

Chapter 11

Rhinocerotidae

Elina Hernesniemi, Ioannis X. Giaourtsakis, Alistair R. Evans, and Mikael Fortelius

Abstract The remains of fossil rhinoceroses from Laetoli represent at least three taxa: *Ceratotherium efficax*, *Ceratotherium* cf. *simum*, and *Diceros* sp. The great majority of the material from the Pliocene Laetoli Beds belongs to *C. efficax*, for which we provide a revised diagnosis. This taxon has been frequently misidentified and inaccurately referred to as *C. praecox*, *C. germanoaffricanum*, or *C. mauritanicum*. A cranium from the Upper Ndolanya Beds shows more derived dental features, but a precise assignment to *C. germanoaffricanum* or *C. simum* is presently not possible. The occurrence of true *Diceros* in the Laetoli Beds is demonstrated by a partial cranium with incomplete dentition, but very few other specimens can be potentially attributed to this genus. Analysis of occlusal wear patterns suggests that *C. efficax* was a grazer or possibly a graze-dominated mixed feeder; in either case it probably included a variable component of browse in its diet. The transition from a *Diceros*-like ectolophodont dentition to the full-fledged plagiolophodonty seen in extant *Ceratotherium simum* included a substantial period of stasis, spanning at least the interval represented by the Laetoli Beds. A shift in the dietary regime towards increased grazing had occurred by the Upper Ndolanya time, and this trend continued from the early Pleistocene to the Recent. Based on the available fossil record, the split of the two lineages leading to the extant species must have taken place in Africa during the Miocene.

Keywords Rhinocerotidae • *Ceratotherium* • *Diceros* • Taxonomy • Evolution • Nomenclature • Paleocology • Paleodiet

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Introduction

Since the first systematic description by the German paleontologist W. O. Dietrich during the Second World War (Dietrich 1942, 1945), fossil remains of rhinoceroses from Laetoli have been described and discussed under a variety of names (Arambourg 1947, 1959; Hooijer 1969, 1972; Groves 1975; Guérin 1979, 1980a, 1987a; Geraads 2005). The Laetoli rhinoceroses are of particular interest for understanding the early evolution of the *Ceratotherium* lineage during the Plio-Pleistocene, as well as for interpreting the paleoecological setting of the locality. In particular, the transition from a generalized ancestral morphology to the specialized grazing condition of the extant white rhinoceros, *Ceratotherium simum*, has been long regarded as a case study for evolutionary research (Osborn 1903; Dietrich 1942; Thenius 1969; Stanley 1979).

Our aim is simple: to revise the taxonomy of the rhinoceros material from Laetoli housed in the collections of the National Museums of Tanzania and Kenya, and in the collections of the Natural History Museum, London. Furthermore, we describe it with emphasis on functional aspects, particularly the dental functional morphology and wear patterns. We consider the implications of our findings for the paleoecology of the Laetoli sequence and the evolutionary history of the taxa, including the origins of *Ceratotherium simum*. We also discuss in detail the complicated taxonomic history of *C. efficax* (Dietrich, 1942), and *Ceratotherium praecox* Hooijer and Patterson, 1972.

Materials and Methods

Institutional Abbreviations

AMPG: Athens Museum of Paleontology and Geology, University of Athens; BMNH: British Museum of Natural History (=Natural History Museum), London; BSPG: Bayerische Staatssammlung für Paläontologie und Geologie,

München; FSL: Faculté des Sciences, University of Lyon; GSN: Geological Survey of Namibia, Windhoek; IPUW: Institut für Paläontologie der Universität, Wien; KMMA: Koninklijk Museum voor Midden-Afrika, Tervuren; KNM: National Museums of Kenya, Nairobi; LGPUT: Laboratory of Geology and Palaeontology, University of Thessaloniki; MNHB: Museum der Naturkunde für Humboldt Universität zu Berlin; MNHN: Muséum National d'Histoire Naturelle, Paris; NHMW: Naturhistorisches Museum, Wien; NME: National Museum of Ethiopia, Addis Ababa; NMT: National Museum of Tanzania, Dar es Salaam; RMNH: Rijkmuseum van Natuurlijke Historie (Naturalis), Leiden; SAM: South African Museum, Cape Town; SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main; SMNK: Staatliches Museum für Naturkunde, Karlsruhe; SMNS: Staatliches Museum für Naturkunde, Stuttgart; ZMA: Zoological Museum, Amsterdam.

Material

The material of fossil rhinoceroses from Laetoli is housed at the National Museum of Tanzania in Dar es Salaam, the National Museums of Kenya in Nairobi, the Museum der Naturkunde für Humboldt Universität in Berlin, and the Natural History Museum of London. Detailed information about the excavation and research history of the locality, as well as of the geological and stratigraphical setting is provided by Harrison (2011), Ditchfield and Harrison (2011), and Harrison and Kweka (2011).

The Laetoli material was compared with selected fossils from the Aterir Beds (Hooijer 1973), Chemeron Formation (Hooijer 1969), Kanapoi (Hooijer and Patterson 1972), and Koobi Fora and West Turkana (Harris 1976, 1983) at the collections of KNM. Additional comparative studies with material from the Plio-Pleistocene localities of Hadar (Guérin 1980b; Geraads 2005) and Dikika (Geraads 2005) were carried out at the NME; from the Omo Valley (Arambourg 1947; Hooijer 1969, 1972, 1973, 1975; Guérin 1985) at NME, RMNH and MNHN. Pleistocene material from Olduvai Gorge, Kanjera, Kanam West, and Rawi (Hooijer 1969; Groves 1975) was studied at BMNH. The Kohl-Larsen fossil collection from East Africa (Dietrich 1942, 1945) was studied at MNHB. Specimens from Bou Hanifia (Arambourg 1959; Geraads 1986), Ternifine (Pomel 1895) and several Plio-Pleistocene North African localities (Arambourg 1970) were examined at MNHN. Materials of “*Diceros*” *neumayri* from Greece (Pikermi, Samos, Axios Valley: Gaudry 1862–1867; Geraads 1988; Geraads and Koufos 1990; Giaourtsakis et al. 2006; Giaourtsakis 2009) were studied at AMPG, LGPUT, MNHN, BMNH, NHMW, IPUW, SMNS, BSPG, SMF and HLMD; those from Turkey (Various localities:

Heissig 1975, 1996; Geraads 1994; Fortelius et al. 2003) were studied at BSPG, SMNK, and MNHN; and those from Iran (Maragheh: Osborn 1900; Thenius 1955) were examined at NHMW and MNHN. Casts of specimens from Fort Ternan (Hooijer 1968) and Langebaanweg (Hooijer 1972) were examined at BMNH and BSPG, respectively. Cranial material of *Diceros douariensis* from Douaria (Guérin 1966) was kindly shown to MF by C. Guérin and digital images of the specimens were provided by C. Guérin and A. Prieur. The rhinoceros material from the following localities was studied based on the referred publications: Arrisdrift, Namibia (Guérin 2000, 2003); Ekora Formation, Kenya (Hooijer and Patterson 1972); Lothagam, Kenya (Hooijer and Patterson 1972; Harris and Leakey 2003); Ahl al Oughlam and Oulad Hamida, Morocco (Geraads 2005). Comparative studies with the extant species *Ceratotherium simum* and *Diceros bicornis* have been also carried out at the zoological collections of the aforementioned institutions.

Stratigraphy

For temporal resolution of the Laetoli Sequence, we used the stratigraphic position of the localities relative to the marker tuffs to create semi-arbitrary Tuff Groups (Harrison and Kweka 2011). The following groups were created: 1-LLB=Lower Laetoli Beds, 2-BT3=below Tuff 3, 3-T3-5=between Tuffs 3 and 5, 4-T5-7=between Tuffs 5 and 7, 5-STRT7=straddles Tuff 7, 6-AT7=above Tuff 7, 7-UND=Upper Ndolanya Beds.

Mesowear

We applied the original mesowear scoring system and analytical techniques introduced by Fortelius and Solounias (2000) for the upper dentition. We also extended the methodology to the cusp sharpness of the buccal enamel band of the lower teeth. We did this by a subjective judgment of equivalences according to the following guideline: distinct phase I facets with sharp boundaries=sharp; distinct phase I facets with fuzzy boundaries=rounded; no phase I facets=blunt. Relief was not scored for lower teeth and, apart from hierarchic clustering, we have limited our comparisons to cusp sharpness only. All teeth that were sufficiently well preserved were scored for mesowear, but only the first and second molars were included in the final analyses, and only the uppers in the hierarchic clustering analysis. Results generally remain similar even if premolars and deciduous teeth are included. We used polysiloxane putty (Provil Novo Putty regular set, Heraeus Kulzer GmbH, Hanau, Germany) to make partial molds of the teeth and synthetic dental stone

(Fujirock by GC Europe n.v., Leuven, Belgium) to make replicas.

The curvature of the facets and enamel were further examined by high-resolution 3D scanning techniques. We used this methodology to study the enamel edges of the upper and lower teeth of *C. efficax*, the derived *Ceratotherium* from latest Pliocene and early Pleistocene, extant *C. simum*, Pliocene *Diceros* and extant *D. bicornis*. An area of at least 2×3 mm around the enamel edge and the facet was scanned using a Nextec Hawk 3D laser scanner at 30×30 µm resolution. The scanned area extended from the vertical buccal side of enamel, over the worn enamel surface, to the dentine on the occlusal surface. Point clouds were realigned using Rhinoceros 3.0 (McNeel, Seattle, WA, USA). They were then imported into Surfer for Windows v. 8 (Golden Software, Colorado, USA) and a 30×30 µm resolution grid was generated using Kriging interpolation. Surface curvature was calculated according to Evans (2005): the surface was smoothed three times using a 9×9 kernel with central weighting of 4 to reduce surface noise, and then directional curvature was calculated at 10° intervals for 180°. The maximum curvature at each x, y point for all directions was determined. Radius of curvature (inverse of curvature) plots were overlain on the smoothed surface plot to visualize flat and curved areas (Evans 2005).

Statistical calculations were carried out using the statistics package JMP 6.0 (SAS Institute, Inc., Cary, NC, USA), except for the polar clustering diagrams (Fig. R.4.1), which were produced in Systat 11.0 (Systat Software, Inc., San Jose, CA, USA).

Systematic Paleontology

Class Mammalia Linnaeus, 1758
 Order Perissodactyla Owen, 1848
 Suborder Ceratomorpha Wood, 1937
 Superfamily Rhinocerotioidea Owen, 1845
 Family Rhinocerotidae Owen, 1845
 Subfamily Rhinocerotinae Owen, 1845
 Tribe Dicerotini Ringström, 1924
 Genus *Ceratotherium* Gray, 1868
Ceratotherium efficax (Dietrich, 1942)

Synonymy

1907. non *Opsiceros simplicidens* sp. nov. – SCOTT: pp. 257–259, pl. 17, Figs. 3–5.
 1926. pro parte sub *Rhinoceros scotti* sp. nov. – HOPWOOD: pp. 216–217, Fig. 3; (Kaiso).

