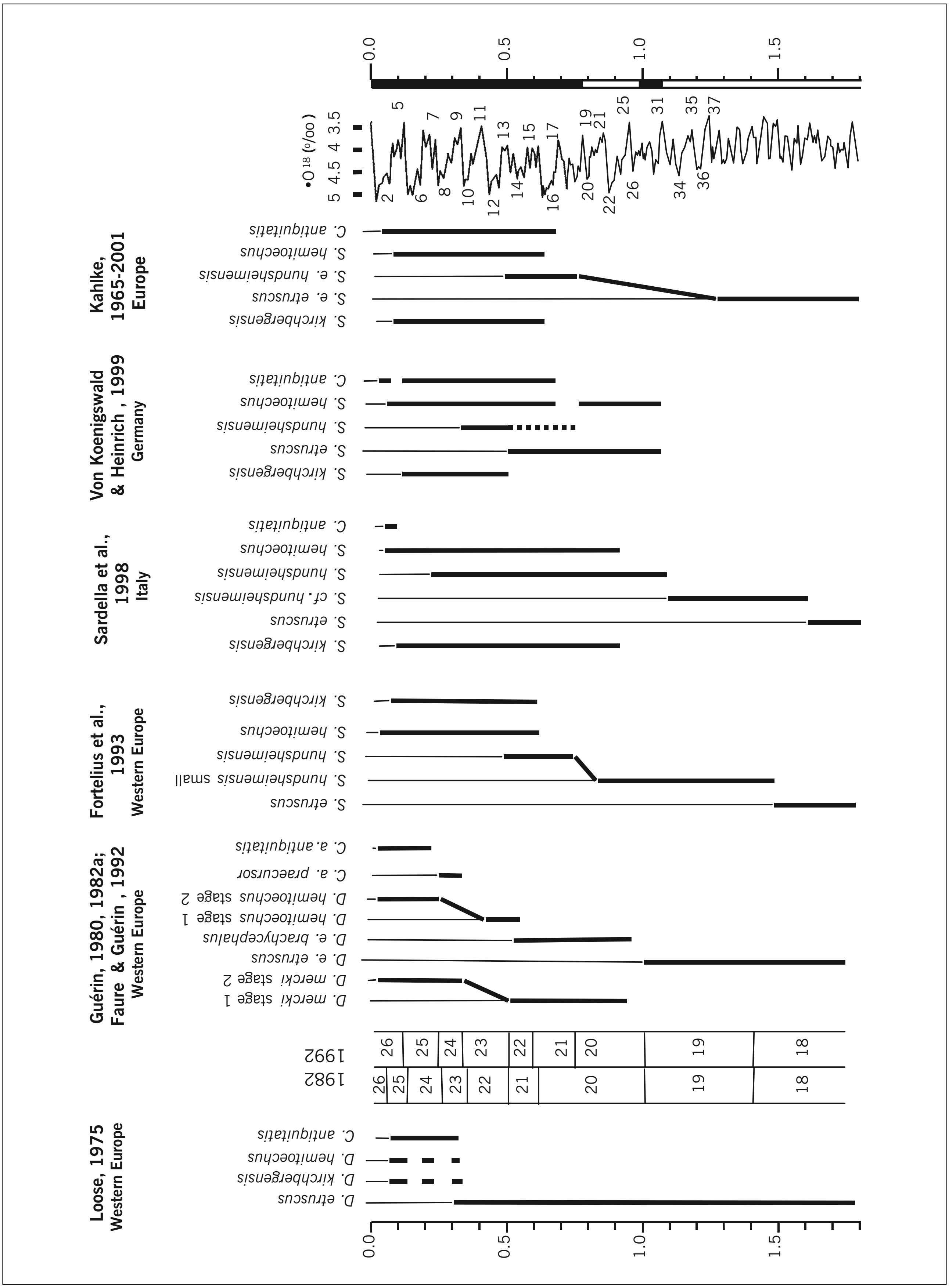


**Fig. 38** The stratigraphic distribution of the different western European Pleistocene rhinos as given by, or interpreted from, Loose (1975), Guérin (1982), Fortelius et. al. (1993), Kahlke (1965; 1969; 1975; 1977; 2001) and Sardella et. al. (1998). Not all these studies provided range charts, and the ages of the localities on which the ranges are based are not estimated the same way by all authors, therefore, this figure should be considered only as an attempt to present the different views in a comparable way. The biochronological units by Guérin (1980; 1982a) are indicated by the numbers 18–26. The ranges of the rhinos are indicated with reference to the updated ages of the units 19–26 by Faure/Guérin (1992). The names *Dicerorhinus, Stephanorhinus, mercki* and *kirchbergensis* are used as by the authors.

sequence, first *Betula*, then *Quercus*, *Corylus* and *Carpinus* are dominant in the pollen counts. There cannot be any doubt as to the presence of *Coelodonta* in the interglacial environment.

Judging from the oxygen isotope stages, the period from OIS13 to OIS15 did not have extreme glacial nor extreme interglacial conditions. If *Coelodonta* was present in OIS7, it could have been present as well in OIS13 to OIS15, however, at present a clear west European record is lacking not only for OIS 13 and 15, but also for the cold periods OIS 12 and 14.

The woolly rhino, *Coelodonta antiquitatis*, is widely seen as a »glacial species«. Species that during glacial or cold periods expanded their distribution into mid-latitude Europe include species that during interglacial periods lived in northern Eurasia, mainly in the tundra (e. g. *Rangifer tarandus*), in arid areas in central Asia (e. g. *Saiga tatarica*) or in mountainous regions (e. g. *Marmota*). Unlike *Mammuthus primigenius*, *Ovibos moschatus*, *Rangifer tarandus* and others, *Coelodonta* did not extend its range into North America, but unlike *Ovibos moschatus* and *Rangifer tarandus*, it did reach the south of Spain (Kahlke 1999). This suggests that the species was more adapted to dry or open landscapes than to polar or extreme glacial conditions. In this sense, its occurrence in an interglacial environment in Europe need not come as a surprise.

