Ardipithecus kadabba

Late Miocene Evidence from the Middle Awash, Ethiopia

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Cover illustration: Lingual view of ASK 3/400, *Ardipithecus kadabba* right upper canine from Asa Koma. Photograph courtesy of David Brill © copyright 2003.

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Rhinocerotidae

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During the Miocene, fossil rhinoceroses were diverse and widespread in Africa. At least five different lineages (aceratheres, brachypotheres, iranotheres, dicerorhines, and dicerotines), comprising about eight genera and thirteen species, have been documented (Hooijer 1978; Guérin 2003). However, only one lineage, the dicerotines, managed to survive the biotic turnover event at the Miocene-Pliocene boundary. It persists today with two ecologically differentiated species: the extant black or hook-lipped rhinoceros, *Diceros bicornis,* a browser; and the extant white or square-lipped rhinoceros, *Ceratotherium simum,* a dedicated grazer.

Fossil representatives of the tribe Dicerotini are relatively poorly documented in Miocene Africa. Few African localities have yielded adequate material for a detailed study, and in each case a new species has been described. Despite the number of Miocene species and the more adequate Plio-Pleistocene fossil record, the early evolutionary history of the tribe and the split between the extant black and white rhinoceroses remain tentative and controversial (Thenius 1955; Hooijer 1968; Hooijer and Patterson 1972; Hooijer 1978; Groves 1975; Guérin 1980b , 1982; Groves 1983; Geraads 1988; Guérin 1989; Heissig 1989; Geraads 2005). Therefore, the discovery of a relatively well-preserved Dicerotini skull close to the Miocene-Pliocene boundary in the Middle Awash Valley is of particular interest. A full listing of the institutional, anatomical, and locality abbreviations used herein can be found in the Appendix at the end of this chapter.

Rhinocerotidae

Diceros Gray, 1821

Diceros douariensis Guérin, 1966

RESTRICTED SYNONYMY 2004 *Ceratotherium* cf. *C. praecox* (Haile-Selassie et al. 2004c: 544, figure 5)

　　2001 *Diceros* sp. (Haile-Selassie 2001a: 318–319)

REVISED DIAGNOSIS *Diceros* of large size; nasal and frontal horns present, nasal bones rostrally rounded with abrupt and broad termination; premaxillary bones reduced;

lower border of orbit sloping laterally downwards; anterior border of orbit above the level between M^1 and M^2; supraorbital process very strong; postorbital process absent; dorsal cranial profile concave; parietal crests widely separate; nuchal crest straight or slightly indented, not extending over the occipital condyles; occipital plane vertically oriented; postglenoid process strong and straight; posttympanic process bending forward, narrowing the external auditory pseudomeatus, but not contacting the postglenoid process. Mandibular symphysis anteriorly abbreviated and narrow, posteriorly extending below the level of P_3; ventral border of mandibular corpus convex without marked angulation at mandibular angle. Lower premolars with open internal valleys, not forming fossetids. Upper and lower incisors absent or vestigial. High-crowned brachydont maxillary dentition with concave occlusal surface, inequalities in enamel thickness, and thin cement coating. Upper premolars with variable persistence of d^1 in adulthood; lingual cingulum strong, crenellated, and continuous; crochet present, crista and medifossette absent; protocone and hypocone not constricted; antecrochet absent; paracone fold present; metacone fold faint or absent. Upper molars (M^1, M^2) with protoloph of M^1 bending slightly distolingually and metaloph vertically oriented; mesial protocone groove present, deep and marked; distal protocone groove absent or faint; lingual protocone groove present; crochet strong, crista and medifossette absent; paracone fold present, moderate; mesostyle swelling developed but weaker than paracone fold; buccal apices of metacone and paracone cusps sharp; M^3 with subtriangular outline and continuous ectometoloph.

DESCRIPTION   KUS-VP-1/20 is a moderately well-preserved adult cranium including the complete right and left permanent dentition (Figure 14.1). The specimen has been restored from numerous fragments and bears multiple fractures, postmortem abrasion, and minor dorsoventral crushing. Most affected are the lateral sides, especially the buccinator region and the zygomatic bones, which are poorly preserved. The temporal bones and their zygomatic processes are better-preserved. In dorsal view, the anterior part of the nasal bones is completely preserved. The intervening area, including the posterior part of the nasals, a significant portion of the frontals, and parts of the dorsal border of the maxilla and the lacrimals, is missing. The parietal and interparietal bones are almost intact, but the occipital bone is more fragmentary. In ventral view, the complete dentition and the palatine processes of the maxilla are very well-preserved, including the two small premaxillary bones. The palatine bones are nearly complete, but most of the vomer is lost. The pterygoid bone is better-preserved on the right side. The basisphenoid and the basioccipital of the occipital are moderately well-preserved.

The nasal bones are thick and wide, bearing a very strong nasal horn boss with extensive, rough vascular impressions. In dorsal view, the nasal bones terminate abruptly, and their rostral end is wide and rounded. The internasal groove is deep and marked only at the rostral tip of the nasal dome. The nasal bones are completely fused posteriorly. The ventral surface of the nasals is transversally concave. In lateral view, the nasal incision extends backward to above the mesial half of the P^3. The nasal notch appears to be U-shaped, although this area is fragmentary, especially on the left side. The infraorbital foramen is situated above the distal half of the P^3. The facial morphology of the buccinator region is

KUS-VP-1/20, cranium of *Diceros douariensis* with complete right and left permanent dentition. A. Dorsal view. B. Ventral view C. Lateral view.

poorly preserved. A significant portion of the frontal bones is missing, but the remaining fragments bear vascular rugosities at the level between the supraorbital processes, indicating the presence of a smaller frontal horn. The supraorbital process is very strong and prominent. The lacrimal process is weaker and more posteriorly oriented, bearing at least two separated lacrimal foramina at its base. A postorbital process is not developed on the frontals. The anterior border of the orbit is approximately situated above the level between M^1 and M^2. The floor of the orbit (dorsal surface of the zygomatic bone) slopes laterally downwards. The ventral border of the zygomatic bone is low, partly covering the maxillary tuber in lateral view. The temporal process of both zygomatic bones is poorly preserved.

The parietal bones are well-preserved. In lateral view, the dorsal profile of the skull is clearly concave, as in the extant *D. bicornis*. In dorsal view, the two oblique parietal crests are well-separated, and the interparietal bone between them remains wide and slightly convex transversally. Anteriorly, they curve smoothly laterally and are continuous with the temporal lines. Posteriorly, they diverge backward into the nuchal crests. The occipital border of the interparietal bone is damaged at the junction with the squamous part of the occipital bone. The nuchal crest appears dorsally indented (Figure 14.1A). However, it is distorted because of the missing fragments, especially on the left side. Based on the morphology of the more complete right side, we can infer that the nuchal crest was straight or only slightly indented in dorsal view, as in the extant *Diceros*. In occipital view, the squamous part of the occipital is fragmentary. The squamous occipital fossa is deep, and the external occipital protuberance was probably weak. There is no sign of an external median occipital crest. The nuchal tubercle is weak. The foramen magnum appears to be rounded, but it is incomplete. Only the right occipital condyle is preserved; it is kidney-shaped. Despite the incompleteness, the occipital plane appears to be almost vertical in lateral view, as in the extant *D. bicornis,* and not backwardly inclined, as in *C. simum*.

In ventral view, the basioccipital part of the occipital bone is moderately well-preserved. A marked and sharp sagittal crest runs along its middle, extending from the intercondylar incision to the basisphenoid. The paraoccipital process is missing its ventral tip on both sides. Its base is fused with the post-tympanic process, which bends forward, approaching very close to, but not contacting, the postglenoid process. The postglenoid process is strong, long, and straight. The bilateral basilar muscular tubercles are fused and demarcate the junction with the body of the basisphenoid. The pterygoid plates are thin and slope evenly, their posterior margin nearly horizontal. The vomer is poorly preserved. The anterior border of the choanae extends forward to the level between the M^2 and M^3. The palatine processes of the maxilla are fused in the middle, and their rostral border must have been indented. Both premaxillary bones are preserved. The left one is in better condition. They are short, thin, and flattened. They are edentulous, and no alveoli for permanent or persisting deciduous incisors are present. The distance between the rostral tip and the second premolar on the left side is less than 75 mm. A palatine process is not developed. The interincisive fissure is wide. It narrows rostrally as the premaxillary bones bend medially and approach each other but do not come in contact.