1942. *Serengeticeros efficax* gen. et sp. nov. – DIETRICH: pp. 297–300, Fig. 2; (Laetoli).
 1945. *Serengeticeros efficax* Dietrich, 1942. – DIETRICH: pp. 56–67; pl. 13, Figs. 1, 3, 4, 6; pl. 14, Figs. 8, 10; pl. 15, Figs. 11–15, 18–20; pl. 16, Figs. 21–23; pl. 17, Fig. 28; pl. 18, Fig. 36; pl. 19, Fig. 42; (Laetoli).
 1947. pro parte *Atelodus germanoaffricanus* (Hilzheimer, 1925). – ARAMBOURG: pp. 299–301. (Laetoli).
 1969. pro parte *Ceratotherium simum germanoaffricanum* (Hilzheimer, 1925). – HOOIJER: pp. 74–75, 85–86, pl. 3; (Laetoli).
 1972. pro parte *Ceratotherium simum germanoaffricanum* (Hilzheimer, 1925). – HOOIJER: p. 153; (Laetoli).
 1976. *Ceratotherium* sp. – LEAKEY et al.: p. 464; (Laetoli).
 1979. *Ceratotherium* sp. – LEAKEY and HAY: p. 4; (Laetoli).
 1980b. pro parte *Ceratotherium praecox* Hooijer and Patterson, 1972. – GUÉRIN: p. 61; (Hadar).
 1987a. pro parte *Ceratotherium praecox* Hooijer and Patterson 1972. – GUÉRIN: pp. 321–326, pl. 9.4, Figs. A–C; (Laetoli, Hadar).
 2005. pro parte *Ceratotherium mauritanicum* (Pomel, 1888). – GERAADS: pp. 452–455, Figs. 1a–b; (Hadar, Dikika, Koobi Fora, Laetoli).

Holotype. Maxillary fragments with left and right M1–M3 of the same individual (MNHB: MB.Ma.42009), illustrated by Dietrich (1945: taf. 13, Fig. 1, 6).

Type Locality. Vogelflussgebiet near the Garrusi River of the Southern Serengeti, known today as Laetoli, Tanzania.

Stratigraphical level. Grey volcanic tuff of the Serengeti Beds (Dietrich 1945), corresponding to the Upper Laetoli Beds of current usage (Hay 1987; Ditchfield and Harrison, 2011).

Age. Pliocene.

Geographical distribution. Presently known from East Africa: Tanzania, Kenya, Ethiopia, Uganda, and perhaps Chad. Fossil evidence from other African countries is presently insufficient.

Revised descriptive diagnosis. *Ceratotherium* of large size; nasal and frontal horns present, nasal bones rostrally rounded with abrupt and broad termination; premaxillary bones reduced; lower border of orbita sloping laterally downwards; supraorbital process very strong, postorbital process absent; average position of the anterior orbital border at the level between the distal half of M2 and the mesial half of M3; dorsal cranial profile gently concave; strong nuchal crest with concave occipital notch, extending posteriorly over the level of the occipital condyles; occipital plane postero-dorsally inclined; postglenoid and posttympanic processes without contact. Upper and lower incisors absent or vestigial. High crowned, functionally hypsodont maxillary dentition with relatively flattened occlusal surface, rather constant enamel thickness, and significant cement coating. D1 not persisting in adulthood. Upper premolars with: protocone

markedly larger than hypocone after moderate stage of wear; protocone constricted only by a mesial groove; distal protocone groove and antecrochet absent; hypocone not constricted; medisinus basin lingually open, protoloph and metaloph fusing only during late to latest stages of wear; lingual cingulum present, moderately expressed, and frequently continuous; crochet always present and well developed; crista mostly present, usually weak; medifossette rarely formed and only after moderate to late stages of wear; paracone fold faint to weak; metacone fold absent. Upper molars (M1, M2) with: protoloph bending markedly distolingually; metaloph shorter and relatively less oblique, particularly on M1; mesial protocone groove present, deep and marked; distal protocone groove absent; lingual protocone groove generally present and well marked; crochet strong; expression of crista variable; formation of closed medifossettes frequent after early to moderate stages of wear; buccal profile of ectoloph in molars slightly undulated; paracone fold present but weak to faint; mesostyle bulge prominent, but not acute and not markedly stronger than the paracone fold; metacone fold absent. M3 with predominately continuous ectometaloph and without postfossette. Lower premolars with lingually open trigonid and talonid basins, forming occasionally closed fossetids; lower molars with buccal wall of the trigonid frequently flattened. Appendicular skeleton with markedly long and relatively slender metapodials.

Differential diagnosis. *Ceratotherium efficax* is distinguished from *C. mauritanicum*, *C. germanoaffricanum* and *C. simum* by its more primitive dentition, as well as from the latter two species by the different size and proportions of its appendicular skeleton, in particular of the metapodials. Based on the available evidence, *C. mauritanicum* differs from *C. efficax* by showing population variants with frequent expression of a shallow buccal depression slightly demarcating the continuity of the ectolometaloph on M3, upper premolars with earlier fusion of protoloph and metaloph, upper premolars with weaker and frequently discontinuous lingual cingulum, and lower premolars forming more frequently closed fossetids during moderate stages of occlusal wear. *C. germanoaffricanum* and *C. simum* differ from *C. efficax* and *C. mauritanicum* by the following dental features: the ectoloph and metaloph on M3 are always markedly separated forming a postfossette; the lingual protocone groove on the molars is absent or only faintly expressed; the metaloph on the molars and premolars is longer and bends more markedly distolingually. Extant *C. simum* differs additionally by at least the following dental features: the teeth are absolutely and relatively more high crowned; the protoloph and metaloph of the premolars fuse after early stages of occlusal wear closing the entrance of the medisinus; the lingual cingulum on the premolars is virtually absent; the paracone fold on the buccal wall of the premolars and particularly of the molars is completely suppressed by a deep parastyle groove; the mesostyle bulge is more acute and always developed as the most prominent

fold on the buccal wall of the ectoloph; the metaloph of the molars and the premolars bends more markedly distolingually; a closed medifossette is very frequently formed on the premolars during early to moderate stages of occlusal wear, and it is almost always formed on the molars during the earliest stages of occlusal wear. *C. efficax* differs from *C. simum* by its absolutely longer and relatively more slender appendicular skeleton. *C. germanoaffricanum* differs from *C. efficax* and *C. simum* by its absolutely larger and relatively more robust appendicular skeleton.

Material

Lower Laetolil Beds (NMT)

Mandibles: EP 062/98, KK 82/294, KK 82/71

Deciduous teeth: Rt DP2 EP 098/98, Lt DP4 EP 066/98

Permanent teeth: Lt P3/4 EP 062/98, rt P3/4 EP 3927/00, rt P/M EP 1343/03, rt M1/2 EP 103/98, Lt M2 EP 100/98, M frgt EP 221/03, Lt m3 KK 82/213, m frgt EP 522/03

Upper Laetolil Beds (NMT)

Crania: LAET 74-323, LAET 78-4979

Mandibles: LAET 74-188, LAET 75-2836

Deciduous teeth: Lt DP1 EP 122/98, LAET 75-2617, EP 458/04, EP 3824/00, LAET 75-1182, LAET 75-1275; rt DP2 EP 1318/04, EP 1358/00a, EP 038/01, EP 1006/04; Lt DP2 EP 458/04, LAET 75-3434, EP 1493/04, LAET 78-4714; rt. DP3 EP 458/04, EP 038/01; Lt DP3 EP 1240/01; rt DP4 LAET 75-3118, EP 038/01; Lt DP4 EP 458/04, LAET 74-215, LAET 75-618; rt dp2 LAET 75-1782; EP 2323/03, EP 512/00; Lt dp2 EP 4120/00; rt dp3 EP 1421/00, EP 1506/03, EP 308/00, EP 331/04, EP 410/00, EP 432/04, EP 673/00, EP 721/04; Lt dp3 EP 1365/98, EP 2879/00, EP 2998/00, LAET 74-214, LAET 75-1855, LAET 75-2209, LAET 75-3531, LAET 78-4884; dp3/4 LAET 74.100, LAET 74-145; rt dp4 EP 1179/98, EP 2198/03, EP 457/00, LAET 75-3747, LAET 75-456; Lt dp4 EP 1297/03, EP 1759/00, EP 2455/00, EP 2646/00, EP 3609/00, EP 418/98, LAET 78-5137, LAET 78-5335

Permanent teeth: rt P2 EP 1218/98, EP 1237/01, EP 1843/00, EP 2574/00, LAET 75-1378, LAET 75-3649, LAET 75-630; Lt P2 EP 1132/04, EP 1358/00c, EP 1366/98, EP 4224/00, EP 660/98, LAET 74-50, LAET 75-1992, LAET 75-2115, LAET 75-2544, LAET 75-3582, LAET 78-5009; rt P3/4 EP 120B/98, EP 454/03, EP 088/00, EP 118/98, EP 121/98, EP 154/00, EP 155/00, EP 366a/98, EP 3927/00, LAET 74-250, LAET 75-3091, LAET 75-3371, LAET 78-4774, EP 1035/98, LAET 75-3647; Lt P3/4 EP 1554/98, EP 117/98, EP 1492/04, EP 1502/00, EP 2402/00,

EP 3692/00, EP 505/98, LAET 75-1194, LAET 75-1385, LAET 75-2150, LAET 75-985, LAET 78-5406, EP 591/00; rt M1/2 EP 038/01, EP 1080/98, EP 120B/98, EP 3664/00, LAET 78-4651, EP 1064/04, EP 1217/98, EP 1611/00, EP 2027/03, EP 2223/00, EP 2401/00, EP 366c/98, EP 3691/00, EP 595/04, LAET 75-1306, LAET 75-1378, LAET 75-1615, LAET 75-2040, EP 1080/98, EP 120B/98, LAET 75-2760, LAET 75-492; lt M1/2 EP 1080/98, EP 982/03, LAET 78-4949, EP 634/98, EP 090/00, EP 1037/98, EP 119/98, EP 1358/00d, EP 1551/03, EP 156/00, EP 264/99, EP 2738/00, EP 761/03, LAET 75-1378, LAET 75-1872, LAET 75-507, LAET 75-543, LAET 78-4964, EP 1080/98, EP 120A/98, LAET 75-3648; rt M3 EP 089/00, EP 1080/98, EP 275/99, LAET 75-1378, LAET 75-2149, LAET 75-2208, LAET 78-4938; lt M3 EP 1080/98, EP 120A/98, EP 1509/03, EP 413/98, EP 414/98, EP 672/00, EP 763/03, EP 865/98, LAET 74-51, LAET 75-3042, LAET 78-4640; rt p2 EP 1178/98, EP 923/01, LAET 78-4651; lt p2 EP 147/03, EP 2645/00, EP 762/04, EP 874/01, LAET 75-1378; rt p3/4 LAET 75-1378, EP 1962/00; lt p3/4 EP 1359d/00, EP 1635/98, EP 556/00, LAET 75-987, LAET 74-188, LAET 75-1378, LAET 78-4755; rt m1/2 EP 027/00, LAET 75-3530, LAET 78-4883, LAET 78-5328, EP 026/00, LAET 75-2760; lt m1/2 EP 3693/00, EP 3883/00, LAET 74-153, LAET 74-188, LAET 75-1378, EP 037/01, EP 1177/98, EP 1239/01, EP 1359c/00, EP 1501/98, LAET 75-1135, LAET 75-544, EP 1359e/00, EP 3883/00, LAET 74-188, LAET 76-3847; rt m3 EP 1039/98, EP 211/01, LAET 78-4742; lt m3 EP 1298/03, EP 3883/00, LAET 74-188, LAET 75-472, LAET 78-4964, LAET 78-5141, LAET 78-5191.