### *Stratigraphic distribution of the west European Pleistocene Rhinocerotidae*

In the past years, there has been a relative consensus on the rhinos that are to be recognised, even though different names have been applied. However, different authors give different temporal ranges for these rhinos, as can be seen in Fig. 38. This, of course, is a problem when interpreting the relationship between evolution and biogeography of the rhinos and global climate and environmental change and faunal change in general. Being large herbivores and prey to early humans, rhinos formed an important part of the world of early man and increasing our knowledge on the evolution and distribution of this group helps us to understand this world. Therefore a discussion of the temporal ranges of the different rhinos of the Pleistocene of western Europe seems useful.

The comparison presented in Fig. 38 is not straightforward, since the ranges are given for different areas (e. g. Italy or western Europe), and there are differences in the estimates of the ages of the localities, the number of glacial cycles recognised, and the ages of the different glacial or interglacial periods. Some authors indicated the presence/absence of a taxon for each cold or warm period, whereas others do not do this or only do it in the case of the Eemian.

Loose gave a time scale, environmental/climatic curves with the following stages from the present to 300 ka: Weichselian, Eemian, Saalian, Holsteinian, Elsterian and the very top of the »Cromerian Complex«. At present, most of these stages are considered to be older, than indicated by Loose, and more warm and cold stages are recognised. Here, the temporal ranges of the rhinos are given more or less corresponding to Loose's chronological scale, but taking the ages of the climatic fluctuations according to the oxygen isotope curves into account. It is noteworthy, that Loose interpreted *C. antiquitatis* as a species with a continuous range, whereas *S. kirchbergensis* and *S. hemitoechus* are considered to have a strictly interglacial distribution.

Guérin (1980; 1982) introduced a biozonation for the Pleistocene, with units with numbers 18–26 (following the units numbers 1–17 of the Neogene) and indicated ages for these units. M. Faure and Guérin (Faure/Guérin 1992) provided slightly older ages for most of the units. Guérin (1980; 1982a) recognised various stages of evolution within the different species of west European rhinos. The extremely rare *Elasmotherium* is omitted here.

Fortelius et. al. (1993) discussed the phylogeny and stratigraphic ranges of the rhinos, but did not give a range chart. They used west European localities and indicated the presence of a small *S. hundsheimensis* in a number of localities and discussed the overlap in temporal distribution of *S. hundsheimensis* and *S. hemitoechus* in Mosbach and other localities. The ranges given in the figure are based on these localities, in combination with the ages that these localities are assumed to have in this study.

Sardella et. al. (1998) gave a large range chart for many species in Italy with numerical ages, and the ranges of the rhinos are taken from that chart.

Von Koenigswald and Heinrich (von Koenigswald/Heinrich 1999) gave faunal lists of a great number of, what they call central European localities (but which are mainly German localities), a range chart and a figure with faunal events (their figures 7 and 6, respectively), but did not give the numerical ages of the faunal events. Their figures contradict each other[6] as well as the figures and the text[7]. Fig. 38 is based on their figure 7, while variations are discussed in the text. These authors believe that there is a glacial cycle between Süssenborn and the Elsterian. They did not treat the earliest Pleistocene faunas.

H.-D. Kahlke (2001) largely reflected his earlier opinions (Kahlke 1965; Kahlke 1969; Kahlke 1975; Kahlke 1977) and indicated that *Coelodonta* appeared during the early Elster, in localities like Süssenborn and Bad Frankenhausen and that *S. kirchbergensis* and *S. hemitoechus* appeared during the following interglacials. No numerical ages are given, however, here Süssenborn is assumed to be about 650 ka old, and the ranges are given accordingly.

The different rhino species dispersed from other parts of Eurasia into western Europe, which implies that they had different temporal distributions in other areas. For this reason, it is meaningless to indicate a temporal range, if no geographical area is defined in which it should be valid. Here this area is western Europe and is taken as Europe west of the eastern boundaries of Germany, Czech Republic, Austria and Italy. In terms of degrees longitude, this is about one third of Europe and also for other reasons this seems a very

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[6] E. g. the entry of *Coelodonta* in the later faunas with *Arvicola cantianus* in Fig. 6, but in the *Mimomys* faunas in Fig. 7.

[7] E. g. *S. hemitoechus* not occurring in the Eemian in figure 7, but being cited from Taubach and Burgtonna.