The complete left and right permanent dentition of the Kuseralee cranium is well-preserved (Figures 14.1B and 14.2A). The left M^3 is fully erupted and moderately worn, indicating a mature adult individual (Hitchins 1978). The right M^2 is severely deformed and pathologically twisted 90° counterclockwise, so that the metaloph and postfossette are facing the lingual side. This malformation has affected the occlusion of the right M^3, which is completely unworn, and also, to some extent, the right M^1 and P^4. Rhinoceroses chew on one side at a time, and during the occlusal stroke the teeth occlude only on the active side (Fortelius 1985). It is therefore reasonable that the animal tried to avoid the pathological side. We have observed a similar dental malformation in a P^4 of extant *C. simum* (USNM: 164592) and a P^4 of *Dicerorhinus sumatrensis* (BMNH: 1868-4-15-1). Several cases of rare dental malformations have been documented in the dentition of extant and fossil rhinoceroses (Patte 1934; Vialli 1955; Guérin 1980b).

Traces of a thin cement layer are evident in all teeth, especially on the buccal side of the ectoloph and in the medisinus valley of the molars. All premolars are molariform (*sensu* Heissig 1989: figure 21.1): The protoloph and metaloph do not fuse lingually, except at the very late stages of wear, keeping the entrance of the medisinus open. The first premolar (a D^1) has not persisted into adulthood. The P^2 is nearly square-shaped and markedly smaller than the succeeding premolars. As is common in P^2s, the metaloph is slightly longer than the protoloph, and the mesial width is greater than the distal. The hypocone, which bends slightly mesially, is also larger than the protocone. Both are unconstricted, and their lingual sides are rounded. The internal cingulum is strong, continuous, and crenellated. It begins on the medial side, projects lingually, surrounding both lingual cusps and the entrance of the medisinus, and bends again on the distal side, where it is almost completely worn down. A simple crochet is the only secondary fold developed; crista and antecrochet are absent. The postfossette forms a perfect circle in the worn metaloph. The ectoloph is gently convex, but a faint paracone fold can be traced.

P^3 and P^4 are similar in morphology, the last premolar somewhat larger than the third, and its protoloph slightly more oblique. The protocone and hypocone are subequal with a rounded lingual side. The mesial, lingual, and distal (worn down) cingula are strong, crenellated, and continuous. The metaloph is vertically oriented and the postfossette rounded. The crochet is simple and well-developed; crista and medifossette are absent. A mesial protocone groove is not developed on P^3 but is weakly present on P^4. A distal protocone groove and an antecrochet are absent in both. On the ectoloph, a weak but evident paracone fold is developed, as well as a faint metacone fold. A small, crenellated cingular trace is restricted to the distal corner of the ectoloph base.

Because of the abnormal right M^2, descriptions of features refer to the left side except where otherwise noted. The first two molars are morphologically similar. As expected, the M^1 is more rectangular, whereas the M^2 is somewhat longer but distally narrower. The enamel is thicker on the sides of the teeth and thinner around the medisinus. The protoloph of the left M^1 is oblique, bending distolingually, and the mesial protocone groove is deep and marked. The protoloph of the right M^1, which remains less affected by wear as a result of the malformation of M^2, shows better the marked degree of obliqueness (Figure 14.1B). The intensity of the distolingual sloping is more apparent with respect to
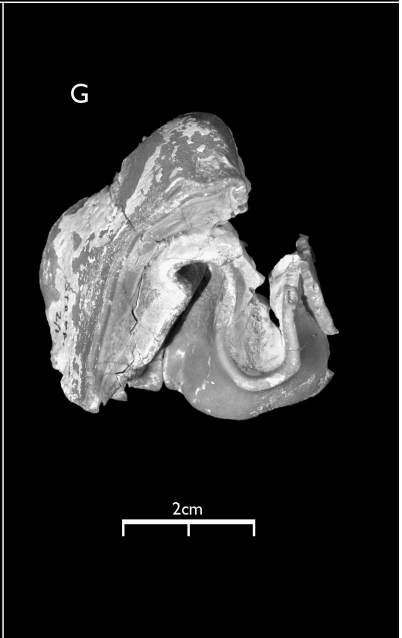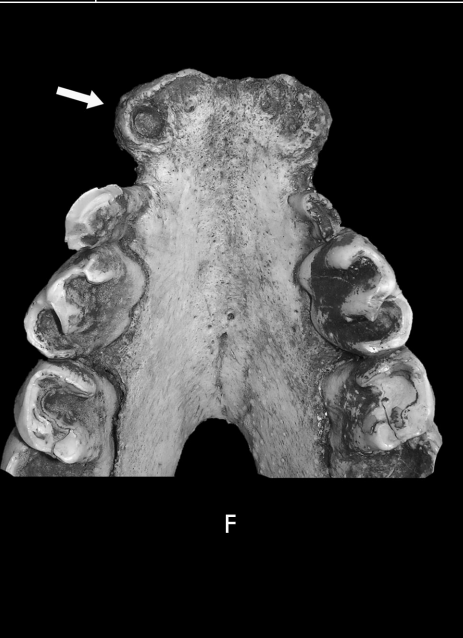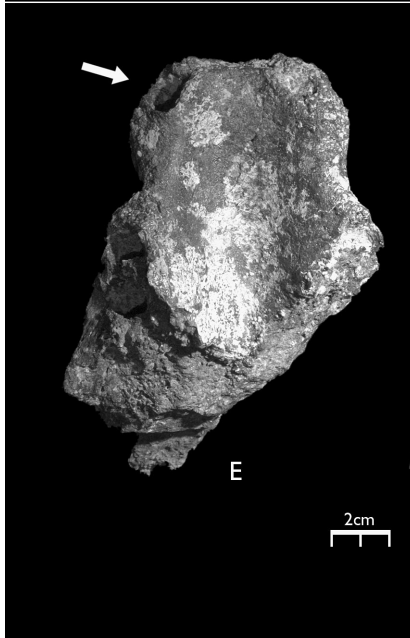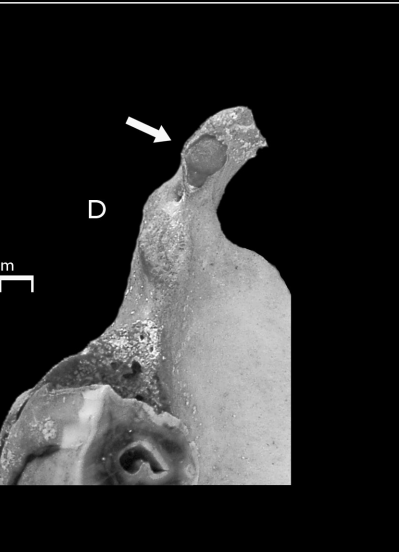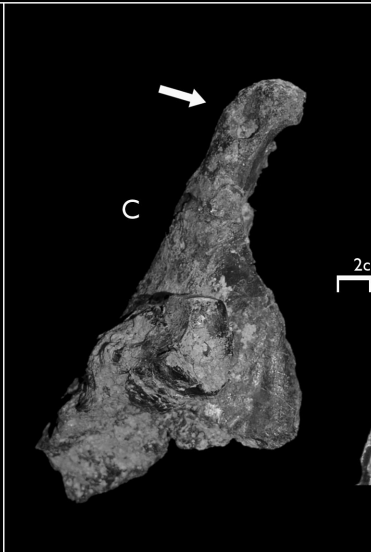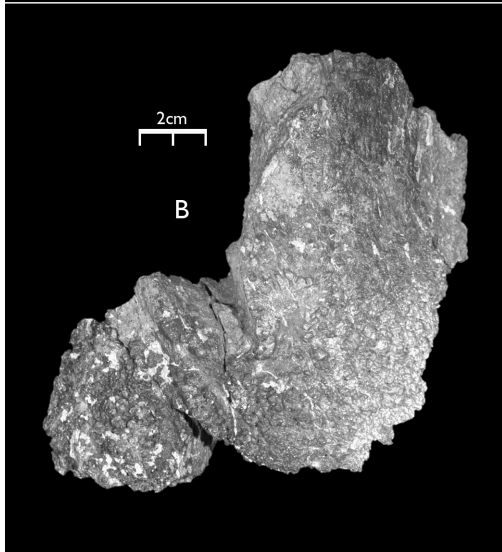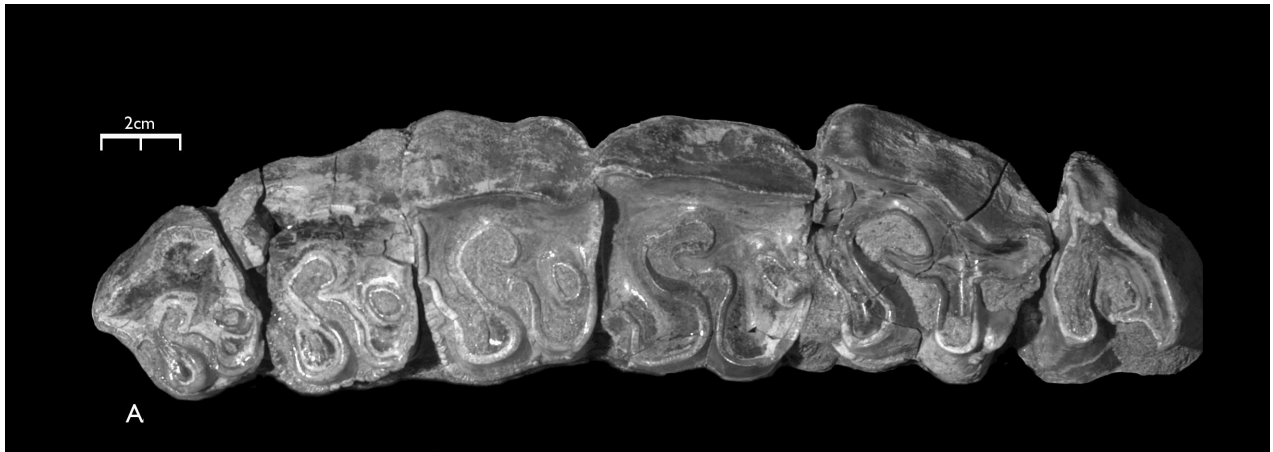
Plio-Pleistocene and extant *Diceros* skulls examined. The intensity of obliqueness closely resembles the morphology of the Langebaanweg molars but is decisively less marked with respect to the Plio-Pleistocene and extant *Ceratotherium* (see discussion). The metaloph does not bend distolingually but remains almost perpendicular with respect to the longitudinal axis of the tooth. The M^2 follows the same protoloph and metaloph arrangment, but both cross lophs are somewhat more tilted with respect to the ectoloph. A distal protocone groove and an antecrochet are not developed. The lingual wall of the protocone is more flattened than in the premolars. On the less worn right M^1 it is slightly depressed, but no marked groove is actually formed. A lingual cingulum is not developed; the mesial cingulum projects slightly on the lingual side of the protocone, particularly on the left M^2, but does not cross the entrance of the medisinus valley. The latter is V-shaped in the less worn right M^1 and left M^2 and would remain open in the very late stages of wear. A closed postfossette is formed only in the much worn metaloph of the left M^1. The only secondary fold projecting in the medisinus valley is a particularly strong and prominent crochet; a crista is absent. The ectoloph of the M^1 is straight and parallel to the longitudinal axis of the tooth row. The M^2 ectoloph is placed more obliquely, forming a bow with the M^3 ectometaloph. The parastyle is narrow and the parastyle groove flat in both M^1 and M^2. A moderate paracone fold is the most prominent vertical fold on the ectoloph. The mesostyle fold is developed as a broader but less prominent swelling, especially on M^2. A metacone fold is absent on the buccal wall of the ectoloph. However, the coronal tip of the metacone is more prominent than the paracone one. Both are sharp, and the intermediate ectoloph relief is concave. The metastyle is somewhat longer than the parastyle, and the metastyle groove is slightly concave.