Probably Upper Laetoli Beds (KNM)

Rt DP3 LIT 59-119; lt DP3 LIT 59-116; lt DP4 LIT 59-195; lt P2 LIT 59-418, rt P3/4, LIT 59-118; lt P3/4 LIT 59-346, LIT 59-439; rt M3 LIT 59-194; P/M frgts LIT 59-117, LIT 59-193

Upper Ndolanya Beds (NMT)

Cranium EP 1041/00; lt p2 LAET 75-413; m/p frgt EP 3786/00

Laetoli Specimens (BMNH)

Almost 60 rhinocerotid specimens from Laetoli are housed in the collections of the Natural History Museum of London. About 35% of them represent dental elements, while the rest are postcranial elements. The specimens originate from the collections made by Louis Leakey during 1935 and bear their original field numbers. Three Laetoli sites are indicated: LIT.AS, LOL.S and 1710.S. The material forms a

rather uniform sample, and there is no indication for the presence of *Diceros*: all dental specimens demonstrate the characteristic morphological features of *Ceratotherium effica* detailed in the diagnosis, and the postcranial elements are consistent in size and proportions. In particular, complete metapodials are absolutely longer and relatively more slender with respect to extant *Ceratotherium simum*.

Remarks and Comparisons

Before proceeding with the description we feel obliged to comment on what differences one may reasonably expect to demonstrate between species of the tribe Dicerotini. As our discussion shows, it has been commonplace in the literature to identify individual specimens at the species level. For complete cranial material and well-preserved dentitions and teeth this is generally entirely reasonable. However, even in these cases it might be difficult to support an identification based solely on metric comparisons. Fig. 11.1 shows that the skulls of the extant *Diceros* and *Ceratotherium* are quite well separated based on a length-width bivariate plot, although, even in this case, some individuals from the two genera overlap. Fig. 11.2 shows that the molars of the same specimens overlap almost completely in terms of their basal length-width measurements. We have accordingly desisted from attempts to use simple linear metrics to assign Laetoli teeth taxonomically, and based our identifications only on clearly defined morphological criteria.

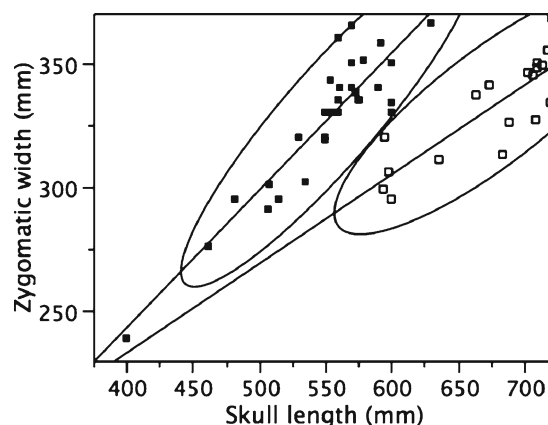


Fig. 11.1 Zygomatic width as a function of total skull length in Recent *Ceratotherium simum* (white) and *Diceros bicornis* (black), including subadult individuals, scale in cm. Some specimens have essentially identical dimensions but separation is good and the allometric relationship is different, *Diceros* having a more rapid increase in width with increasing length. Least squares regression lines and 95% density ellipses shown. Unpublished data; specimens from the collections of (Tervuren, Leiden, Copenhagen, Stockholm, Gothenburg, and Helsinki)

Crania

Guérin (1987a) assigned the crania LAET 74-323 (Loc. 7) and LAET 78-4979 (Loc. 3) from the Upper Laetolil Beds to *C. praecox*, reporting a close resemblance between the concave frontal profile of the latter specimen and the type cranium of “*C. praecox*” from Kanapoi (Hooijer and Patterson 1972). However, as noted by Geraads (2005), the frontal area of the LAET 78-4979 cranium is deformed rather than origi-

nally concave, and the cranial morphology is, in fact, very similar to the skulls from the Lower Awash Valley, which he referred to as *C. mauritanicum*. The dentition of the LAET 78-4979 cranium is very incomplete; the axis of the metaloph appears to pass distally to the medifossette, similar to the Lower Awash specimens. The dentition of the cranium LAET 74-323 is completely missing and the nuchal crest is seriously damaged; the available morphology of the occipital and frontal portion clearly distinguishes it from *Diceros*. The partial cranium EP 1041/00 from the Upper Ndolanya Beds is poorly preserved, but its dentition is in excellent condition and demonstrates all characteristic features of *C. efficax* described in the diagnosis (Fig. 11.3).

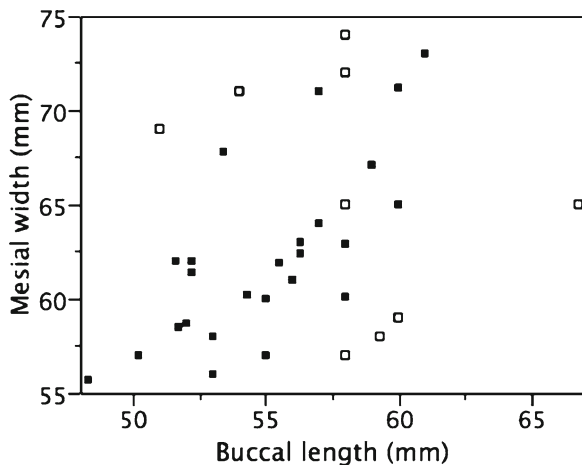


Fig. 11.2 Plot of mesial width as a function of buccal length in second upper molars of Recent *Ceratotherium simum* (white) and *Diceros bicornis* (black), from the skulls shown in Fig. 11.1. Note complete lack of separation of teeth by size or proportions

Permanent Upper Dentition

Although the Laetoli teeth assigned by us to *C. efficax* appear quite similar to those of modern *C. simum* in general characteristics, there are several distinct and constant differences. The dentition of *C. efficax* is absolutely and relatively less high crowned than *C. simum* and the occlusal surfaces of the teeth are less flattened. In *C. efficax*, the protoloph and particularly the metaloph bend less markedly distolingually than in *C. simum*. On the premolars of *C. efficax*, a moderately expressed and usually continuous cingulum is developed, the crista is weak and forms rarely after moderate stages of wear a closed medifossette with the strong crochet, the entrance of the medisinus remains usually open until late

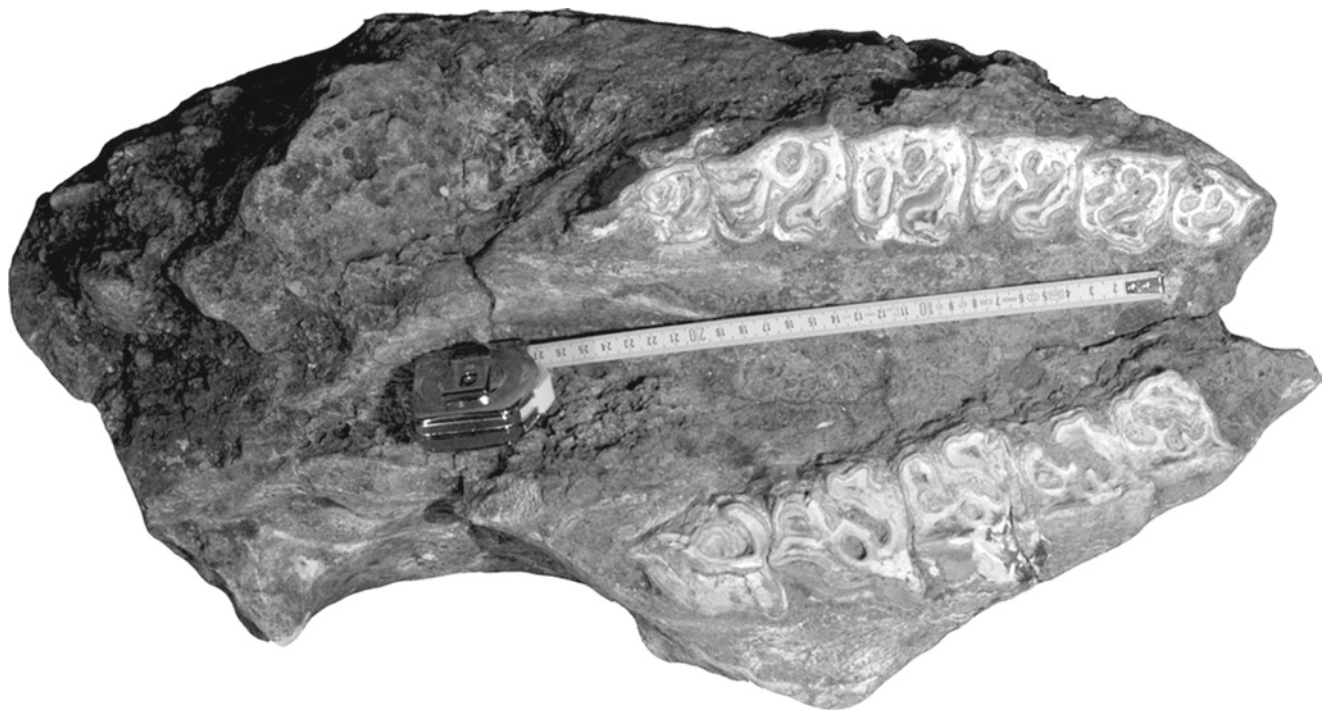


Fig. 11.3 *Ceratotherium efficax*, cranium NMT: EP 1041/00

stages of wear (except on P2), and a weak paracone fold is present on the buccal wall of the ectoloph. On the premolars of *C. simum*, the lingual cingulum is virtually absent, a closed medifossette is mostly formed during early stages of occlusal wear, the protoloph and metaloph fuse early closing the entrance of the medisinus, and the mesostyle bulge is the most prominent fold on the buccal wall of the ectoloph. On the molars of *C. efficax*, a conspicuous lingual protocone groove is nearly always present (sometimes also on premolars, but much weaker), a closed medifossette is variably formed, a faint protocone fold is usually evident, and the M3 features a continuous ectometaloph without postfossette. On the molars of *C. simum*, a marked lingual protocone groove is not developed (due to the more extreme bending of the protoloph), a closed medifossette is always formed at very early stages of wear, the paracone fold is completely suppressed by a deep parastyle groove, the mesostyle bulge is more acute, and on the M3 the ectoloph and metaloph are always markedly separated forming a postfossette.

Upper Deciduous Dentition

The upper deciduous teeth are generally quite similar to those of *C. simum*, with a slightly undulating ectoloph and a prominent parastyle, which is more markedly expressed than in *D. bicornis*. The mesial cingulum is weaker than in *D. bicornis* and the protoloph bends more markedly distolingually. The crista is strong and often expressed as multiple folds. The buccal enamel surface is rough, suggesting that a cement covering was originally present, but has not been preserved.