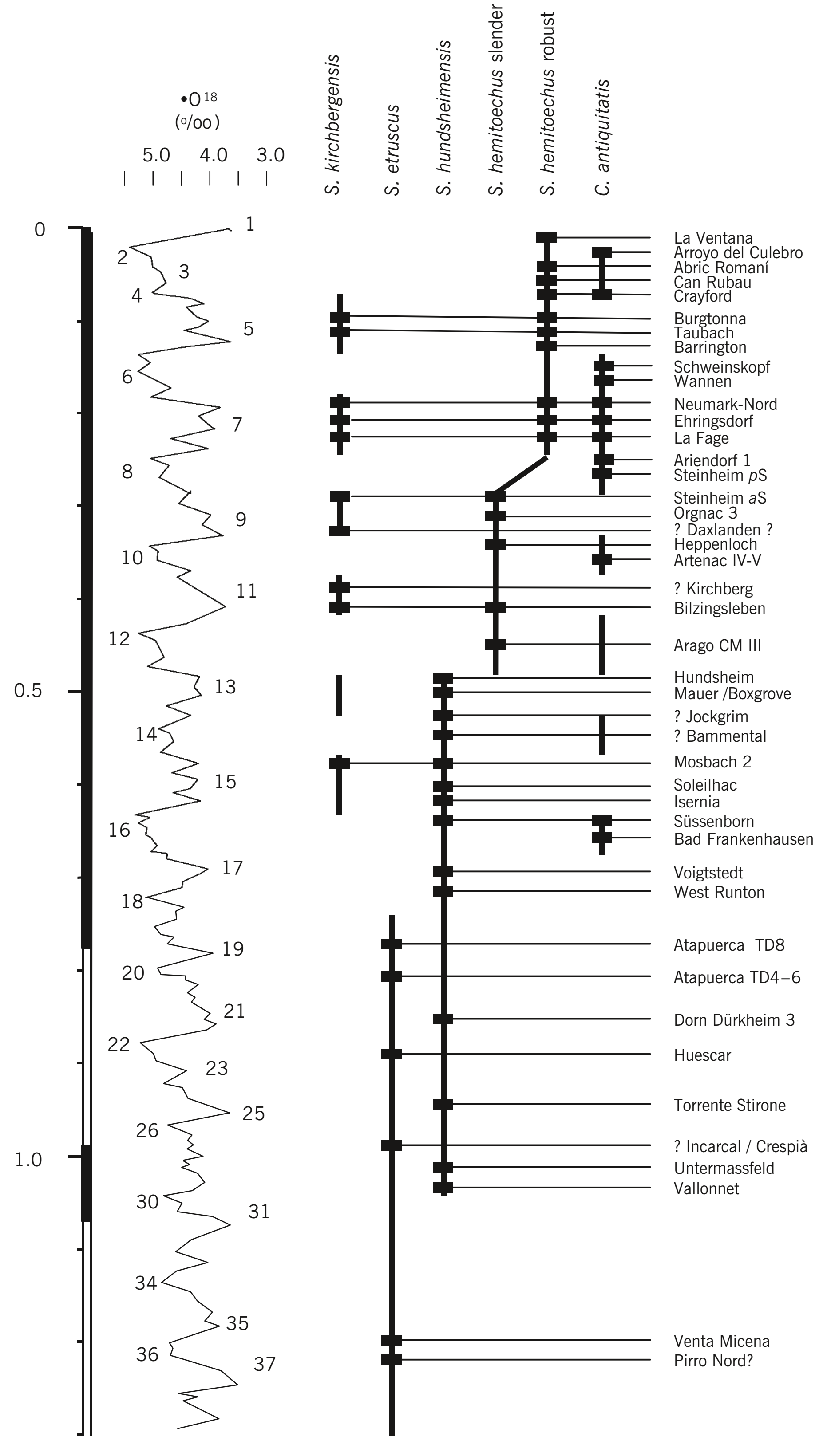

**Fig. 39** The stratigraphic distribution of the different west European rhinos. On the left is the time in Ma, the palaeomagnetic scale and oxygen isotope curve (after Shackleton 1995). On the right are the localities that are used to construct the temporal distribution of the rhinos. The position of these localities relative to the oxygen isotope stages is largely after (Van der Made 2001; Van der Made et. al. 2003). A question mark in front of the name of a locality indicates that its exact stratigraphic position relative to OIS or palaeomagnetism is not known and a question mark after the name indicates that the presence of this species is tentative.