The M^3 is subtriangular, bearing a continuous ectometaloph. The paracone fold is better-marked than on the previous two molars, as the tooth is less worn. A mesostyle swelling is evident on the middle of the ectometaloph. The lingual side of the ectometaloph is pointed. The protoloph is vertically oriented, and the mesial groove is very weak. As with the rest of the teeth, a distal groove and an antecrochet are not developed. However, a faint but conspicuous lingual protocone groove is developed on the base of the protocone. A prominent crochet is the only secondary fold developed, as on the two preceding molars; a crista is absent. The crown height of the unworn right M^3 measures 72.6 mm by an ectometaloph length of 62.8 mm; this provides a height/length index of 115.

FIGURE 14.2

A. *Diceros douariensis* from Kuseralee, left upper permanent dentition of the skull KUS-VP1/20 with P^2–M^3 in occlusal view. STD-VP-2/12, *Diceros* sp. from Saitune Dora. B. Nasal bone fragment in dorsal view. C. Right maxillary bone fragment with P^1 and premaxillary bone in ventral view; arrow indicates the presence of rudimentary I^1 alveolus. D. Extant specimen of *Diceros bicornis* (NHMW: 4292), detail of maxillary and premaxillary bone in ventral view; arrow indicates the presence of a rudimentary, unerupted I^1 inside the diminutive alveoli. E. *Diceros* sp. from Saitune Dora, STD-VP-2/12, mandibular symphysis fragment in dorsal view; arrow indicates the presence of a rudimentary I_2 alveolus. F. Extant specimen of *Diceros bicornis* (RMNH: Cat-B), detail of mandibular symphysis in dorsal view; arrow indicates the presence of a rudimentary I_2 alveolus. G. *Diceros* sp. from Saitune Dora, STD-VP-2/1, right M^3 in occlusal view.

Diceros sp.

RESTRICTED SYNONYMY   2004 *Diceros* sp. (Haile-Selassie et al. 2004c: 544, figure 5)
    2004 cf. *Brachypotherium lewisi* (Haile-Selassie et al. 2004c: 544, figure 5)
    2001 cf. *Brachypotherium lewisi* (Haile-Selassie 2001a: figure 5.45)

DESCRIPTION   The remaining identifiable material in the Middle Awash sample under consideration consists mainly of worn upper and lower cheek teeth that cannot be presently assigned with certainty to the species level. An association with *Diceros douariensis* is possible. All specimens recovered from the locality of STD-VP-2 could represent one individual. This material was collected from the same spot during three different field seasons. The dental specimens have been restored from many fragments. The stage of wear and the state of preservation of the recovered teeth correspond perfectly to one another, and there is no repetition of elements. However, for some teeth, a direct contact could not be established, and therefore the different catalog numbers have been preserved (STD-VP-2/1, STD-VP-2/2, STD-VP-2/12, STD-VP-2/113). From the other localities of the Adu-Asa Formation, three dental (STD-VP-1/53, ASK-VP-1/10, ASK-VP-3/71) and two postcranial specimens (STD-VP-1/19, ASK-VP-3/202) have been recovered.

Cranial Elements   STD-VP-2/12 comprises the majority of the material from STD-VP-2, including two important cranial fragments (part of the nasal bone and the right premaxillary bone) and the mandibular symphysis.

The nasal fragment retains only the rostral part of the bone, mostly the left side (Figure 14.2B). It is very similar to the nasals of KUS-VP-1/20, displaying the typical Dicerotini morphology. The rostral end is very broad and rounded. Extensive vascular impressions are developed, demonstrating the presence of a strong nasal horn. The internasal groove is deep and marked, but its posterior termination cannot be located because of the fragmentary condition.

The right premaxillary bone is well-preserved, including a small part of the maxilla with the right P^1 (Figure 14.2C). The bone is extremely reduced, and the distance between its anterior tip and the P^1 (probably a persisting d^1) is about 60 mm. The most interesting feature is the presence of a diminutive alveolus for a vestigial I^1. The presence of a rudimentary I^1 (or persisting di^1?) can also be occasionally observed in the extant African species (Figure 14.2D).

The mandibular symphysis is moderately well-preserved (Figure 14.2E). The symphysis is very short and narrow. The lingual face is evenly concave. The labial face is convex and bears several small foramina. There are no marked bilateral ridges developed along the interalveolar margin. The most interesting feature is the presence of a pair of diminutive alveoli, measuring about 11 mm in diameter, for a rudimentary I_2. These are also occasionally observed in the extant species (Figure 14.2F; Hitchins 1978: 72). The posterior part of the symphysis is poorly preserved, and the position of the posterior margin cannot be specified exactly. It must have extended at least to the middle of the P_3 roots, another characteristic feature of the tribe Dicerotini.