Mandible and Lower Dentition

Several mandibular fragments have been recovered from the Laetoli Beds, but unfortunately they are rather incompletely preserved. The mandibular symphysis and the ascending rami are usually broken off or severely crushed. The mandibular ramus, which is usually better preserved, is relatively high and features a concave dorsal profile. On its lingual side, the mylohyoid line is often expressed as a shallow longitudinal depression. The posterior margin of the symphysis extends variably below the level of p3. The enamel of the lower teeth is rough and cement traces can be often observed on the buccal wall and the internal valleys of the teeth. The dp1 does not persist in adulthood. On p2, the paralophid is single and there is no evident buccal groove or depression on the buccal wall of the trigonid. A rising mesiobuccal cingulum can be observed in some molars. The buccal wall of the metalophid is often slightly flattened, especially on the upper part of the crown, but not to the extent observed in extant *C. simum*,

where it can be even slightly depressed, particularly on the molars. The ectoflexid is smoothly marked, but not particularly deep. It usually terminates before the base of the crown, especially on the premolars. The hypolophid is oblique and rounded, except sometimes on m3, where it may be less markedly rounded. In extant *C. simum*, the hypolophid on m3 and sometimes on m2 is less oblique and nearly straight. The lingual sinuses are situated high above the base; in molars, the profile of the anterior sinus is U-shaped and the distal sinus V-shaped. The lingual wall of the metaconid is rather flattened; in extant *C. simum*, the lingual wall of the metaconid is usually shallowly depressed. On the premolars, the metaconid bends frequently distolingually, but, contrary to the extant *C. simum*, the formation of closed fossetids is rare.

Tribe Dicerotini Ringström, 1924

Genus *Ceratotherium* (Gray, 1868)

Ceratotherium cf. *simum*

Material

Upper Ndolanya Beds (NMT)

Cranium LAET 81-74 (Fig. 11.4); lt p2 LAET 78-5017

Remarks and Comparisons

The LAET 81-74 cranium (Fig. 11.4) from Loc. 14 of the Upper Ndolanya Beds was assigned to *C. simum* by Guérin (1987a). The left P4-M3 are moderately well-preserved and show several derived features with respect to *C. efficax*. On



Fig. 11.4 *Ceratotherium* cf. *simum*, cranium NMT: LAET 81-74, left P4-M3

P4 a closed medifossette is formed, the metaloph is relatively longer than in *C. efficax*, and the mesostyle bulge more prominent. However, contrary to extant *C. simum*, the protoloph and metaloph of the P4 do not fuse lingually and the medisinus valley remains open even during this late stage of wear. The molars are fragmentary. The axis of the metaloph passes clearly through the medifossette. On the buccal wall of the ectoloph, the mesostyle bulge is the dominant fold, but it is not as prominent as in extant *C. simum*. The available comparative material presently prevents a more accurate assignment of this specimen to *C. germanoaffricanum* or primitive *C. simum*, since the molars of both species share the features listed above.

Tribe Dicerotini Ringström, 1924
Genus *Ceratotherium* Gray, 1868
Ceratotherium sp.

Material

Upper Ndolanya Beds (NMT)

Lt mandible LAET 75-2469; P frgt EP 4022/00

Remarks and Comparisons

LAET 75-2469 is an incompletely preserved mandibular fragment, which may be referred to *Ceratotherium*.

Tribe Dicerotini Ringström, 1924
Genus *Diceros* Gray, 1821
Diceros sp.

Restricted Synonymy

- 1987a. *Diceros bicornis* (L.) - GUÉRIN: p. 327, pl. 9.5, Figs. A, B; (Laetoli).
2005. *Diceros* cf. *praecox* (Hooijer and Patterson, 1972). - GERAADS: p. 457, tab. 4; (Laetoli).

Material

Upper Laetoli Beds (NMT)

Cranium LAET 75-3065

Remarks and Comparisons

The genus *Diceros* has generally been regarded as morphologically constant from the Early Pliocene to the present day. According to Harris and Leakey (2003) even the teeth from 6.24–5.5 Ma (Leakey et al. 1996) Upper Nawata, Lothagam, are similar to the teeth of the recent *D. bicornis*, even though, as Hooijer (1978) and Geraads (2005) noted, such longevity is extremely rare for a recent mammal species. Although *Diceros* appears to have been a less common element in the Laetoli fauna than it may have been previously assumed (Guérin 1987a), it clearly was present as evidenced by the LAET 75-3065 cranium. During an exhaustive survey of the entire collections of the Laetoli rhinoceros material preserved in the National Museums of Tanzania and Kenya, as well as in London and Berlin, we found only a few dental specimens that potentially could be attributed to *Diceros*. It is possible that some of the postcranial elements may also represent *Diceros*, as Guérin (1987a) has suggested, but we were not able to document reliable quantitative or qualitative criteria for distinguishing two genera among the available material.

Cranium

The cranium LAET 75-3065 originates from Loc. 10W of the Upper Laetoli Beds and was described and figured by Guérin (1987a, pl. 9.5). The cranium is crushed and deformed, and bears multiple fractures. It belongs to a very old individual, as indicated by its heavily worn teeth. The right P3-M3, as well as the left M2 and part of the left M3, are fragmentary. All molars are lingually broken and their ectoloph is poorly preserved. The relatively complete P4 shows a well-developed and continuous lingual cingulum, and an ectoloph coronal profile similar to extant *D. bicornis*. There is no evidence of a paracone fold at this late stage of wear. Both the protoloph and metaloph are rather straight and only slightly oblique, similar to extant *D. bicornis*. These features are in sharp contrast to *Ceratotherium efficax* (and subsequent congeneric species), where the lingual cingulum is weaker, the ectoloph profile more flattened, and the protoloph is bending markedly distolingually.

Geraads (2005) proposed that the cranium LAET 75-3065 might be referred to *Diceros praecox* (Hooijer and Patterson 1972) from Kanapoi, together with the skull AL-126-21 from Hadar. According to Geraads (2005), both specimens combine a dental morphology similar to extant *Diceros* with a “primitive” [sic] *Ceratotherium* occipital morphology. However, we could not detect the combination of cranial and dental features described by Geraads (2005) for the Hadar and Laetoli crania. The teeth of the Laetoli specimen LAET 75-3065 are too worn to show any reliable differences, while the apparent shortness

of the transverse lophs noted by Geraads (2005) for the Hadar specimen AL-126-21 does not, in our opinion, differ significantly from extant *D. bicornis* teeth at a similar early stage of wear. The large size of the teeth reported for the Hadar specimen actually fall within the range of variation of the large-sized genotypic subspecies *Diceros bicornis bicornis*. In addition, the teeth of the holotype cranium of the purported *Diceros praecox* from Kanapoi (KNM-KP 36) are too worn and incomplete to allow metric comparisons (Hooijer and Patterson 1972: Fig. 9a). The occipital region of both Laetoli and Hadar specimens is quite fragmentary. According to our comparisons, the available morphology seems to fall well within the range of variation that we have observed among the various subspecies of extant *D. bicornis*, for both the extension of the nuchal crest and the angle of the occipital level; a resemblance with the derived occipital morphology of *Ceratotherium* is not justified.

Tribe Dicerotini Ringström, 1924
Dicerotini gen. et sp. indet.

Material

Lower Laetolil Beds (NMT)

Postcrania (incomplete listing): Ulna EP 1184/04; magnum LAET 78-5023; unciform EP 005/99, EP 200/03.

Upper Laetolil Beds (NMT)

Permanent teeth: Rt P3 EP 1061/03; Lt M1/2 LAET 75-757; rt p3 EP 628/98.

Postcrania (incomplete listing): Scapula EP 1761/00; humerus EP 462/04; radius EP 160/98, EP 413/04, EP 2163/00, scaphoid EP 154/98, EP 871/03, EP 602/98, EP 2674/00, EP 1963/00, LAET 75-581, EP 2783/00, EP 3826/00, EP 3908/00, EP 1043/98, EP 462/04; lunar EP 908/04, EP 1526/98, EP 1041/98; cuneiform EP 2484/00, EP 1322/04; trapezoid EP 424/98; magnum EP 809/98, EP 1322/04, EP 1504/00, EP 1183/98, unciform EP 496/98, LAET 75-2358, LAET 75-3284, EP 039/04, EP 124/98, EP 125/98, LAET 78-4743, EP 1133/04, EP 1363/98, LAET 78-4811, EP 2335/00, LAET 75-3048, EP 2648/00, EP 677/00, LAET 75-3653, EP 212/01, EP 1646/04, LAET 75-2890, EP 1322/04, EP 2134/03, EP 2518/00, EP 758/03, EP 462/04, mc II EP 3610/00, EP 1491/04, EP 383/03, EP 1361/00, LAET 75-1110, LAET 75-1118, EP 1505a/00, EP 1045/98; mc III EP 1844/00, EP 676/00A, EP 676/00B, LAET 75-1729, EP 515/00, EP 679/03, LAET 78-4924, EP 1361/00, EP 1423/04, LAET 75-1246, LAET 75-819, LAET 9b; mc

IV LAET 75-3562, LAET 75-3564, EP 659/98, EP 810/98, EP 4300/00, LAET 78-4800, LAET 75-3656, LAET 76-3888, EP 1614/00, EP 1320/04, EP 1423/04, EP 1505b/00, EP 2517/00, EP 1236/01, tibia EP 2994/00, EP 3926/00; astragalus EP 039/01, EP 1009/98, EP 1146/00, EP 1319/04, EP 1429/01, EP 1434/98, EP 1572/03, EP 1845/00, EP 1964/00, EP 2199/03, EP 2219/00, EP 2363/00, EP 2456/00, EP 2457/00, EP 408/00, EP 4229/00, EP 751/00, EP 788/98, EP 789/98, EP 879/04, LAET 75-1231, LAET 78-5079; calcaneum EP 1141/00, EP 1142/00, EP 2051/00, EP 2133/03, EP 2293/00, EP 2483/00, EP 2647/00, EP 309/00, EP 3828/00, EP 879/04, LAET 75-1117; navicular EP 1697/00, EP 2135/03; ectocuneiform EP 1070/98, EP 462/04, EP 654/98; cuboid EP 1695/00, EP 2050/00, EP 3064/00; mt II EP 1107/98, EP 1262/00, EP 1364/98, EP 406/00, EP 462/04, LAET 75-3445, LAET 75-3529; mt III EP 337/99, EP 038/04, EP 1061/04, EP 1255/04, EP 1299/03, EP 1364/98, EP 462/04, EP 514/00, EP 793/98, LAET 74-18, LAET 75-1227, LAET 75-1339, LAET 75-2171, LAET 75-2825, LAET 75-3207, LAET 75-3654, LAET 75-583; mt IV EP 128/04, EP 1479/03, EP 267/03, EP 462/04, EP 978/01, LAET 74-9, LAET 75-3657, LAET 75-3658, LAET 75-814.

Probably Upper Laetolil Beds (KNM)

Permanent tooth: Lt P2 LIT 59-582.

Postcrania (incomplete listing): Mc II LIT 59-265; mc III LIT 59-580; mc IV LIT 59-263, LIT 59-263; tibia LIT 59-423; astragalus LIT 59-248, LIT 59-433; calcaneum LIT 59-22, LIT 59-23, LIT 59-345; mt II LIT 59-262, LIT 59-343; mt IV LIT 59-264.

Upper Ndolanya Beds (NMT)

Postcrania (incomplete listing): Magnum LAET 78-5023; unciform LAET 75-1653; femur, EP 1038/00; calcaneum EP 1214/03; navicular EP 705/03.