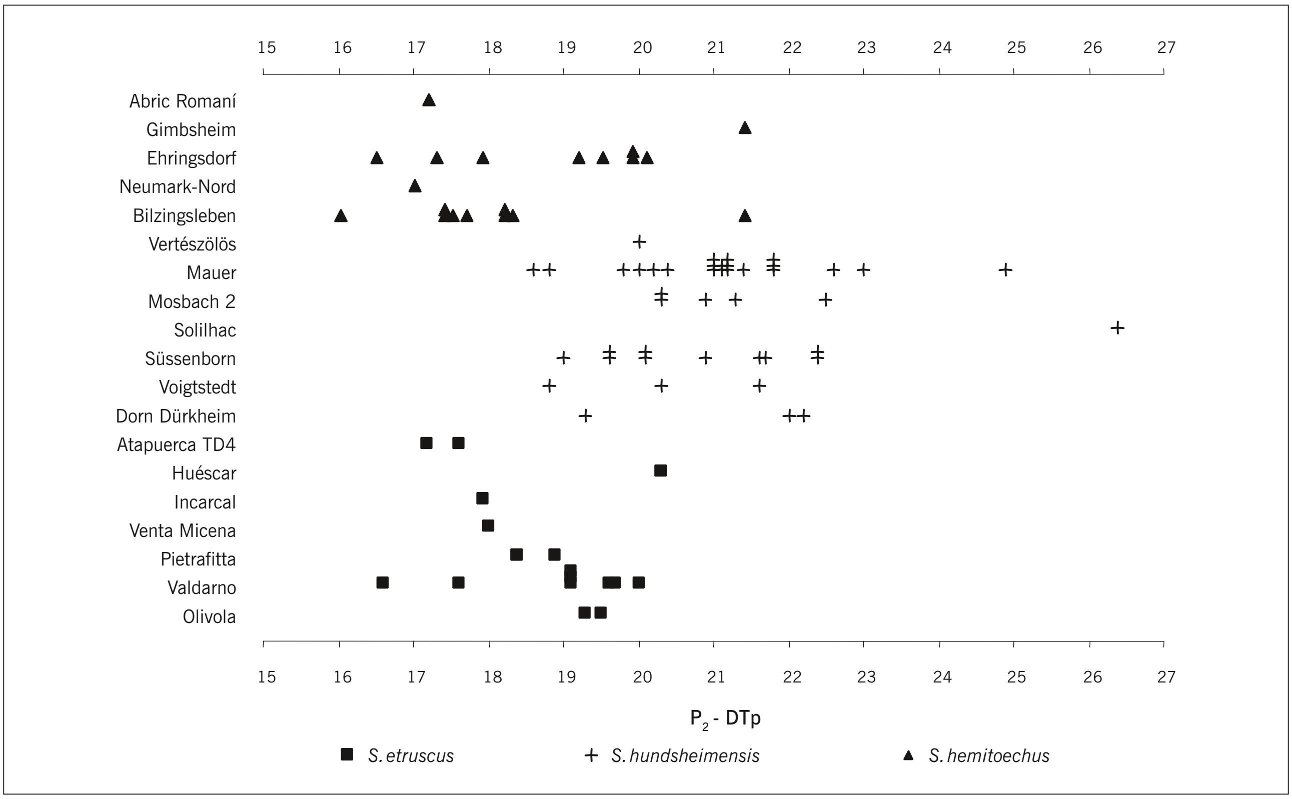

**Fig. 40** The width of the posterior lobe of the $P_2$ in the smaller species of the genus *Stephanorhinus*. The localities are in approximate order from old (bottom) to young (top). *Stephanorhinus etruscus* from Olivola (IGF), Valdarno (IGF, IQW), Pietrafitta (Mazza et. al. 1993), Venta Micena (Santafé-Llopis/Casanovas-Cladellas 1987), Huéscar (MNCN) and Atapuerca TD4 (MB). *Stephanorhinus hundsheimensis* from Dorn-Dürkheim (FISF), Voigtstedt (IQW), Süssenborn (IQW), Solilhac (MCP), Mosbach 2 (NMM, SMNS), Mauer (SMNK) and Vertészölös (HGSB). *Stephanorhinus hemitoechus* from Bilzingsleben (FBFSUJB), Neumark-Nord (LVH), Ehringsdorf (IQW), Gimbsheim (NMM) and Abric Romaní (LAUT).

useful limitation. There is very little record north of Germany and England, which further limits the area. Fig. 39 gives localities in this area and the rhinos that occur in them. The localities are positioned relative to the palaeomagnetic scale and oxygen isotope stages as indicated by Van der Made (2001) and Van der Made et. al. (2003).

### *The extinction of* S. etruscus *and appearance of* S. hundsheimensis

In particular the perception of the *Stephanorhinus etruscus/S. hundsheimensis* »group« became progressively more complex. *Dicerorhinus etruscus* of Loose became the lineage *D. e. etruscus - D. e. brachycephalus* of Guérin. Fortelius et. al. substituted the name *Dicerorhinus* by *Stephanorhinus* and applied the name *hundsheimensis* to most of what was called *brachycephalus* by Guérin, but more importantly considered this group as two different species, that might represent a lineage, or not. Von Koenigswald and Heinrich considered *S. etruscus* and *S. hundsheimensis* two different species that may have overlapping ranges. Kahlke (2001) maintained a model of evolution similar to that of Guérin, but with updated nomenclature. There are thus basically two opinions: a single lineage and a two lineage model, and within the latter, there are differences as to the moment of extinction of *S. etruscus*.

*Stephanorhinus etruscus* was present already in the Late Pliocene. It does not seem likely that it increased in size and evolved into *S. hundsheimensis* for various reasons: 1) *S. hundsheimensis* is more primitive than *S. etruscus* in having larger P2 and cheek teeth with lower crowns (Van der Made 2001; Van der Made et. al.2003, Figs 40–43) the two species have overlapping temporal distributions. *Stephanorhinus etruscus* is present in Atapuerca levels TD4, TD6 and TD8 (Van der Made 1998; Van der Made 1999) and in Huéscar and Venta Micena (see descriptions by Cerdeño 1987; Santafé-Llopis/Casanovas-Cladellas 1987). TD8 is just above the Brunhes-Matuyama boundary and TD4–6 just below (Parés/Pérez-González 1995). *Stephanorhinus etruscus* is also present in Incarcal and Crespià (García-Fernández et. al. 2003; García-Fernández et. al. 2003a). Incarcal is reported to have *Bison* and *Capreolus*, indicating a latest Early Pleistocene age, otherwise the earliest record of *Capreolus* is in the Jaramillo in Untermassfeld. A slightly larger size, lesser hypsodonty and smaller P2, suggest that material from Vallonnet, Untermassfeld and Dorn-Dürkheim 3 more probably belongs to *S. hundsheimensis* than to *S. etruscus*. Palaeomagnetically, Dorn-Dürkheim is dated to the very end of the Early Pleistocene (Franzen et. al. 2000) and the other two localities to the Jaramillo Event (de Lumley 1996; Wiegank 1997). As a result, there is a temporal overlap between the two species of at least 300 ka.