Upper Dentition   The specimen STD-VP-2/12 comprises the right P^1 and the left P^1–P^3 and M^3. All the teeth are much more worn than those of the KUS-VP-1/20 cranium,

indicating a very old adult individual. As described, the right P^1 remains attached on the maxillary fragment (Figure 14.2C). The isolated left P^1 (Figure 14.3C) is a small subtriangular tooth retaining its roots. No particular feature can be observed on the completely worn occlusal surface. A small mesiolingual cingulum appears to have been present. The left P^2 is very well-preserved (Figure 14.3C). In contrast to P^3, its mesial width is smaller than its distal one, and the hypocone is larger than the protocone. Both are unconstricted. The mesial cingulum projects lingually, surrounding the base of the protocone. It terminates at the entrance of the medisinus. The presence of a crochet during this late stage of wear cannot be verified. The same is true for the crista and the medifossette. The postfossette forms a small ring in the metaloph. The ectoloph is slightly sinuous, but no vertical folds can be distinguished. The left P^3 is also well-preserved (Figure 14.3C) and, apart from the differences mentioned, it is morphologically similar with the P^2 but significantly larger. Since it is slightly less worn, the presence of a remnant crochet can be verified. The lingual cingulum is longer, surrounding the base of the hypocone. It is less crenellated than the cingulum of the P^3 from the KUS-VP-1/20 skull. The left M^3 is very poorly preserved. Only a part of the ectometaloph is available. It is a perfect reflection of the more complete right M^3 of STD-VP-2/1 described below, supporting that they probably belong to the same individual.

STD-VP-2/1 consists of a very fragmentary right M^2 and a more complete right M^3. The slightly different color of the teeth with respect to STD-VP-2/12 is a result of more extended surface weathering. Only the metaloph and a small part of the protoloph of the right M^2 are preserved (Figure 14.3E). A worn crochet is present in the medisinus valley. A crista and medifossette are absent. The hypocone is not constricted. The deep postfossette remains distolingually open at this late stage of wear, supporting its identification as M^2. The right M^3 is better preserved; only a small portion of the protoloph is missing (Figure 14.2G). The morphology is similar to the M^3 of KUS-VP-1/20, except for the more worn crochet, which is not as prominent. On the protoloph the mesial protocone groove is marked, and the distal one is absent. An antecrochet is not developed. Crista and medifossette are also absent. The hypocone is angular, nearly V-shaped, and not constricted. The ectometaloph bears a weak paracone fold and is covered by a thin cement layer. Some traces of cement are also observable in the entrance of the medisinus valley. Neither lingual nor buccal cingula are developed.

STD-VP-2/2 is a moderately well-preserved left P^4 missing the mesiobuccal part of the ectoloph (Figure 14.3D). The tooth is very worn. The protocone is larger and more rounded than the hypocone; both are unconstricted. The mesial cingulum projects lingually into a crenellated lingual cingulum surrounding the base of the protocone and the entrance of the medisinus. A crochet was present, but it has been completely worn down. As in the other teeth, the antecrochet, crista, and medifossette are absent. The ectoloph of the tooth is poorly preserved. The coronal apex of the metacone cusp is sharp. A crenellated cingular trace is restricted to the distal corner of the ectoloph base.

STD-VP-2/113 is a bulk specimen including all remaining small dental fragments recovered from STS-VP-2, which could not be restored and securely associated with the larger specimens described.
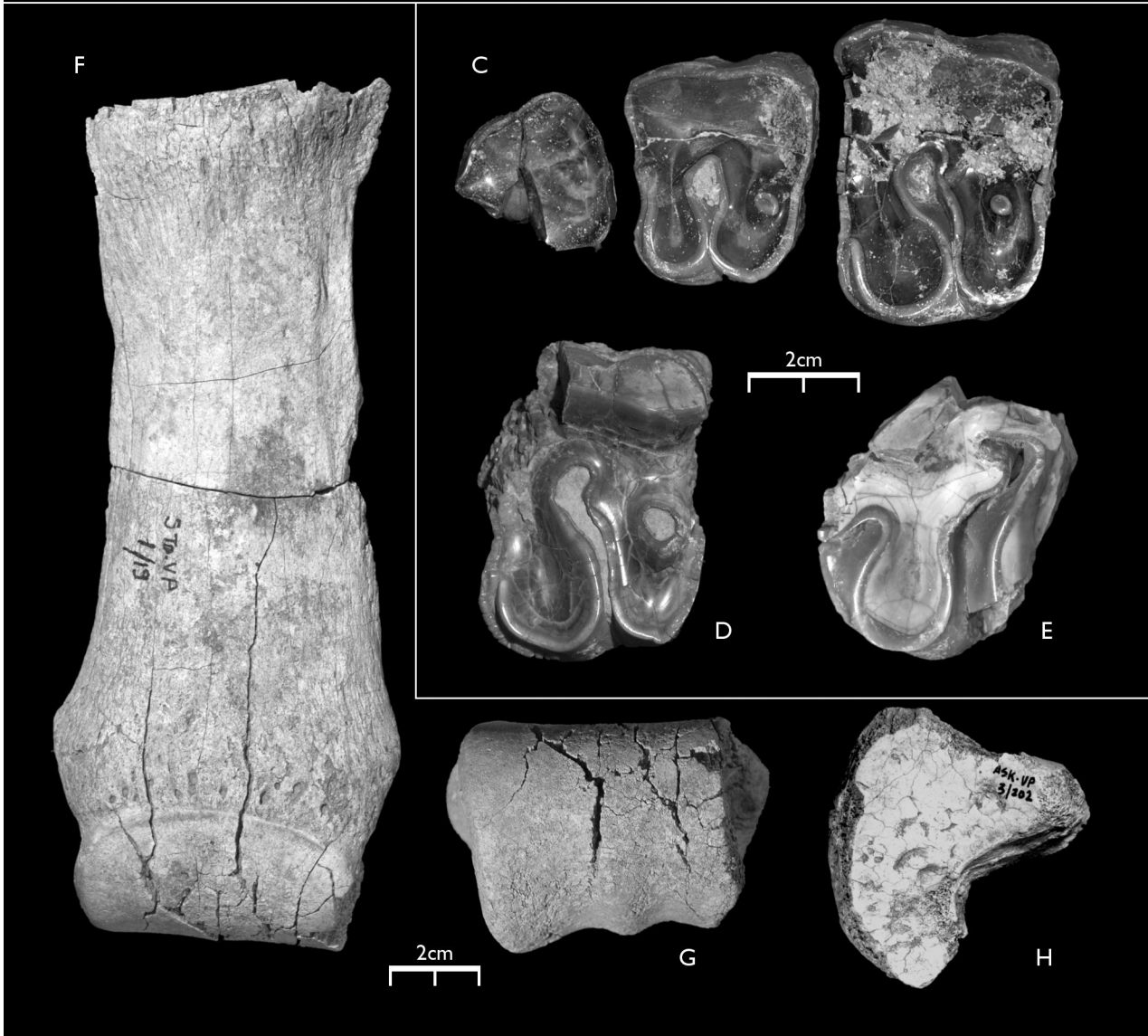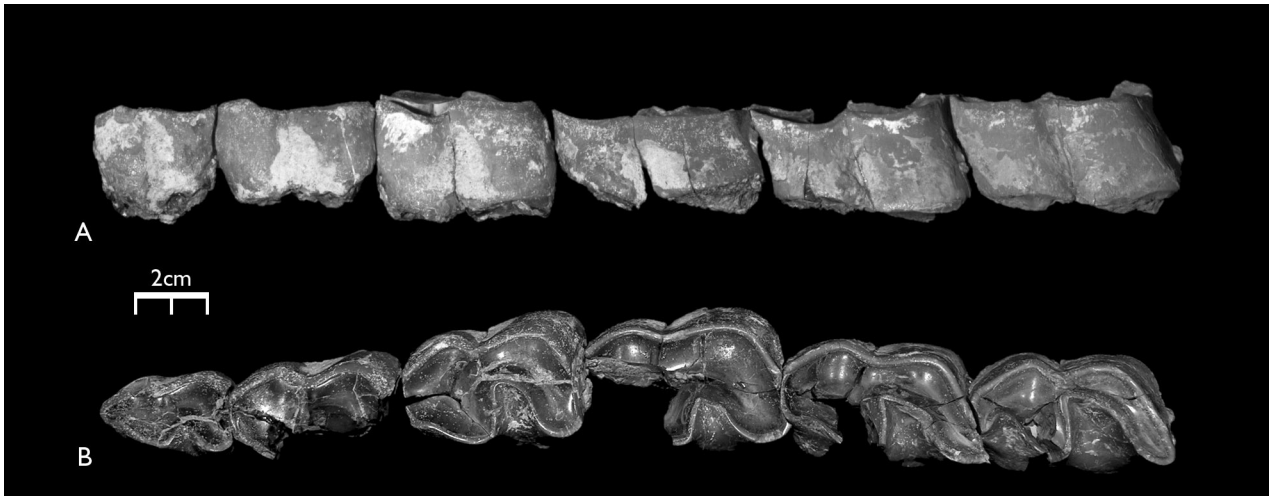
STD-VP-1/53 is the only dental specimen recovered from the locality of STD-VP-1. It represents a right permanent upper molar, probably a M^1. The tooth is fragmentary and completely worn, so that no particular features on the occlusal surface can be described. Although it cannot be accurately measured, the size corresponds well to the described specimens from STD-VP-2.