Ngaloba Beds (NMT)

Permanent tooth: Lt P3 EP 381/04

Remarks and Comparisons

Permanent Dentition

For some isolated dental fragments, a definite identification as *Ceratotherium* or *Diceros* is very difficult. The upper

premolars LIT 59-582 and EP 1061/03, and the lower premolar EP 628/98 are incompletely preserved and do not offer reliable diagnostic features. The ectoloph profile of the upper molar LAET 75-757 appears to have some similarity with *Diceros* morphology, but it is difficult to ascertain, as almost half of the tooth is missing. The upper premolar EP 381/04 is clearly rounded by transportation and it may actually be subrecent.

Postcrania

Among the available postcranial material the most notable specimens are several complete metapodials. They are absolutely longer than the metapodials of both extant African species, and relatively slender. There is little doubt that these specimens represent *C. efficax*. The size and proportions of the Laetoli metapodials are closer to the size and proportions of the abundant Langebaanweg sample (Hooijer 1972; Guérin 1979, 1987a). This was one of the key arguments used by Guérin (1987a) for referring the Laetoli material to *C. praecox*, since this name was previously widely used for the Langebaanweg sample. Guérin (1987a) did not assign any metapodials or long bones to *Diceros*, but only a few carpal and tarsal bones with somewhat smaller dimensions. Based on the proportions and morphology, it seems difficult to unequivocally recognize different groups among the carpals and tarsal bones. Since the majority of cranial and dental specimens belong to *C. efficax*, one could reasonably assume that the majority of the postcranials, if not all, represent this species. Alternatively, some of the smallest postcranial elements may indeed belong to the genus *Diceros*, as Guérin (1987a) has suggested. We believe that more postcranial material and comparative studies are required to establish reliable quantitative and/or qualitative criteria for their discrimination and we have accordingly not attempted an identification of the Laetoli postcranial specimens in the present study.

Discussion

Taxonomic History of the Laetoli Rhinoceroses

The first detailed studies of fossil rhinoceroses from Laetoli were published by Dietrich (1942, 1945). His material, consisting of a large number of isolated teeth and bones, had been collected by the Kohl-Larsen Expedition from 1938–1939 in the volcanic tuffs of the Garusi River area (“Vogelflussgebiet”; Dietrich 1941; T. Harrison, personal communication) of the Southern Serengeti, known today as

Laetoli (Leakey 1987). Dietrich identified specimens that in his opinion could not be referred to either of the living African species, the white rhino *Ceratotherium simum* or the black rhino *Diceros bicornis* (Dietrich 1942). He considered these specimens to represent a species intermediate between the living species, although closer to *C. simum*. He named this species *Serengeticeros efficax* and believed it to be the direct ancestor of *C. simum*. According to Dietrich the diagnostic character of *S. efficax* was found in the upper molar teeth, in which the protoloph curves towards distal but the metaloph is straight (Dietrich 1942). In a more detailed description of the stratigraphic context of the rhinoceros remains (Dietrich 1945), he noted that *S. efficax* was found in the grey volcanic tuff, corresponding to the Upper Laetoli Beds of current usage (T. Harrison, personal communication). According to Dietrich, fossils attributable to the living species were only found in younger strata, probably corresponding to the Ndolanya Beds or the Pleistocene Ngaloba Beds (Leakey 1987; T. Harrison, personal communication).

The specimens described and illustrated by Dietrich as *Serengeticeros efficax* (e.g., Dietrich 1942, Fig. 2; Dietrich 1945, Table XII:1, 6) correspond precisely to subsequently collected material of the most common rhinoceros species from Laetoli. Dietrich's line drawings show the characteristics of this species well, including the lingual curvature of the protoloph towards the distal, the straight metaloph with an axis that does not bisect the medifossette, the lingual protocone groove, and the mesostyle bulge, distinct but less developed than in *C. simum*. The lack of any specimens of *Diceros bicornis* from the grey tuffs as noted by Dietrich matches our finding that *Diceros* is very rare in the Laetoli Beds.

Much earlier, Pomel (1885) had mentioned and later described (Pomel 1888, 1895) a Pleistocene rhinoceros from Ternifine (age ca. 0.8 Ma, see e.g., Guérin 1987b), Algeria, as *Rhinoceros mauritanicus*. Pomel did not assign a holotype, but Geraads (2005) selected an isolated M2 (MNHN PTER-2261) drawn by Pomel (1895, plate 1, Fig. 2) as the lectotype of this species, and transferred it to *Ceratotherium* as *C. mauritanicum*. In Pomel's drawing the specimen appears rather similar to second upper molars from Laetoli: the medifossette is closed, the metaloph axis runs distal to the postfossette, the protoloph turns linguallly towards distal, and the mesostyle bulge is significantly less pronounced than in *C. simum*. Among other specimens, Pomel also illustrates a right M3 (1895, Plate 1, Fig. 4), which also resembles specimens from Laetoli to a large degree.

Geraads (2005) attributed the Pliocene material from the Lower Awash to *C. mauritanicum*. The skull AL-129-25 figured by him (Geraads 2005, Fig. 1) matches the material from Laetoli perfectly in both cranial and dental features. We, however, feel that the name *Ceratotherium efficax* (Dietrich 1942) is more appropriate for this East African Pliocene species than the name *Ceratotherium mauritanicum* suggested by Geraads (2005).

North African Pleistocene *C. mauritanicum* retains similar craniodental and postcranial sizes and proportions as *C. effica*x, but demonstrates slightly more derived dental features. For example, M3s are more frequently quadrangular in shape with an expression of a shallow buccal depression slightly demarcating the continuity of the ectoloph. Also in upper premolars the lingual cingulum is often weaker and discontinuous, and the fusion of the protoloph and the metaloph happens earlier, and lower premolars more often form closed fossetids during moderate stages of wear. The morphology of *C. mauritanicum* is thus closer to the common ancestor of *C. germanoaffricanum* and *C. simum*. *C. mauritanicum* managed to retain the *C. effica*x morphotype with few modifications in North Africa considerably longer than in East Africa, where *C. effica*x was replaced by the more derived species *C. germanoaffricanum* and *C. simum* (Geraads 2005; Giaourtsakis et al. 2009). According to the interpretation presented here, the Pliocene *C. effica*x represents the common ancestor of *C. mauritanicum*, *C. germanoaffricanum* and *C. simum*.

Hilzheimer (1925) described a subspecies of the white rhino from Olduvai Gorge as *Rhinoceros simus germanoaffricanus*. Hilzheimer's description was based mostly on a broken skull, which according to Geraads (2005) has since been lost. Hilzheimer did not publish a stratigraphy of his material, but according to Dietrich, Hilzheimer's taxon was probably based on material of mixed provenance and age, an opinion supported by the notes of the original collector, Reck, who was uncertain whether the skull was derived from the basal Olduvai Beds proper or from a much younger horizon ("Steppensinter") (Dietrich 1945). Dietrich excluded Hilzheimer's material from *S. effica*x and suggested that *R. simus germanoaffricanus* might be synonymized with the white rhino, *Ceratotherium simum*, an opinion with which Geraads (2005) concurred.

Hilzheimer's drawing (Hilzheimer 1925, text Fig. 1) shows two teeth, M2 and M3, which appear somewhat less derived compared to those of modern *C. simum*, and are, in our opinion, best associated to the species *Ceratotherium germanoaffricanum*. As already noted by Geraads (2005), the metaloph axis of M2 bisects the medifossette, resembling in this feature the modern *C. simum* and differing from the Pliocene *C. effica*x and Pleistocene *C. mauritanicum*. However, the protolophs of the M2 and M3 are straighter than in the modern *C. simum*, so that they do not turn distally except at their lingual tips. In addition, the protocone of the M3 is clearly marked by a lingual protocone groove, which is absent or only faintly expressed in molars of *C. simum*. The medifossette of the M3 is open, with a tiny crista and faint ectoloph bulge, and the overall shape of the tooth is rather triangular. Another of Hilzheimer's drawings (Hilzheimer 1925, text Fig. 2) shows an isolated M3 similar to modern *C. simum* with a closed medifossette and a quadrangular form.

In published Laetoli faunal lists, *C. simum germanoaffricanum* remained the only rhinoceros taxon until Leakey et al. (1976) reported finding skulls belonging to both *Diceros* and *Ceratotherium* from Laetoli (Guérin 1987a). Soon after, Leakey and Hay (1979) reported numerous teeth and some postcranial remains from Laetoli attributed to *Diceros*, and expressed the opinion that both *Diceros* and *Ceratotherium* were represented by tracks in the footprint tuff, even though their separation by other criteria than size was not possible (Leakey and Hay 1979; Leakey 1987).

Guérin (1987a) found three species of fossil rhinoceros at Laetoli: *Ceratotherium praecox* and *Diceros bicornis* in the Laetoli Beds, and *Ceratotherium simum* in the overlying Upper Ndolanya Beds. He regarded *Serengeticerus effica*x Dietrich, 1942 as synonymous with *Ceratotherium praecox* Hooijer and Patterson, 1972, but preferred to use the junior nomen because of its wider usage, pending a decision by the ICZN that does not appear to have materialized. Guérin, (1987a) did, however, note that the dental material assigned by him to *C. praecox* differed from the teeth assigned to this species from Kanapoi, Ekora, Lothagam, and Langebaanweg, in it being more derived, similar to teeth from Hadar also assigned to *C. praecox*. Earlier Guérin (1980b) had also remarked that dental material from Sidi Hakoma of Hadar was morphologically intermediate between the species *C. praecox* and *C. simum*, and referred it to *Ceratotherium* cf. *praecox*. Given the wide concept of *C. praecox* adopted by other workers at the time (see below), Guérin's decision to call the Laetoli species *C. praecox* was understandable. However, as noted above, the name *C. effica*x now appears appropriate for this material.

Relationships of the Plio-Pleistocene Dicerotini

Scott (1907, plate XVII Fig. 3) erected the new species *Opsiceros simplicidens* based on an isolated left M2 from superficial coastal deposits in Zululand. From the same deposits, he illustrated also two isolated teeth of *Diceros bicornis* (Scott 1907, Plate XVII, Fig. 4, 5). Scott (1907) compared this mixed material with the extant *Diceros bicornis* only, and the unusual morphology of the isolated M2 led him to the creation of a new species. However, the tooth is morphologically indistinguishable from fossil and extant *Ceratotherium simum*. Hopwood (1926) inappropriately reported that the species name *Opsiceros simplicidens* was a previously occupied (junior homonym of *Rhinoceros simplicidens* Lydekker) and proposed the species name *Rhinoceros scotti* as a replacement. Thus, *Rhinoceros scotti* Hopwood, 1926 is an objective junior synonym of *Opsiceros simplicidens* Scott, 1907, which is a subjective junior synonym of *Ceratotherium simum* and therefore neither of these

names affects the usage of *Ceratotherium efficax*. Hopwood (1926, Fig. 3) referred an upper molar (BMNH 12616) from the Kaiso Bone Beds in Uganda to his *Rhinoceros scotti*. Dietrich (1945) considered that this molar may be conspecific with *C. efficax* from Laetoli and our direct comparisons seem to support this assignment, although the stratigraphic context of the specimen is somewhat imprecise.