The very late record of *S. etruscus* indicated by von Koenigswald and Heinrich is partially based on material from Voigtstedt, Süssenborn and Jockgrim, which is identical in these and other features to material from Mauer assigned by the same authors to *S. hundsheimensis* (Van der Made 2001; Van der Made et. al. 2003) and the species is possibly also present in some other localities, where these authors list

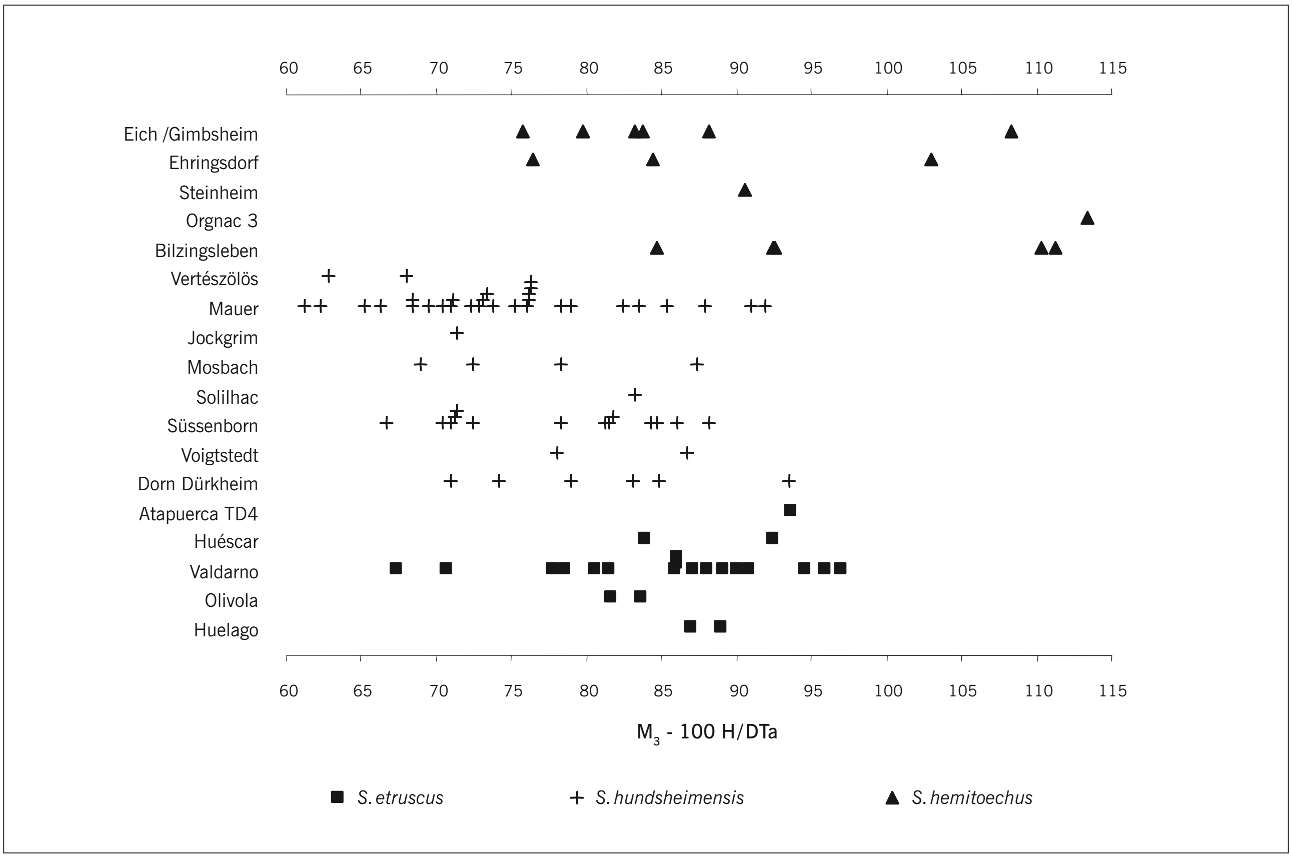

**Fig. 41** The hypsodonty of the smaller species of the genus *Stephanorhinus*. The hypsodonty index 100 H/DTa is given for the $M_3$. The localities are in approximate order from old (bottom) to young (top). *Stephanorhinus etruscus* from Huelago (MNCN), Olivola (IGF), Valdarno (IGF, IQW), Huéscar (MNCN) and Atapuerca TD4 (MB). *Stephanorhinus hundsheimensis* from Dorn-Dürkheim (FISF), Voigtstedt (IQW), Süssenborn (IQW), Solilhac (MCP), Mosbach 2 (NMM, SMNS), Jockgrim (SMNK), Mauer (SMNK) and Vertészölös (HGSB). *Stephanorhinus hemitoechus* from Bilzingsleben (FBFSUJB), Orgnac 3 (LPTUP), Steinheim (SMNS), Ehringsdorf (IQW) and Eich and Gimbsheim (NMM).

*S. etruscus*. The fact that they indicated the possible (but not certain) presence of *S. hundsheimensis* in the Middle Pleistocene *Mimomys* faunas in their figure 7 suggests that the authors were aware of the problem of these rhinos' identification.

Whereas Fortelius et. al. (1993) leave it open whether *S. hundsheimensis* evolved from *S. etruscus*, Mazza et. al. (1993) seem more inclined to consider a »small *S.* cf. *hundsheimensis*« to be an intermediate evolutionary stage between the two species and seem to consider the species to be different from *S. etruscus*, partly because of its smaller size. This form is present in Pietrafitta, Pirro Nord and Westerhoven[8]. Mazza et. al. (1993, Fig. 1; 2) indicated that *S. etruscus* is used as a standard, but comparison with Fig. 3 and 4 of Fortelius et. al. (1993), who use the same comparative data, suggests that *S. hundsheimensis* is the standard and that the curve with the dots is *S. etruscus*. If this is taken into account, the rhino from Pietrafitta resembles *S. etruscus* more than *S. hundsheimensis*, not only in size, but also in proportions, notably in having a relatively small and narrow $P_2$ (see also Fig. 40 and 43). Mazza et. al. did not give a legend with the ratio diagrams of the metapodials, and I was not able to find out which signature represents which sample. The material from Atapuerca TD4–8 and Huéscar is small and very similar to *S. etruscus* and I get the impression that this is also the case for Pietrafitta, though I did not study this material. Here all the »small *S.* cf. *hundsheimensis*« are tentatively included in *S. etruscus*.