ASK-VP-1/10 is a fragment of a worn right M^2 from ASK-VP-1. The specimen also includes some small indeterminable fragments of other teeth that belong to the same individual. The assignment to *Diceros* sp. is supported by the absence of a distal protocone groove (no constriction), the absence of an antecrochet, the absence of hypoconone constriction, and the presence of crenellated cingular traces in front of the medisinus entrance. A much worn crochet is also present.

ASK-VP-3/71 is a bulk sample comprising numerous upper and lower dental fragments from at least two individuals. Traces of a thin cement layer are excellently preserved on all ectoloph fragments of the upper dentition. The paracone fold is also well-developed. On the most complete ectoloph fragment, probably a right P^3, neither mesostyle nor metacone fold are developed. Buccal cingula are absent. A medisinus fragment of a much worn premolar shows the presence of a closed mediofossete. Another fragment, probably from a left molar, shows only the typical crochet. Traces of a crenellated lingual cingulum can be observed in some isolated medisinus fragments. Overall, these dental characters are in accordance with the generic morphology of *Diceros*.

Lower Dentition   Both lower tooth rows of STD-VP-2/12 are almost completely preserved. They have been restored from many small dental fragments. Most of the teeth are very worn, hindering detailed description of the occlusal morphology (Figure 14.3A and B). The buccal wall of all the teeth is covered by thin cement traces that are more apparent in the ectoflexid groove (sometimes also preserved under the sediment). Cement traces are also preserved in some trigonid and talonid basins of the less worn teeth. Lingual and buccal cingula are not developed, the exception being some crenellated cingular traces at the base of the buccal wall. The mesial and distal cingula are moderately developed. The talonid basin of all teeth is lingually open, even at this late stage of wear (absence of closed fossettids). The P_2 has a reduced trigonid as is the case in advanced rhinocerotids. The paralophid of the P_2 is unconstricted, mesially rounded, and not prominent at this late stage of wear. The ectoflexid is not particularly deep, but better marked than those of the succeeding teeth. A mesial groove on the buccal wall of the trigonid is not developed. The talonid basin is open lingually, even at this late stage of wear. The P_3 and P_4 are very similar in morphology, with the latter being larger in size. Compared to the molars, both

FIGURE 14.3

Specimens of *Diceros* sp. from late Miocene deposits of the Middle Awash. A. STD-VP-2/12, right P_2–M_3, buccal view. B. STD-VP-2/12, right P_2–M_3, occlusal view. C. STD-VP-2/12, left P^1–P^3, occlusal view. D. STD-VP-2/2, left P^4, occlusal view. E. STD-VP-2/1, right M^2, occlusal view. F. STD-VP-1/19, left third metatarsal, dorsal view. G. STD-VP-1/19, left third metatarsal, distal view. H. ASK-VP-3/202, right ectocuneiform.

teeth have a more reduced trigonid and a more angular hypolophid. The M_1 is worn and still retains a rather angular hypolophid. The last two lower molars are morphologically more similar. Their most notable feature is the less angular hypolophid, especially of the M_3. The ectoflexid is moderately marked.

Postcranial Elements STD-VP-1/19 is a nearly complete left third metatarsal (Figures 14.3F and G). Only the morphology of the proximal epiphysis, which bears the articular facets for the adjacent bones, is obscured by abrasion and surface loss. On its medial side, the poorly preserved small dorsal and plantar facets for the second metatarsal are separated. On the proximal side, the facet for the ectocuneiform is very fragmentary, allowing only an estimation of its size. On the lateral side, the dorsal facet for the fourth metatarsal is completely missing. The plantar facet is better-preserved. It is round and separated by a very narrow groove from the proximal ectocuneiform facet. The diaphysis of the bone is rather straight proximally but widens distally. Its dorsal surface is transversally slightly convex. The plantar surface is flattened, bearing longitudinal rugose depressions for the interosseus metatarsal ligaments on either side of the proximal two-thirds of the shaft. The medial and lateral borders are rounded. On the distal part of the shaft, the medial and lateral tubercles for the attachment of the collateral ligaments of the fetlock joint are well-developed, but they do not project dorsally in distal view. The bilateral depressions for the attachments of the collateral sesamoidean ligaments are circular and deep. The distal epiphysis is well-preserved. In dorsal view, the proximal border of the trochlea is slightly convex. In plantar view, the proximal border of the trochlea is slightly sinuous and remains below the level of the bilateral tubercles. There are no deep supratrochlear depressions developed on the diaphysis above this border, only faint traces caused by the sesamoid contact. In distal view, the median sagittal keel of the trochlea is only weakly developed and remains much lower than the medial rim of the trochlea (Figure 14.3G).

ASK-VP-3/202 is a well-preserved right ectocuneiform (Figure 14.3H). The proximal and distal sides are flattened. On the medial side, the dorsal and plantar facets for the second metatarsal are separated, and there is no contact with the small proximal facet for the mesocuneiform. On the lateral side a dorsodistal and a proximoplantar facet are present for the cuboid.

Rhinocerotidae gen. et sp. indet.

DESCRIPTION   At ASK-VP-2, an indeterminate ectolophid fragment of a moderately worn left P_3 or P_4 was recovered (ASK-VP-2/1). It has a well-marked and deep ectoflexid, a regularly developed mesial cingulum, and no buccal cingulum.

The presence of a rhinocerotid at Alayla is indicated by an indeterminate small tooth fragment, ALA-VP-2/136.

Discussion and Comparisons

Extant horned rhinoceroses and their fossil relatives are generally classified in three lineages: the dicerotines (includes extant *Diceros bicornis* and *Ceratotherium simum*), the rhinocerotines (includes extant *Rhinoceros unicornis* and *Rhinoceros sondaicus*), and the dicerorhines (includes

extant *Dicerorhinus sumatrensis*). Their phylogenetic relationships and suprageneric classification have been highly controversial, with numerous arrangements proposed and debated (Guérin 1980b; Heissig 1981; Guérin 1982; Groves 1983; Prothero et al.1986; Geraads 1988; Heissig 1989; Prothero and Schoch 1989; Cerdeño 1995; McKenna and Bell 1997; Antoine 2002). They are considered here conditionally as three different tribes (Dicerotini Ringström, 1924; Rhinocerotini Owen, 1845; Dicerorhinini Ringström, 1924), forming the subfamily Rhinocerotinae Owen, 1845, of the "true (modern) horned rhinoceroses." Even molecular studies on the five extant species have failed to resolve this trichotomy satisfactorily, resulting in contradicting conclusions (Morales and Melnick 1994; Tougard et al. 2001; Orlando et al. 2003; Hsieh et al. 2003). As a result, molecular clock estimates must be considered cautiously, given that the fossil record for the early radiation of the subfamily is still inadequate. It is generally accepted that the radiation of the three lineages occurred early and rapidly, causing the existing difficulties and disagreements. The monophyly of the dicerotines within all rhinoceroses has been unequivocally supported by all morphological and molecular hypotheses proposed so far.

Because of its key stratigraphic position close to the Miocene-Pliocene boundary, the Kuseralee cranium KUS-VP-1/20 offers valuable indications regarding the potential evolutionary relationships within the tribe Dicerotini and necessitates a detailed and broad discussion. The comparisons begin with the extant and Plio-Pleistocene representatives of the tribe, where material is more abundant and the differences between the craniodental characters can be better analyzed. Then the Miocene African species are discussed, where available material is more limited and the differences more subtle. We finish the comparison with the particular case of the extra-African late Miocene lineage of *"D." neumayri*.