Arambourg (1947), in his study of fossil rhinoceros material from the Omo, synonymized *Serengeticerus efficax* with Hilzheimer's taxon, which he referred to as *Atelodus simus germano-africanus*. Furthermore, Arambourg synonymized Hopwood's *Rhinoceros scotti* (and Scott's *R. simplicidens*) with *A. simus germano-africanus*. Like Arambourg, Hooijer (1959, 1969) and Harris (1983) regarded *R. simus germano-africanus* Hilzheimer as synonymous with *Serengeticerus efficax* Dietrich. According to Hooijer (1972), this taxon, named *C. simum germanoaffricanum*, occurs at Laetoli, Chemeron, and Olduvai. In Hooijer's view, its skull is indistinguishable from that of *C. simum*, but its upper molars differ from those of *C. simum* in having a transverse metaloph and a protoloph that begins to curve towards distal only at its lingual end (Hooijer 1969). Hooijer (1969, Plate 1, Figs. 1–2) illustrated a skull of *C. simum germanoaffricanum* from Chemeron, J.M.91, which he considered similar to the material from Laetoli described by Dietrich as *S. efficax*, an opinion with which we concur; under the nomenclature employed here, this skull would thus be assigned to *Ceratotherium efficax*. In the same publication, Hooijer illustrated material from Olduvai, which he assigned either to *C. simum germanoaffricanum* or to *C. simum* subsp. Unfortunately the quality of the figures does not permit a precise identification of the species in all cases.

The species *Ceratotherium praecox* was described by Hooijer and Patterson (1972), who interpreted it as an offshoot of *Diceros*, the first representative of *Ceratotherium* and a direct ancestor of the living *C. simum* by way of the intermediate form *C. simum germanoaffricanum* (Hooijer and Patterson 1972; Hooijer 1973). They selected a rather poorly preserved skull from Kanapoi, KNM-KP 36 (Hooijer and Patterson 1972, Fig. 9A) for the holotype. Both sides of this skull as well as the occiput are damaged; the teeth are very worn as well as damaged, making comparisons with other material difficult. Hooijer and Patterson also referred to *C. praecox* a somewhat younger crushed skull from the Ekora Formation (KNM-KP 41; Hooijer and Patterson 1972, Fig 10 A-B) and a rather older isolated upper molar from the late Miocene of the Lower Nawata Formation of Lothagam (KNM-LT 89; Hooijer and Patterson 1972, Fig 8 C-D). Hooijer and Patterson regarded the holotype skull as not far removed from living *Diceros* in shape, but somewhat larger and postdentally more elongated. As for molar morphology, they noted that the metaloph is transverse and the protoloph bulges posteriorly in its lingual third, and that the molars of the type skull are similar to those of the isolated specimen

from Lothagam KNM-LT 89. In the Ekora skull KNM-KP 41 Hooijer and Patterson also observed postdental elongation, but the skull is badly crushed and distorted. Its molars are damaged on the buccal sides, but the relatively well preserved premolars were observed by Hooijer and Patterson to be very similar to those of *Diceros bicornis*, differing only in the lack of a paracone style and in the ectoloph being flatter and undulating. The molars of the Ekora skull have a weak lingual cingulum, noted by Hooijer and Patterson as their only difference from the Lothagam molar KNM-LT 89.

According to Geraads (2005), *Ceratotherium praecox* should be transferred to *Diceros*. He regarded the Ekora skull KNM-KP 41 as belonging to *Diceros bicornis*, but retained the cranium KNM-KP 36 for *Diceros praecox*. We agree that both the Kanapoi skull KNM-KP 36 and the Ekora skull KNM-KP 41 belong to *Diceros*, but see no compelling reason to assign them to different species. Instead, we observe other signs of heterogeneity in the original *C. praecox* hypodigm. Thus, the teeth of the Kanapoi skull are in our opinion indistinguishable from those of modern *D. bicornis*, including the distal bulging of the protoloph noted by Hooijer and Patterson (1972), commonly seen in worn specimens. We would add that some Kanapoi specimens, such as KNM-KP 32, KNM-KP 30216 and KNM-KP 30472, are morphologically similar to *D. bicornis* in shape, but others, such as KNM-KP 38, KNM-KP 30217 and KNM-KP 30554 appear distinctly derived, and can be assigned to *C. efficax*. KNM-KP 38, a right P4, has a closed medifossette and, despite loss of the lingual enamel, a distinct vertical groove is observable on the lingual face of the protocone. KNM-KP 30217 is a left mandibular fragment with a lightly worn p3 in place. This tooth is quite hypsodont, with derived features such as a flattened buccal wall of the metalophid, flattened lingual walls, deep V-shaped lingual sinuses and rough enamel. KNM-KP 30554 is a worn left first or second molar with a flattened lingual wall, with the crown flaring out towards mesial and distal above the base, and rough enamel.

The dentition of the Ekora skull is similar to *D. bicornis*, as noted by Geraads (2005). Of the features noted by Hooijer and Patterson, the presence or absence of a paracone style in the molars cannot be determined on the buccally damaged molars, while in the premolars this feature, which depends very much on the stage of wear, is often weak or even missing in the living species; the ectoloph profile of these teeth also appears *D. bicornis*-like to us. In contrast, the isolated upper molar KNM-LT 89 again shows a more derived morphology: the ectoloph is slightly swollen in its middle part and the protocone has a vertical groove lingually.

Hooijer (1972) referred the rhinoceros from Langebaanweg to *C. praecox*, although the teeth show distinctly more derived features than in the Kanapoi and Ekora skulls. In particular the M1s show the presence of a lingual protocone groove (Hooijer 1972, Plates 21–24). We agree with

Hooijer that the Langebaanweg rhinoceros is a primitive form of the *Ceratotherium* lineage, as also noted by Geraads (2005) and Giaourtsakis et al. (2009). Since the Langebaanweg material, however, clearly represents a less derived form, with respect to both dental features and the features of the posterior part of the skull, than the Laetoli material attributed to *C. efficax* (see Giaourtsakis et al. 2009), we leave the actual taxon to be specified in later works.

Hooijer (1972) also transferred to *C. praecox* several specimens from the Mursi Formation of the Omo Basin and from the Chemeron Formation in Kenya, previously assigned by him to *C. simum germanoaffricanum* (Hooijer 1969). These Mursi specimens are a palatal portion of a skull with the left M2-3 in place and a skull fragment with a broken left P4 (Hooijer 1969, Plate 5, Figs. 4–5). They are definitely more derived than those of the *C. praecox* type cranium from Kanapoi (which actually represents *Diceros*), and also more derived than the dental material of the Langebaanweg *Ceratotherium*, suggesting that an attribution to *C. efficax* would be reasonable. Both P4 and M2 have a lingual vertical groove on the protocone, the protocones expand towards distal, and the metaloph of the M2 is straight. The medifossettes are open on these teeth but closed in the M3, as noted by Hooijer (1972) as exceptional for the Langebaanweg material; the ectolophs are damaged and their shape cannot be assessed. In *C. efficax* the medifossettes are usually, but not always, closed on the molars and often open on the premolars. The Chemeron specimen is a left maxilla with poorly preserved M1-3 (Hooijer 1969, Plate 2, Fig. 1). Only the M2 is sufficiently complete to allow comparisons; Hooijer (1972) regarded it as similar to the Mursi specimens, and it appears derived in comparison with the *Ceratotherium* material from Langebaanweg. Hooijer continued to add such morphologically derived specimens to *C. praecox*, from the Aterir Beds in the Baringo area, Kenya (Hooijer 1973, Plate 1, Figs. 1–3) and from the Omo (Hooijer 1975, Plate 2, Figs. 1–2). The latter material consists of milk teeth, which are considered indeterminate Dicerotini by Geraads (2005). They appear more derived than corresponding deciduous teeth from Langebaanweg and might therefore fit *C. efficax* better than other known forms.

The material referred to the species *C. praecox* by its original authors is thus quite heterogeneous, and the applied concept rather quickly drifted away from the original type material towards a more derived state. A considerable amount of fossil material has subsequently been assigned to what appears to be this secondary concept of *C. praecox*. Harris (1983) found this species in the Kubi Algi Formation of Koobi Fora, Guérin (1987a) found it at Laetoli, Harris et al. (2003) found more material at Kanapoi, and Harris and Leakey (2003) found it at Lothagam. Geraads (2005) noted that the type material of *C. praecox* belongs to the genus *Diceros* (as *Diceros praecox*), and he found that species at Hadar.

Early Evolution of Dicerotini

Several Miocene taxa have been described and phylogenetically associated with the extant African genera (Wagner 1848; Gaudry 1862–1867; Osborn 1900; Thenius 1955; Hooijer 1968, 1978; Guérin 1966, 2000, 2003; Arambourg 1959; Geraads 1986, 1988, 2005). Their status has been recently reviewed and updated by Giaourtsakis et al. (2009). Despite the number of described species, the early evolutionary history and radiation of the Dicerotini tribe remains presently unresolved, primarily due to the insufficient African Miocene record.

“*Diceros*” *neumayri* was the first recognized fossil relative of the extant African species (Wagner 1848; Gaudry 1862–1867) and until the 1960s their only Miocene representative. It is a very common element of the Hipparion faunas of the sub-Paratethyan mammalian province (*sensu* Bernor 1984) and has been documented in numerous localities from the Eastern Mediterranean, the Middle East and adjacent regions (Giaourtsakis 2009 and references therein). Because of its dental similarities with the extant *Diceros*, the taxon has been commonly assigned to this genus (Ringström 1924; Thenius 1955; Hooijer 1972, 1978; Heissig 1975, 1989; Guérin 1966, 1980a, 2003; Tsiskarishvili 1987). Geraads (1988) pointed out cranial similarities with *Ceratotherium*, which, however, represent early convergences (Giaourtsakis et al. 2009). Later, Geraads (2005) deemed “*Diceros*” *neumayri* (which he called *Ceratotherium neumayri*) as the common ancestor of both extant species, arguing that it is morphologically and ecologically intermediate between them. In his context, the known African Miocene taxa *Paradiceros mukirii* and *Diceros primaevus* were considered as being related forms with “*D.*” *neumayri*, and *Diceros douariensis* as potentially conspecific. However, no arguments were provided by Geraads (2005) to support this grouping or the implied relationships among the Miocene taxa, whereas *Diceros australis* was excluded from the comparisons. Geraads (2005) further suggested that the two extant lineages split soon after the Miocene-Pliocene boundary, leading from an ancestral mixed feeder (“*Ceratotherium neumayri*”) to a lineage of grazers (*Ceratotherium*) and a lineage of browsers (*Diceros*). However, based on our observations, the Late Miocene “*Diceros*” *neumayri* forms a monophyletic extra-African evolutionary lineage with no Pliocene descendants. The dispersal of these populations in the eastern Mediterranean and adjacent regions was followed by the gradual establishment of a unique combination of primitive and derived craniodental features, as well as several autapomorphies, notably in the postcranial skeleton (Giaourtsakis et al. 2009). The available Miocene fossil record indicates that the split between the extant lineages of *Diceros* and *Ceratotherium* must have taken place in Africa during the Miocene and that not only the common ancestor

of the extant lineages should have been a browser, but also the ancestral stock of the *Ceratotherium* lineage probably favored a browsing diet for as long as available habitats could supply it.

A potential candidate of the ancestral Dicerotini morphology is the relatively complete rhinocerotid sample from the early late Miocene locality of Bou Hanifia (Oued el Hammam), Algeria, recovered above a volcanic tuff radiometrically dated at 12.18 ± 1.03 Ma (Ameur et al. 1976). The material was originally described as *Dicerorhinus primaevus* by Arambourg (1959), partly due to misleading comparisons (Giaourtsakis et al. 2009), but was later properly allocated to the genus *Diceros* by Geraads (1986). *Diceros primaevus* shows a dental and postcranial morphology that essentially persists, with relatively few modifications, in the extant black rhinoceros. The conservative morphology of *D. primaevus* may support a placement close to the split between the extant black and white rhinoceros lineages. In addition, populations similar to *D. primaevus* might have migrated outside Africa, around the middle-late Miocene boundary, and independently evolved into the Eastern Mediterranean “*Diceros*” *neumayri*.