### *The extinction of* S. hundsheimensis *and appearance of* S. hemitoechus

Guérin (1980) considered *D. hemitoechus* a descendant of *D. etruscus etruscus*, but not of *D. etruscus brachycephalus* (~*S. hundsheimensis*), which implies that the transition should be outside western Europe and that *S. hemitoechus* arrived here by dispersal. Most other authors coincide in a close relationship, but not direct descendance of these forms, and the arrival of *S. hemitoechus* by dispersal. Loose (1975), Guérin (1980, 1982; 1982a) and Kahlke (2001) considered that *S. hemitoechus* replaced *S. hundsheimensis*. However, Fortelius et. al. (1993) discuss the possibility of overlapping ranges and indicate a very late presence of *S. hundsheimensis* in the later Middle Pleistocene of Torrente Conca, along with *S. hemitoechus*, but did not give this material in their list of specimens studied and tables of measurements. Sardella et. al. (1998) indicate a huge overlap, *S. hundsheimensis* occurring possibly as late as OIS 7. This is probably based on the same record. Verteszölös (just outside of what is here defined as western Europe) yielded some material of a rhino

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[8] For the latter locality see also Stromer von Reichenbach 1899; Van Kolfschoten 1989.

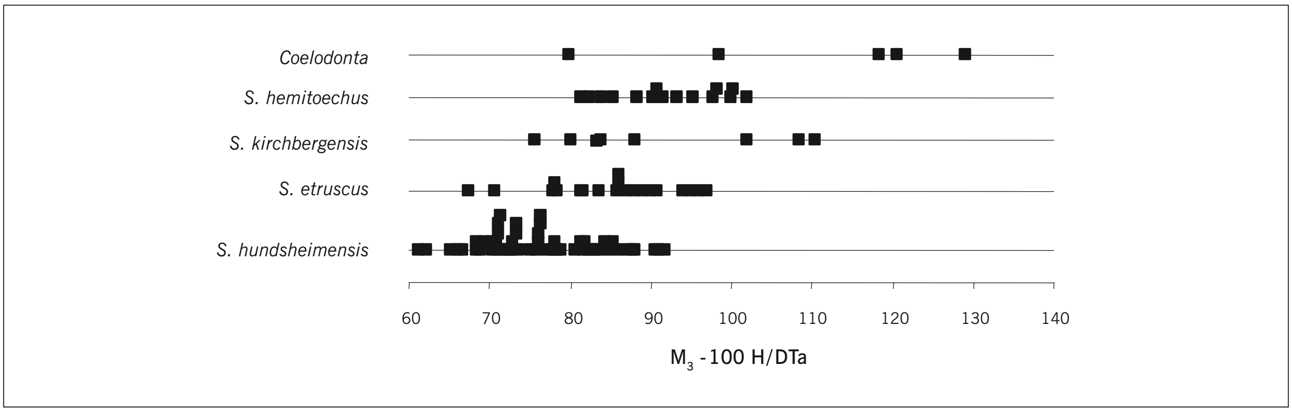

**Fig. 42** Hypsodonty as indicated by the M$_3$. Provenance of data largely as in Fig. 15. *Stephanorhinus hundsheimensis* from Voigtstedt (IQW), Süssenborn (IQW), Solilhac (MCP), Mosbach (NMM, SMNS), Jockgrim (NMM) and Mauer (SMNK), *S. etruscus* from Olivola (IGF), Valdarno (IGF), Monte Pulgnasco (IGF) and Atapuerca TD4 (MB), *S. hemitoechus* from Steinheim (SMNS), Eich (NMM) and Gimbsheim (NMM), *S. kirchbergensis* from Mosbach (NMM, SMNS), Bilzingsleben (FBFSUJB), Steinheim (SMNS), Taubach (IQW), Eich (NMM) and Gimbsheim (NMM) and *Coelodonta antiquitatis* from Steinheim (SMNS), Ehringsdorf (IQW), Backleben (IQW) and Heldrungen (IQW).

(HGSB), including teeth with low crowns and a P$_2$ that is not very small (Fig. 40; 41), and which therefore seems to belong to *S. hundsheimensis*. Information given by Jánossy (1986) suggests that the material I studied is accompanied in the »marly layer« of locality 1 by *Arvicola*, whereas a higher layer in the same locality still contains a saber-tooth cat. The deer is *Cervus elaphus priscus*. The exact age of this locality is not quite clear to me, but seems more likely to be equivalent to OIS13 than to OIS 11. Otherwise, the last occurrence of *S. hundsheimensis* known to me is in Mauer and Hundsheim (Soergel 1914; Toula 1902; Toula 1906) and probably Boxgrove (Parfitt 1999). These localities are assumed to be about 500 ka old, or a time equivalent to OIS 13. Jockgrim has the species and might be as old, or a cycle older.