The genus *Diceros* Gray, 1821, as understood here, is paraphyletic. It includes all Dicerotini except the monophyletic lineage of Plio-Pleistocene and extant *Ceratotherium* Gray, 1868, as well as a monophyletic late Miocene extra-African lineage (provisionally referred to as *"Diceros" neumayri*) that arose independently. In this definition, the genus *Diceros* also includes Miocene and early Pliocene species and specimens exhibiting some progressive dental features that apparently represent an ancestral morphology with respect to the true Plio-Pleistocene *Ceratotherium*. These retain an overall craniodental morphology much closer to *Diceros* and do not warrant a generic ascription to *Ceratotherium*. In this aspect, the position of the material from Langebaanweg is left provisionally undecided and to be discussed separately. A complete phylogenetic analysis of the tribe is beyond the scope of the present contribution, since additional fossil evidence is still required, especially from the African Miocene.

Comparison with the Plio-Pleistocene and Extant Ceratotherium *sp.*

The extant white rhinoceros *Ceratotherium simum* (Gray, 1821) has two well-founded subspecies with a strikingly discontinuous range: *C. s. simum* from the southern part of the continent and the critically endangered northern *C. s. cottoni* (Lydekker 1908) from parts of central and eastern Africa. Only 25 animals of *C. s. cottoni* survive today, whereas *C. s. simum* has recovered from a bottleneck of ca. 20 individuals in 1895 to more than

11,000 animals today. A detailed account of their recent and historical status is provided by Emslie and Brooks (1999).

Heller (1913) was the first to point out two important morphological differences between the two subspecies: the length of the tooth row and the depth of the dorsal concavity. Groves (1975) statistically tested and verified these differences using a sample of over 60 skulls. *Ceratotherium simum simum* has a longer toothrow (80 percent joint nonoverlap) and a deeper dorsal profile (95 percent joint nonoverlap) compared to *C. s. cottoni*. Recent molecular studies confirm that the two subspecies are genetically distinct and require separate conservation (George et al. 1983; Merenlender et al. 1989). The genetic difference observed between them is greater than the genetic difference recorded between the various *Diceros* subspecies (Emslie and Brooks 1999). A rare case of a *Ceratotherium–Diceros* hybrid has been documented in captivity (Robinson et al. 2005).

During the middle-late Pliocene and Pleistocene, the white rhinoceros lineage (*Ceratotherium* sp.) was widespread across Africa (Guerin 1980b and references therein), following the expansion of open grasslands and signifying a remarkable example of herbivore adaptation to an exclusively abrasive diet. The distinction from the synchronic Plio-Pleistocene black rhinoceros lineage is easy, since the white rhinoceros lineage had already developed most of its apomorphic craniodental characters. Four fossil (sub)species have been erected based on Pleistocene *Ceratotherium* material: *Rhinoceros mauritanicus* Pomel, 1888; *Rhinoceros simus germanoafricanus* Hilzheimer, 1925; *Rhinoceros scotti* Hopwood, 1926; *Serengeticeros efficax* Dietrich, 1942. Several contradicting arrangements pertaining to their synonymy, specific or subspecific status, and spatiotemporal distribution have been proposed and debated (Arambourg 1938; Dietrich 1945; Arambourg 1948; Dietrich 1945; Cooke 1950; Hooijer 1969; Arambourg 1970; Groves 1972, 1975; Harris 1976a; Guérin 1979, 1980b; Harris 1983a; Guérin 1985, 1987a, 1987b; Geraads 2005). A (sub)specific evolutionary pattern of geographically/ecologically differentiated populations is feasible, but a revision of the Plio-Pleistocene true *Ceratotherium* lineage is beyond the scope of the present contribution. All Pliocene and early Pleistocene specimens assigned to the genus *Ceratotherium* (for a correct generic allocation of the principal cranial material from eastern Africa compare Geraads 2005: table 4) differ from the Middle Awash rhinoceros material described here by the following set of apomorphic features.

The skull is longer and more dolichocephalic with a dorsal cranial profile less concave; the anterior border of the orbit is usually retracted behind the middle of M^2; the occipital plane is inclined backward (posterodorsally), with a strong nuchal crest extending beyond the occipital condyles; the occipital notch of the nuchal crest is deeply concave or forked; the external occipital protuberance is strong with deep bilateral depressions (attachment for the funicular part of the nuchal ligament). The dentition is hypsodont, with constant enamel thickness and thicker cement investment. In the premolars, a crista or medifossette is variably present during the late Pliocene and more frequently in the Pleistocene; the lingual cingulum is progressively reduced. In the upper molars, a crista is usually present, forming in most cases a closed medifossette with the crochet; the protoloph is more oblique, bending markedly distolingually; the metaloph also becomes gradually more oblique; the paracone fold on the ectoloph weakens or disappears; the mesostyle fold becomes stronger than the paracone fold; the occlusal relief of the ectoloph

is low or flattened. Furthermore, the middle-late Pleistocene and extant white rhinoceros (*C. simum* ssp.) differ additionally by the following features: the teeth are very high-crowned hypsodont and cement investment is abundant; the protoloph and metaloph fuse after early wear, closing the entrance of the medisinus in the premolars; the lingual cingulum on P^2–P^4 is very reduced or absent; M^1–M^2 with protoloph and metaloph both bending markedly distolingually; a closed medifossette is always present; the paracone fold is completely suppressed by a deep parastyle groove; the mesostyle fold is very prominent; the M^3 is subrectangular with separate ectoloph and metaloph; the mandibular symphysis is anteriorly widened; the lower premolars almost always form closed fossetids after moderate wear, and the lower molars have buccally flattened lophids.

These marked differences do not justify the ascription of the Kuseralee cranium to the genus *Ceratotherium*. All these features reflect the increasing adaptation of the white rhinoceros lineage to an exclusive grass diet: The head is more inclined toward the ground, bearing a more hypsodont and plagiolophodont dentition with abrasion-dominated wear. Effectively, these characters can be also used to distinguish *Ceratotherium* from the synchronic and partly sympatric Plio-Pleistocene and extant *Diceros*.

Review of "Ceratotherium praecox"

A species frequently used to describe Pliocene *Ceratotherium* material was *Ceratotherium praecox*. Hooijer and Patterson (1972) defined *Ceratotherium praecox* based on a fragmentary cranium (KNM-KP 36) with incomplete dentition from Kanapoi, Kenya (~4.2 Ma). The authors complemented their diagnosis with a more complete but crushed cranium from Ekora (KNM-KP 41), estimated to be younger than Kanapoi. They also assigned to the new species a single M^2 (KNM-LT 89) from Lothagam (which indeed bears progressive features). In the same year, Hooijer (1972) described abundant material from Langebaanweg under this name. Subsequently, and based largely on the Langebaanweg sample, the binomen *Ceratotherium praecox* was widely used to refer to the direct ancestor of the extant *Ceratotherium simum* (Hooijer 1973, 1976, 1978; Harris 1976a, 1983a; Guérin 1979, 1980b, 1985, 1987b, 1989; Hooijer and Churcher 1985; Harris and Leakey 2003a; Harris et al. 2003). However, as Geraads (2005) has recently demonstrated, both skulls from Kanapoi and Ekora belong undoubtedly to the Pliocene *Diceros* lineage, and so the former usage has been a source of confusion.

Hooijer and Patterson (1972: 19) themselves underlined the similarities of the type cranium (KNM-KP 36) with the extant *D. bicornis* and its differences with respect to extant *C. simum*: The anterior border of the orbit is placed over the anterior border of the M^2; the posterior elongation of the occipital is missing; the occipital plane appears not to be inclined; and the nuchal crest is not markedly indented. The very incomplete dentition (much worn right P^4–M^2 without ectolophs) bears only *Diceros* characters and is missing all progressive features, not only of the late Pliocene *Ceratotherium* but also of the stratigraphically older Kuseralee cranium and the Langenbaanweg sample (~5 Ma). The protoloph is not bending markedly distolingually (despite accentuation by the very worn rounded protocone); the mesial protocone groove is faint, even at this late wear stage; a lingual protocone groove is absent; a weak crochet is the only secondary fold developed.

The cranium from Ekora that retains a more complete and less worn dentition (P^2–M^2), also shows the same *Diceros* features (Hooijer and Patterson 1972: figures 10A, B).