A species considerably older than *D. primaevus* has been recently described by Guérin (2000, 2003) as *Diceros australis* from the locality of Arrisdrift in the Orange River Valley of Namibia, dated close to the early-middle Miocene boundary (ca. 17.5–17.0 Ma after Pickford and Senut 2003). Besides a small occipital and a few mandibular fragments, the hypodigm of *D. australis* comprises several isolated dental and postcranial elements. Based on Guérin’s (2000, 2003) descriptions and illustrations, the morphology of the upper permanent cheek teeth indeed seems to follow the unspecialized Dicerotini pattern, similar to the extant *Diceros*. The well preserved, slightly worn P4 (Guérin 2000, Plate 1, Fig. 3) has a strong paracone fold, the mesostyle and metacone folds are not developed, a weak crochet is present but no crista, the protocone is not constricted by a distal groove, and a strong continuous crenulated lingual cingulum is developed. The described molars also bear a strong paracone fold, a weakly developed crochet without a crista and a distally unconstricted protocone (Guérin 2000, 2003). The most prominent feature of *D. australis*, however, is the significant size of its postcranial elements, especially the metapodials that are considerably longer than the maximum values recorded for the two extant species, as well as the early late Miocene *D. primaevus* and the side branch of the extra-African “*D.*” *neumayri*. Similar size and proportions can be found on isolated specimens from the significantly younger Mpesida Beds of Kenya (~6.2 to 6.9 Ma), and Saitune Dora (~5.6 Ma, Giaourtsakis et al. 2009), as well as in the abundant material from the early Pliocene of Langebaanweg (Hooijer 1972) and the Late Pliocene

C. efficax. If correctly identified and dated, the puzzling discovery of the large-sized *D. australis* as the oldest known representative of the Tribe Dicerotini perplexes the early radiation of the Tribe and the split between the black and white rhinoceros (sensu lato), as it would clearly pose a second center of evolution next to the younger and apparently more conservative *D. primaevus*.

Another Middle Miocene taxon traditionally associated with the Dicerotini lineage has been inaccurately described from the locality of Fort Ternan in Kenya (ca. 13.7 ± 0.3 Ma, after Pickford et al. 2006). Hooijer (1968) originally portrayed *Paradiceros mukirii* as a primitive collateral species of the ancestral *Diceros* stock, differing from extant and fossil *Diceros* in a combination of primitive and progressive features. However, the holotype and the majority of the specimens from Fort Ternan, if not the complete hypodigm, belong to “*Dicerorhinus*” *leakeyi* Hooijer, 1969, an early member of the Dicerorhinini tribe (Giaourtsakis et al. 2009).

The first Miocene taxon to show some progressive dental features similar to *Ceratotherium*, appears to be *Diceros douariensis*, Guérin, 1966 (Heissig 1989; Giaourtsakis et al. 2009). The type material originates from the Mines of Douaria, 2.5 km SW of the village Sedjerane, in the plateau of Couchet el Douharia in North Tunisia. The biostratigraphical context of the locality warrants a Late Miocene age (Guérin 1966, 2003). The material comprises an adult holotype and a juvenile paratype skull, however the latter belongs clearly to a different, hornless rhinoceros species (Geraads 2005; Giaourtsakis et al. 2009). Guérin (1966) originally considered *D. douariensis* as a circum-Mediterranean species showing a mixture of progressive and primitive features with respect to the Eastern Mediterranean “*D.*” *neumayri*, the only established Miocene Dicerotini species at that time. Besides the reported large size and the apparent high crowned teeth of the holotype adult skull (Guérin 1966; Giaourtsakis et al. 2009), some derived dental features characterize the Douaria rhinocerotid and distinguish it from Plio-Pleistocene and extant *D. bicornis*, as well as from the extra-African *D. neumayri*. These include the obliquity of the protocone on the molars and the development of a lingual protocone groove (Guérin 1966, Fig. 8). A similar dental morphology is also observed on an isolated upper molar (KNM LT-89) from the Lower Nawata formation of Lothagam (~7.5–6.5 Ma; McDougall and Feibel 1999, reprinted in 2003), originally referred to as *C. praecox* by Hooijer and Patterson (1972), and an almost complete cranium from Kuseralee of the Middle Awash Valley of Ethiopia (Giaourtsakis et al. 2009). The dental complexity was further advanced during the Pliocene by populations similar to the Langebaanweg sample (Hooijer 1972) and the late Pliocene *Ceratotherium efficax* detailed herein as a response to the expansion of more open habitats and the adaptation to more abrasive diet.

Paleoecology of the Laetoli Rhinoceroses

The available cranial morphology of the LAET 75-3065 *Diceros* falls within the variation observed in the extant *D. bicornis*. The Laetoli *Ceratotherium* crania are markedly longer, more dolichocephalic, and demonstrate an increased posterodorsal inclination of the occiput similar to extant *C. simum*. These cranial features suggest a lowering of the resting position of the head, and by implication, a shift towards feeding on lower vegetation, as originally suggested by Zeuner (1934) and Loose (1975). These observations are consistent with the commonly held view that *Diceros* has remained a browser throughout its history, whereas *Ceratotherium* experienced a more or less gradual shift towards grazing (Osborn 1900; Zeuner 1934; Dietrich 1945; Thenius 1955; Hooijer 1969, 1978; Guérin 1980a, 1987a; Heissig 1989; Harris and Leakey 2003; Giaourtsakis et al. 2009). The available data do not favor a sudden shift in proportions as caused by a mutation acting on ontogenetic development (Stanley 1979), and it is difficult to reconcile with the scenario of Geraads (2005), which suggests that *Diceros* arose from *Ceratotherium* through a process of evolutionary reversal from mixed feeding, or grazing, to browsing.

The available dental morphology of the Laetoli *Diceros* shows no significant difference with respect to extant *D. bicornis*. The recovered teeth are too few (as only the teeth of the cranium LAET 75-3065 can be securely assigned to *Diceros*), and too worn to allow a meaningful study of dental wear patterns. However, nothing suggests that the teeth were worn much differently from what is seen in the extant species. On the contrary, the dental morphology of the Laetoli *Ceratotherium* is functionally informative, since a sufficient number of specimens exist to allow a paleodietary reconstruction using the mesowear analysis (Fortelius and Solounias 2000).

The functionally relevant morphological features of the *Ceratotherium* teeth from Laetoli all point to a state intermediate between extant *Diceros* and extant *Ceratotherium*. These include, among others, the moderate degree of hypsodonty, the presence of thickened cement covering the crown, the mild distolingual bending of the transverse lophs, the incipient closing-off of the medifossette and the medially bulging curvature of the ectoloph. The distribution of these character states is discussed in detail in the taxonomic part of this chapter; here we only note that the dental morphology of the Laetoli *C. efficax*, while indeed intermediate, is significantly closer to the *C. simum* end of the spectrum and well separated from the plesiomorphic rhinoceros morphology demonstrated by *Diceros*, including *D. praecox* as understood by Geraads (2005). However, rather than trying to quantify the relative development of these features of long-term evolutionary change, we focus our attention here on the

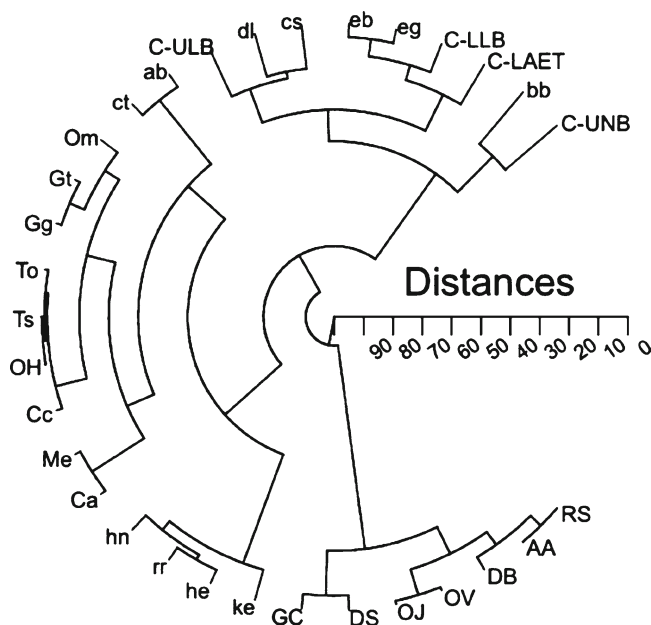


Fig. 11.5 Hierarchic cluster diagram of mesowear (Fortelius and Solounias 2000) in all *Ceratotherium* (C-LAET) from Laetoli and in stratigraphic subsamples from the Lower Laetoli Beds, Upper Laetoli Beds, and upper Ndolanya Beds (C-LLB, C-ULB, and C-UNB, respectively). Note that all samples cluster in the grazer part of the tree, indicated by species acronyms in lower case. Acronyms in upper case indicate browsers and acronyms in mixed case indicate mixed feeders. Species abbreviations: Browsers (conservative): AA=*Alces alces*, DB=*Diceros bicornis*, DS=*Dicerorhinus sumatrensis*, GC=*Giraffa camelopardalis*, OH=*Odocoileus hemionus*, OJ=*Okapia johnstoni*, OV=*Odocoileus virginianus*, RS=*Rhinoceros sondaicus*. Grazers (conservative): ab=*Alcelaphus buselaphus*, bb=*Bison bison*, cs=*Ceratotherium simum*, ct=*Connocchaetes taurinus*, dl=*Damaliscus lunatus*, eb=*Equus burchelli*, eg=*Equus grevyi*, he=*Hippotragus equinus*, hn=*Hippotragus niger*, ke=*Kobus ellipsiprymnus*, rr=*Redunca redunca*. Mixed feeders (conservative): Ca=*Capricornis sumatrensis*, Cc=*Cervyceros melampus*, Gt=*Gazella thompsoni*, Gg=*Gazella granti*, Me=*Aepyceros melampus*, Om=*Ovibos moschatus*, To=*Taurotragus oryx*, Ts=*Tragelaphus scriptus*

analysis of wear patterns reflecting the immediate dietary regimes of the animals.

Hierarchic clustering of *C. efficax* from Laetoli, based on classical mesowear, places it within the grazer cluster, with stratigraphically defined subclusters ending up in distinct parts (Fig. 11.5). The result is insensitive with respect to which two of the three cusp sharpness states are included in the analysis, and to whether the relief is included as a parameter or not.