Sardella et. al. (1988) indicated that *S. hemitoechus* appeared in Italy around the Early-Middle Pleistocene transition, but did not indicate on which record this is based. Possibly this is based on Cigala-Fulgosi (1976), who assigned a skull to that species, which comes from sediments near the Torrente Stirone with reversed polarisation assigned to the late Matuyama just above the Jaramillo. The occiput does not overhang the occipital condyles and in general is primitive, as in *S. etruscus* and *S. hundsheimensis*. The origin of the horn is wide (Zeuner's index, calculated as indicated above, is 0.18) as in *S. hundsheimensis*. The molars are not very large, but the second premolar is very large; the anterior width is indicated as 42 mm, which is in the upper range for *S. hundsheimensis*. Most probably the skull belongs to *S. hundsheimensis*. Von Koenigswald and Heinrich (von Koenigswald/Heinrich 1999, Fig. 7) indicated the presence of *S. hemitoechus* in the Early Pleistocene and in the latest *Mimomys* faunas, but the basis for this cannot be found in their faunal lists, where *S. etruscus* is cited. Fortelius et. al. (1993) and von Koenigswald and Heinrich (von Koenigswald/Heinrich 1999) mentioned the presence of this species in Mosbach 2. However, the material is from old collections and no other locality of this age with *S. hemitoechus* is known, and therefore it seems much more likely that the material of that species is from the younger »Mosbach 3«. However, it is not clear how old »Mosbach 3« is. The earliest occurrences of *S. hemitoechus* are here considered to be in Arago (OIS 12) and Bilzingsleben (OIS 11).

### *Evolutionary stages of Stephanorhinus hemitoechus*

Azzaroli (1962) recognised two subspecies of *D. hemitoechus*, a primitive one for Mosbach, Clacton and Bucine and a more advanced one from the localities that he believed to be of Late Pleistocene age. Also Fortelius et. al. (1993, 120) recognised evolutionary changes in *S. hemitoechus*, but the localities that Azzaroli believed to be Late Pleistocene are listed by them as »Late Middle or Late Pleistocene« (Fortelius et. al.

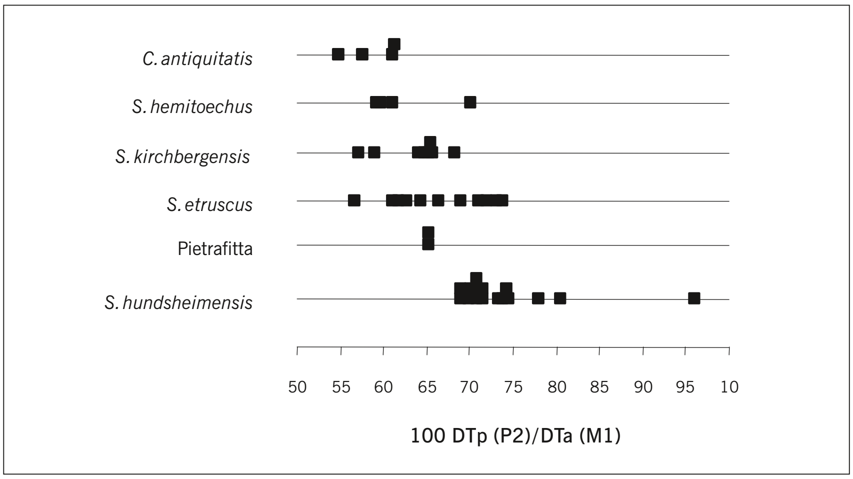

**Fig. 43** The relative size of the P$_2$ (the width of its anterior and posterior lobes expressed as a percentage of the width of the first lobe of the M$_1$ in the same mandible). *Stephanorhinus hundsheimensis* from Voigtstedt (IQW), Süssenborn (IQW), Solilhac (MCP) and Mauer (SMNK), *S. etruscus* from Olivola (IGF), Valdarno (IGF), Monte Pulgnasco (IGF) and Atapuerca TD4 (MB), *S. hemitoechus* from Neumark-Nord (LVH), Ehringsdorf (IQW) and Gimbsheim (NMM), *S. kirchbergensis* from Mosbach (NMM, SMNS), Bilzingsleben (FBFSUJB), Eich (NMM) and *Coelodonta antiquitatis* from Gimbsheim (NMM) and Eich (NMM).

1993, 67). Guérin (1980, 1982) indicated that the change from one to the other stage of evolution occurred during stage 24. Probably the changes were slow and gradual, but the material from Neumark-Nord is here assigned to *S. hemitoechus hemitoechus*, which implies that the transition of one subspecies to the other occurred before OIS7.

### *The entry of* Stephanorhinus kirchbergensis

In more or less recent times, all authors consider this species to have arrived by dispersal from another part of Eurasia, most assumed this to have occurred more or less at the same time as the dispersal of *S. hemitoechus* and the oldest locality mentioned or cited by them tends to be Mosbach 2. However, Guérin (1980, 1982 a) assumed *S. kirchbergensis* (or *D. mercki*) to have dispersed considerably earlier into western Europe, early in his zone 20 (0.6–1 Ma) in the localities Tegelen, Mosbach and Solilhac. Tegelen is a latest Pliocene locality (Freudenthal et. al. 1976). Though material from that locality has been assigned to *S. kirchbergensis* (or *»R. mercki«*) (Bernsen 1927), others have suggested the material belongs to *S. etruscus* (Loose, 1975; Van Kolfschoten 1989). However, the rhino from Tegelen resembles metrically *S. hundsheimensis*, though there are some specimens that differ morphologically. Solilhac is a locality that was excavated already in the early part of the 19th century. Remains of ungulates from this locality in the MCP suggest a similar age as Mosbach 2 (Van der Made 2001, Fig. 6). Mosbach 2 and Solilhac are here believed to be about 0.6 Ma old and to be correlated to OIS 15 (Van der Made 2001; Van der Made et. al. 2003). Sardella et. al. (1998) indicted the entry of *S. kirchbergensis* in Italy just before the Early-Middle Pleistocene transition. It is not clear on which fossils this is based. However, already Azzaroli (1962) indicate that numerous remains in Italy have been attributed to *S. kirchbergensis* (*»Rh. mercki«*), which in his opinion belong to *S. hemitoechus*. Historically the species have frequently been confused, and maybe some older literature has been used. In Tiraspol, *S. kirchbergensis* occurs (coll.), apparently together with *Mimomys* (Nikiforova et. al. 1971), suggesting that the dispersal of this species into Europe was diachronic. The species is considered to be a strictly »interglacial« species, dispersing each interglacial into mid-latitude Europe. Since it is not known from Spain, this was probably not its refuge area in glacial times.