It is apparent that the combinations *Diceros praecox* or *Diceros bicornis praecox* are available for the Kanapoi *Diceros* population. Geraads (2005) has suggested a broader usage including skulls from Lothgam, Hadar, Laetoli, and Koobi Fora; the Ekora skull was assigned to *D. bicornis*. The revised diagnosis of *D. praecox* provided by Geraads (2005: 455) comprises "a few apomorphic (cranial) features with respect to its likely ancestor *C. neumayri*." However, according to our comparisons, neither is *C. neumayri* its likely ancestor, nor are the suggested cranial features apomorphic. Since a broader evaluation with the Plio-Pleistocene and extant *Diceros* is required, we suggest that more and better-preserved material from the type locality needs to be documented before assessing evolutionary patterns. During recent excavations, the hypodigm of Kanapoi has not increased significantly (Harris et al. 2003).

Unlike the stratigraphically younger Kanapoi and Ekora material, the M^2 from Lothagam (KNM-LT 89) described by Hooijer and Patterson (1972: figures 8c, d) displays indeed several progressive morphological features similar to the Kuseralee cranium and the Langebaanweg sample. The most salient are its large size and relatively high crown, the weak paracone fold combined with a broad and evident mesostyle fold, the strong crochet, the somewhat distolingually bending protoloph, the deep mesial protocone groove, and the presence of a marked lingual protocone groove. A small crista is also developed, as in some teeth of the Langebaanweg sample. Despite its progressive features, isotopic analysis of the tooth indicates a C_3 browsing diet (Harris and Leakey 2003a), and is thus in accordance with our paleoecological inferences for the Kuseralee cranium. According to Harris and Leakey (2003a), the M^2 originates from the Lower Nawata (~6.5–7.5 Ma; McDougall and Feibel 2003) and bridges somewhat the gap between the Douaria and Kuseralee material.

Comparison with the Plio-Pleistocene and Extant Diceros *sp.*

During historical times, the extant black rhinoceros had a nearly continuous distribution throughout most of sub-Saharan Africa. Because of its wide distribution and adaptation to diverse habitats, extant black rhinoceroses show greater variability of locally adapted populations than do white rhinoceroses. This has led to the recognition of several subspecies or ecotypes, whose affinities are still under refinement (Hopwood 1939b; Zukowsky 1965; Mertens 1966; Groves 1967; Du Toit 1986, 1987; Groves 1993; Rookmaaker 1995; Hillman-Smith and Groves 1994). Molecular and biochemical studies generally support the separate management of different subspecies, although their results regarding the degree of genetic variation within populations may vary according to the applied methodology and sample (Ashley et al. 1990; Swart et al. 1994; O'Ryan et al. 1994; Swart and Ferguson 1997; Brown and Houlden 2000). Based on analysis of mtDNA restriction fragment length polymorphism, Ashley et al. (1990) estimated an average divergence of 0.29 percent between the subspecies *D. b. michaeli* and *D. b. minor* and suggested a common ancestry no further than 100,000 years ago. Analysis of the genetic variation in mtDNA control region, which has a higher rate of evolution to detect intraspecific

variation than restriction enzymes, found a 2.6 percent nucleotide divergence between the same subspecies and suggested a divergence time of between 0.93 Ma and 1.3 Ma (Brown and Houlden 2000).

During the Plio-Pleistocene, the black rhinoceros lineage had a distribution quite similar to its historic one and is absent from North African localities (Guérin 1980a and references therein). Because of the close morphological resemblance with the extant species and the limitations of the fossil record, all Plio-Pleistocene *Diceros* material has been commonly assigned to the extant species *Diceros bicornis,* with the consideration of a subspecific treatment when more fossil material becomes available (Hooijer 1969, 1973, Harris 1976a; Hooijer 1978; Guérin 1979, 1985, 1987b; Harris and Leakey 2003a).

There are many similarities between the Kuseralee cranium (KUS-VP-1/20) and the Plio-Pleistocene and extant *Diceros bicornis*. The most significant common features include a markedly concave dorsal cranial profile, a straight or only slightly indented nuchal crest that does not extend posteriorly over the occipital condyles, a nearly vertical occipital plane, and anterior border of the orbit not extending behind the middle of M^2. The maxillary dentition is functionally brachyodont, with a concave occlusal surface, irregular enamel thickness, and thin cement coating. The upper premolars have a strong and continuous lingual cingulum, a paracone fold is developed, and a faint metacone fold is occasionally present. The upper molars (M^1, M^2) do not have a closed medifossette; the metaloph is vertically oriented; a paracone fold is present; a mesostyle fold is often developed as a broad swelling but is not stronger than the paracone fold; and the buccal apices of the metacone and paracone cusps are sharp. The M^3 has a subtriangular outline with continuous ecto-metaloph, lacking crista and medifossette.

All these craniodental similarities and the marked differences with respect to the Plio-Pleistocene and extant true *Ceratotherium* justify the ascription of the Kuseralee cranium to the genus *Diceros*. However, the Kuseralee cranium also displays some derived features with respect to the Plio-Pleistocene and extant *Diceros bicornis*. These include the particularly large size, the relatively high-crowned teeth, the distolingually bending protoloph, the deep mesial protocone groove, and the presence of a faint lingual protocone groove on the molars. The first two need to be carefully evaluated, because they seem to increase independently in some locally adapted *Diceros* populations during the Plio-Pleistocene.

The measurements of the Kuseralee cranium are slightly above or close to the maximum values, and much greater than the mean documented by Guérin (1980b), for ca. 50 skulls of extant *Diceros bicornis* ssp. (Table 14.1). Guérin (1980b: 29, 171) notes that the larger measurements in his sample originate from the "individus vraiment gigantesques" of the Cape black rhinoceros, but a more detailed subspecific analysis was beyond the scope of his study and refers to the work by Groves (1967). Groves (1967) used a larger sample of ca. 84 skulls, but with fewer measurements. He was able to demonstrate subspecific patterns within geographic populations, although the integrity of some of his groups based on a few skulls might be debatable (Du Toit 1987; Groves 1993). The large samples of *D. b. michaeli* (n = 22; occipitonasal length: 532 ± 20.9 mm) and *D. b. minor* (n = 23; occipitonasal length: 576.0 ± 17.0 mm) could indicate that variation within well-founded subspecies might not be much. Nevertheless, intergrades and overlapping with other groups undoubtedly occur (Groves 1967: 274, Tables 1, 2; Groves, 1993). In any case, out of the

TABLE 14.1 Skull Measurements of *Diceros douariensis* from Kuseralee Dora Compared with Other Dicerotini

	Kuseralee Dora D. DOUARIENSIS KUS-VP-1/19	*Omo* DICEROS SP. SHUNGURA D L.68-1	*Koobi Fora* DICEROS SP. (GUÉRIN 1980A)	*Various* CERATOTH. SP. PLIOCENE- PLEISTOCENE	*Africa, Extant* D. BICORNIS (GUÉRIN 1980A)	*Africa, Extant* C. SIMUM (GUÉRIN 1980A)
1 L cond.-prmx.	640			720–750	494–619	649–748
n =				5	27 (563)	25 (708)
2 L cond.-nas.	ca. 680		561		519–676	661–786
n =					45 (584)	23 (742)
3 L occ.-nas.	ca. 660	585	537	742–920	480–655	667–836
n =				7	46 (567)	23 (797)
5 W min. of the braincase	128		107	103–154	96–147	94–121
n =				6	53 (116)	26 (112)
7 L nuchal crest-supraorb. proc.	ca. 345	301	308	414–502	285–390	406–454
n =				4	53 (324)	7 (428)
8 L nuchal crest-lacrymal proc.	ca. 405	363	332	470–535	325–424	395–515
n =				6	53 (364)	25 (486)
13 L cond.-M3	ca. 320		236	333–430	235–346	315–430
n =				7	45 (286)	24 (374)
15 W nuchal crest	ca. 208		168	224–280	114–211	181–249
n =				5	53 (186)	(224)
16 W between proc. paraocc.	262		218	250–299	191–264	212–291
n =				5	53 (230)	26 (257)
17 W min. parietal crests	78		76		30–101	30–101
n =					53 (69)	26 (65)
20 W between lacrymal proc.	ca. 305		228		211–312	232–328
n =					51 (255)	25 (290)
21 W bizygomatic	ca. 375		307	337–404	286–363	300–373
n =				5	53 (328)	26 (339)
22 W at nas.inc.	172	ca. 130	129	158–175	127–162	149–178
n =				3	48 (143)	25 (164)