In order to evaluate the conventional mesowear study presented here, we used curvature analyses of scanned enamel profiles to illustrate and to compare the wear profiles in a small selection of upper and lower teeth from Laetoli with teeth of the extant species (Fig. 11.6). These profiles clearly show the exceptionally sharp edges (high curvature) seen in *Diceros*, indicated by a narrow band of white along the buccal edge of an otherwise smooth (black-colored) surface. In contrast, the teeth of derived *Ceratotherium* from the latest Pliocene and

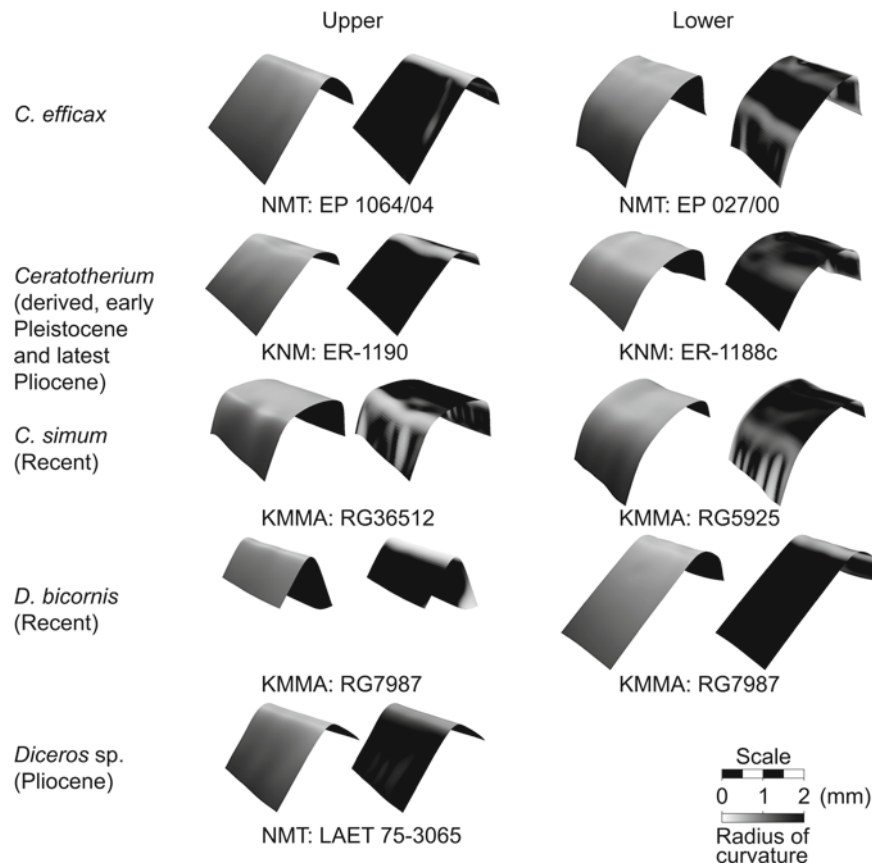


Fig. 11.6 Profiles and curvature maps of buccal upper and lower teeth enamel facets (all teeth are M2/m2, except KNM ER-1190 and LAET 75-3065, which are P4s) of *C. efficax* compared with the early Pleistocene (left) and the latest Pliocene (right) derived *Ceratotherium*, Recent *C. simum*, Pliocene *Dicerops* and Recent *D. bicornis*. For each

specimen, a topographic surface is shown on the left, and a curvature map overlaying the surface is shown on the right. Higher curvature (lower radius of curvature) is shown in white, with lower curvature in black. Topographic scale bar in mm, radius of curvature scale (grayscale) in mm

early Pleistocene, and particularly extant *Ceratotherium simum* show moderate curvature along the crest and a profusion of locally high curvature due to irregularities in the enamel surfaces. *C. efficax* from Laetoli occupies an intermediate state between these extremes, with relatively well-demarcated curvature maxima along the profile, but decidedly lower values at the edge between the main surfaces and with more irregularities within them than is seen in *Dicerops*. This comparison also reveals that the profiles of the lower teeth, while geometrically different from those of the upper teeth, nevertheless show the same overall similarities and differences as the upper teeth, lending some independent support to our inclusion of lower teeth in the cusp sharpness analyses.

A box plot of cusp sharpness among selected taxa (Fig. 11.7) shows a clear separation between *Dicerops* and *Ceratotherium*, with *C. efficax* occupying an intermediate position closer to *C. simum* than to *Dicerops*. A marked but statistically insignificant difference is observed between the late Pliocene and early Pleistocene derived *Ceratotherium* and extant *C. simum*, suggesting that the extreme grazing diet of the extant species may

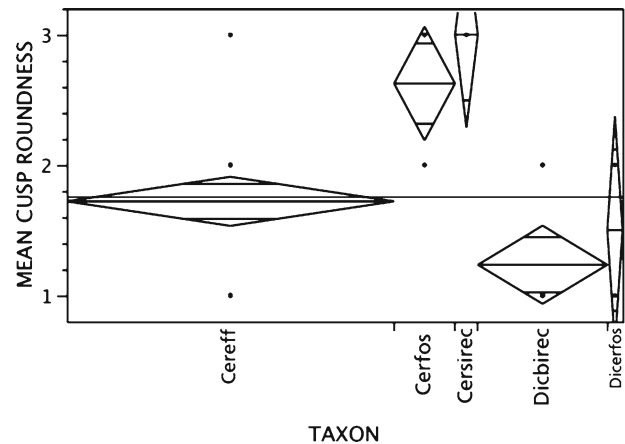


Fig. 11.7 Comparison of mean molar cusp roundedness in selected rhinoceros taxa: Cereff=*C. efficax*, Cerfos=derived *Ceratotherium* from the late Pliocene and the early Pleistocene, Cersirec=*C. simum* (recent), Dibirec=*D. bicornis* (recent), Dicerfos=fossil *Dicerops*. Note low rounding in *Dicerops*, high in *C. simum*, and intermediate in *C. efficax*. Top and bottom of diamond, 95% CI; horizontal lines are “overlap marks”, width of diamond signifies number of specimens

have developed during the beginning of the Pleistocene or even later. A similar plot for *Ceratotherium* across temporal groups within the Laetoli sequence shows the same relationships but with more resolution (Fig. 11.8). The minor fluctuations observed within the Laetoli Beds cannot be distinguished from random noise, but the small sample from the Upper Ndolanya Beds shows significantly higher rounding, indicating a more abrasive diet at this time. Thus, the dietary regime of *C. efficax* appears to fall within the grazing realm, but may still have included variable amounts of browse. In any case the food eaten was clearly less abrasive than the graze consumed by the late Pliocene and early Pleistocene *Ceratotherium* and especially extant *C. simum*. Figure 11.9 illustrates the mean molar cusp roundness of *Ceratotherium* in East Africa over time.

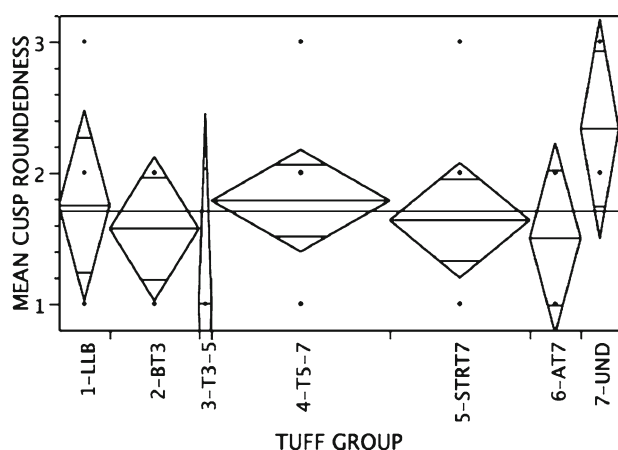


Fig. 11.8 Mean cusp roundedness in *Ceratotherium* in the Laetoli Sequence, separated into Tuff Groups. Note increase in unit 7-UND (Upper Ndolanya Beds). Other abbreviations: 1-LLB=Lower Laetoli Beds, 2-BT3=below Tuff 3, 3-T3-5=between Tuffs 3 and 5, 4-T5-7=between Tuffs 5 and 7, 5-STRT7=straddles Tuff 7, 6-AT7=above Tuff 7. See Fig. 11.7 for diamond description

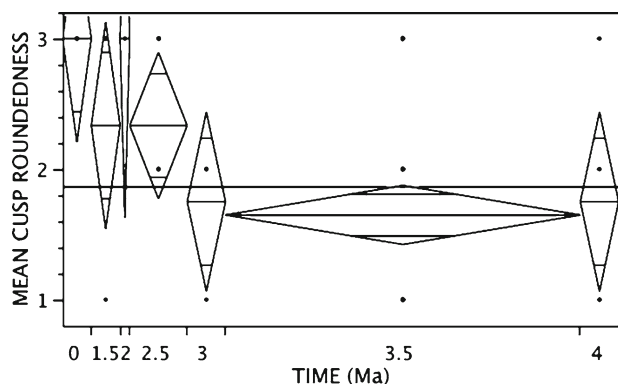


Fig. 11.9 Mean molar cusp roundedness in East African *Ceratotherium* over time. Note sustained increase in food abrasion through Late Pliocene and Pleistocene. See Fig. 11.7 for diamond description

Conclusions

The occurrence of true *Diceros* in the Laetoli Beds is indisputable, but, in contrast to Guérin (1987a), we find few specimens attributable with any confidence to this genus. We are also unwilling to assign the Laetoli *Diceros* material at the species level. We agree with Hooijer (1978) and Geraads (2005) that the existence of an extant species *D. bicornis* even in the Late Miocene locality Lothagam (Harris and Leakey 2003) would make its longevity rather unique among mammals. We were, however, unable to detect in the *Diceros* material from Laetoli features described by Geraads (2005) in *D. praecox* from Lower Awash. We agree with Guérin (1987a) on the identity of the larger and more abundant rhinoceros at Laetoli, which he assigned to *Ceratotherium praecox*, while mentioning the alternative nomenclatorial choice of *C. efficax*. We, however, chose to use the name *C. efficax* for this material, because of the mismatch with the holotype and the heterogeneity of the material referred to the species *C. praecox* by its original authors. The name *C. mauritanicum*, proposed by Geraads (2005), is restricted to the Pleistocene North African species, which is most likely a descendant of *C. efficax* and can be viewed as a “sister taxon” of *C. germanoaffricanum* and *C. simum*. The more advanced cranium LAET 81-74 is so poorly preserved, that the precise identification to either *C. germanoaffricanum* or *C. simum* is impossible. The vast majority of the Laetoli postcranials most likely belong to *C. efficax*.

As noted by several authors (Osborn 1900; Dietrich 1942; Fortelius 1985), the dental evolution of *Ceratotherium* shows a transition from a *Diceros*-like ectolophodont condition to the full-fledged plagiolophodonty seen in extant *Ceratotherium simum*. There cannot be any doubt that this morphological transition somehow reflects a dietary shift from browsing to grazing, but the rate and timing of these changes, as well as their precise relationship to the diet has largely remained a matter of speculation. Our results suggest, that the transition included a substantial period of stasis, spanning at least the interval represented by the Laetoli Beds, during which the dietary regime varied in the range from mixed feeding to grazing (Fig. 11.8). Our results clearly show that a shift in the dietary regime towards grazing had occurred by Upper Ndolanya times, and that the trend towards increased grazing continued from the Early Pleistocene to the Recent (Fig. 11.9).

Geraads (2005) proposed an alternative scenario according to which African *Ceratotherium* arose through an immigration of the Eurasian species “*Diceros*” *neumayri*, and in turn gave rise to *Diceros* through an evolutionary reversal to a browsing mode of life. However, we find this scenario difficult to reconcile with the available evidence, and believe that the Late Miocene “*Diceros*” *neumayri* actually forms a monophyletic extra-African evolutionary lineage with no Pliocene descendants (see Giaourtsakis et al. 2009).

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