### *The entry of* Coelodonta

*Coelodonta* has a well known record in East Asia anterior to its dispersal into Europe. Its dispersal into western Europe is usually assumed to have occurred during the Elsterian, but not by Guérin, who assumed the dispersal of *Coelodonta* to have occurred during the Saalian, between 0.25 and 0.15 Ma (or 0.35 and 0.25 Ma). Kahlke (2001) cited three early Elsterian localities for the earliest occurrence of *Coelodonta*: Bornhausen, Bad Frankenhausen and Süssenborn. The first two are cited by Guérin to have *Coelodonta*, but Bornhausen is assumed to be younger than the Elsterian and the age for Bad Frankenhausen is not given. Von Koenigswald and Heinrich (von Koenigswald/Heinrich 2001), indicate *Coelodonta* to be present in the first two localities, which they believe to be Elsterian, but not in Süssenborn, which they believe to be older (but in their figure 7, they indicate *Coelodonta* to be present in the *Mimomys* faunas). In any case, *Coelodonta* seems to have appeared later in France than in Germany; it also seems to have appeared relatively late in England (Stuart 1982) and still later in Italy (Sardella et. al. 1998, Fig. 37), and Spain, where it may have entered only during the latest glacial. In France, the oldest record might be in Artenac, where J. F. Tournepiche (1996) indicates it to be present in levels IV and V (a composite list is given) together with *Dinoblastis latidens*, *Canis lupus* cf. *lunellensis*, *Rangifer tarandus*, *Gulo gulo* and others, and suggests these units to cover OIS 10–11. The cold elements fit very well for OIS10.

For most authors, the appearance of *Coelodonta* in western Europe appears thus to be linked to the age of the Elsterian. Loose recognised few glacial cycles and assumed the Elsterian to be about 200–300 ka old. Guérin (1982) situated the Elsterian between 0.5 and 0.35 Ma. Süssenborn is said to be in early Elsterian sediments and has *Mimomys savini*, which became an important marker, initially for the Early Pleistocene, later also for the early Middle Pleistocene. Von Koenigswald and Heinrich (von Koenigswald/Heinrich 1999) discussed the age of the Elsterian and argued that the Elsterian in its type area should be much younger than Süssenborn because of the age of the Anglian in England (which is supposed to be as old as the Elsterian in its type area) and on the Cromerian of the Netherlands (which seems to be younger than the type Cromerian, but is assumed to be older than the Elsterian), and the augite-hornblende transition in the Rhine sediments. If there is doubt whether Süssenborn is in Elsterian sediments so close to the typical Elsterian, is the correlation of a lithostratigraphical level in the Rhine valley or the Anglian Till to the Elsterian more reliable? Or the correlation of the Dutch »Cromerian« to the English Cromerian and from there to the area where the Elsterian is defined? In any case, if we accept Kahlke's statement that *Coelodonta* is present in Süssenborn, an early presence in western Europe seems likely. Nevertheless, it is striking that there is no record of the genus in several of the following cycles.

### *The extinction of* S. kirchbergensis, S. hemitoechus *and* Coelodonta

Loose (1975) indicated that all these species became extinct in the early Weichselian. Guérin (1982) indicated all three species to be present in (and till the end of) his zone 26, which corresponds to the Weichselian. For the latest occurrences of *S. kirchbergensis* (= *D. mercki*) he indicated Villefranche-sur-Saône and Grimaldi-Prince (lower zone 26) and Grimaldi-Enfants (zone 26 and with Mousterian industry). Von Koenigswald and Heinrich indicated in their figure 7 that *S. hemitoechus* went extinct before the Eemian, *S. kirchbergensis* after the Eemian and *Coelodonta* after the Weichselian, but indicate the presence of *S. hemitoechus* in a number of Eemian localities (von Koenigswald/Heinrich 1999, 99–102).

It seems likely that *Coelodonta* became extinct at the end of the last cold stage. *S. kirchbergensis* may have survived till the beginning of the last glacial stage, but if truly an interglacial species, its survival till the end of this cold stage would be surprising. One of the last records of *S. hemitoechus* might be in La Ventana, close to the Pleisto-Holocene transition (Sánchez et. al. 2003).

## Acknowledgements

I thank Prof. Dr. D. Mania and U. Mania for inviting me to study material from Neumark-Nord, for help, stimulating discussions, and hospitality. Andy Currant was so kind to let me use his notes on the problems concerning the type material and type locality of *S. hemitoechus* and the early literature on the species. I thank the following persons for access to material or help of any other kind while working in their institutes: Amprimoz, G. Bossinski, E. Carbonell, B. Castillo, E. Cioppi, A. Currant, E. Frey, K. Heissig, J. L. Franzen, E. Frey, J. Jagt, A. Justus, H.-D. Kahlke, L. Kordos, O. Kullmer, H. Lutz, L. Maul, H. Meller, A. M. Moigne, W. Munk, L. Rook, G. Rössner, B. Sánchez Chillón, E. Turner, J. de Vos, R. Ziegler and the staff of the Instituut voor Aardwetenschappen, Utrecht library. While carrying out this research, I received support from the Deutsche Forschungs Gemeinschaft through Prof. Mania, but also from projects CGL 2009-12703-C03-01 and CGL 2008-03881 of the Spanish Ministry of Science and Innovation and the Unidades Asociadas programme of the Consejo Superiror de Investigaciones Científicas.

Date of submission of the manuscript: march 2004

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