NOTE: All measurements are in mm. Measurement numbers follow Guérin (1980a). Data for extant *D. bicornis* and *C. simum* are after Guérin (1980a). First row of each measurement shows either the value of single specimens or the range for the species. Second row presents the sample size and mean value for species. The Pliocene-Pleistocene material refers to *Ceratotherium* sp. skulls from Hadar, Dikika, Laetoli, Koobi Fora, Chemeron Formation, Olduvai, Rawi, and Ain Hanech. The sample is only used to demonstrate the size difference between the Plio-Pleistocene *Ceratotherium* sp. and the Kuseralee skull and, as such, no mean values are calculated. Data are based on Harris (1983a), Groves (1975), Guérin (1987a), Geraads (2005), and personal observations. Repetition of material is avoided by accepting the minimum and maximum values and the minimum number of skulls for each measurement.

seven subspecies recognized by Groves (1967), six subspecies (representing 79 out of 84 skulls) have maximum values well below that of the Kuseralee cranium. The only subspecies somewhat comparable to the Kuseralee cranium in size is indeed the Cape black rhinoceros, which constitutes the nominate subspecies *D. bicornis bicornis* (Linnaeus 1758), according to Thomas (1911) and Rookmaaker (1998, 2005). The available material of this subspecies was revised by Rookmaker and Groves (1978), including an important amendment of the statistical values of Groves (1967). In Groves (1967: Table 3) the occipitonasal length of *D. b. bicornis* is given as 667.0 ± 37.7 mm based on a sample of five adult skulls. In Rookmaker and Groves (1978: table 1) the same dimension is given as 629–653 mm (mean: 641.3 mm) based on a sample of four skulls. Similar differences occur in other measurements as well. As explained by Rookmaker and Groves (1978), this discrepancy is owed to the fact that Groves (1967) has uncritically included in his calculations the values of the "Groningen skull" as provided by Zukowsky (1965), for example, the occipitonasal length of 732 mm. Zukowsky (1965) had overestimated its dimensions based on the illustrations provided by Camper (1780, 1782). From the remaining four adult skulls of the Cape black rhinoceros (RMNH: cat-A; BMNH: 1838.6.9.101; MNHN: A.7969; SAM: 21383), we have examined the first three and can verify the analysis provided by Rookmaker and Groves (1978: table 1). Compared to the largest extant subspecies, the size of the Kuseralee cranium is slightly above or close to the maximum values.

Unfortunately, very few fossil *Diceros* skulls are available to document any spatiotemporal evolutionary patterns in size and proportions during the Plio-Pleistocene. They are smaller than the Kuseralee cranium and close to the mean values of the extant *Diceros bicornis* ssp. A quite well-preserved late Pliocene subadult skull (KNM-ER 636) was described by Harris (1976a, 1983a) from the KBS Member of Koobi Fora (the KBS tuff at the bottom of the member is dated to 1.88 Ma; McDougall and Brown 2006). Guérin (1980b: 165, table 39) analyzed it statistically and found that it falls within the values of the extant *D. bicornis* ssp. subadult and adult skulls (Table 14.1). A crushed adult skull from Laetoli has an occipitonasal length of 580 mm (Guérin 1987b: table 9.24). Two partial *Diceros* skulls from the Apak Member of Lothagam are reported as comparable in size to the extant species (Harris and Leakey 2003a: 378, figure 9.5), but no measurements are provided. From the ~2 Ma Shungura Member D level of the Omo Valley, a fairly complete but laterally compressed skull (L.68-1) was recovered (Hooijer 1973: Table 6, 1975). Its size is also smaller with respect to the Kuseralee cranium and closer to the mean of the extant *D. bicornis* ssp. (Table 14.1). Other incomplete cranial fragments (NME: Omo-54-2090, Omo-58-2085) from Omo are similar in size to L.68-1. From Hadar, only an incomplete *Diceros* cranium has been recovered so far (Geraads 2005) and no significant measurements can be taken. The holotype cranium (KNM-KP 36) of *"Ceratotherium praecox"* from Kanapoi (~4.2 Ma) is also very incomplete, as well as a second cranium from Kanapoi (KNM-KP 30). The cranium (KNM-KP 41) from the stratigraphically younger Ekora Formation, used by Hooijer and Patterson (1972) to complement the hypodigm of *"C." praecox*, is more complete, but crushed and distorted, and no measurements were provided.

The evolution of dental proportions is somewhat better-documented during the Plio-Pleistocene. Hooijer (1969: 87, 1972: 160, 1973: 165) and Guérin (1980b: 165) have

demonstrated that during the early Pliocene, *Diceros bicornis* teeth are less high-crowned and that during the late Pliocene and Pleistocene some specimens achieve crown height similar to the extant species. Dental remains from the Mursi (~4.0 Ma) and the Usno (~3.0 Ma) Formations of the Omo sequence are relatively low-crowned. From Shungura Member D (~2.5 Ma) and younger levels they are similar to the extant form. Compared to the M^3 from the Kuseralee cranium (KUS-VP-1/20), an unworn M^3 from the Usno Formation (White sands W-12) is reported with a height/length index of 100 (Hooijer 1969: 87, 1973: 162). Guérin (1980b: 165, 1985: 81) also reports an index of 100 for a M^3 from the stratigraphically younger Shungura G level. Similar patterns are evident in other eastern African localities (Guérin 1980b: 165). The size of the permanent dentition of fossil specimens of *D. bicornis* falls within the mean values of the extant species (Hooijer 1959; Hooijer and Singer 1960; Hooijer 1969, 1973; Guérin 1980b; Harris 1983a; Guérin 1985; Hooijer and Churcher 1985; Guérin 1987b, 1994). Our observations verify these results, and, although the available record is insufficient for a more detailed analysis, it clearly demonstrates that smaller, medium-sized, lower-crowned *Diceros* populations existed throughout the Plio-Pleistocene. Dentitions from the late Pliocene of Hadar also indicate the presence of large-sized *Diceros* (Geraads 2005: Table 3). Geraads has assigned them, along with some of the Pliocene specimens already discussed, to *Diceros praecox*. However, morphometric comparison between them was not provided, nor were published metrical data from other Plio-Pleistocene localities and extant subspecies considered. The dentition of the Kanapoi cranium is very incomplete (P^4–M^2 without ectolophs) and too worn to allow any usable measurements. The morphology alone falls within the variation observed in the extant species. Certainly, based on its antiquity, we cannot exclude *D. praecox* as the ancestor of the Hadar *Diceros*. But it is equally plausible that it represents an extinct subspecies with no descendants or a subspecies evolving parallel to Hadar and other Plio-Pleistocene populations. We suggest that the Hadar *Diceros,* and eventually some other large-sized Plio-Pleistocene specimens as indicated by Geraads (2005: 457), most likely represent locally adapted populations, similar to the extant large-sized *D. b. bicornis* and *D. b. chobiensis*. They must have temporarily coexisted with the smaller, medium-sized, lower-crowned populations that appear closer to the mean values of the extant species. Groves (1967, 1993) has demonstrated a three-way clinal variation in eastern Africa between the extant subspecies *D. b. minor, D. b. michaeli,* and *D. b. ladoensis,* with geographic intergrades. As Hooijer (1969: 72) has noted, such a pattern of geographic subspeciation must have also existed during the past, but the available material is too limited to evaluate this variability. The same consideration was expressed by all subsequent studies (Hooijer 1973; Harris 1976a; Hooijer 1978; Guérin 1979, 1980b, 1985, 1987a, b, 1994; Harris and Leakey 2003a). Because the fossil record still remains insufficient to establish spatiotemporal subspecific (and perhaps specific) patterns during the Plio-Pleistocene, we also provisionally refer all Plio-Pleistocene black rhinoceroses as *Diceros bicornis* ssp.

The Kuseralee cranium (KUS-VP-1/20) demonstrates more craniodental similarities with the extant *Diceros* than with the extant *Ceratotherium*. However, its particularly large size, the high-crowned teeth, and some progressive dental features indicate that it cannot be the direct ancestor of the Plio-Pleistocene and extant black rhinoceros lineage as a whole. Contrarily, the dental morphology observed in the Kuseralee rhinoceros is

further accentuated by even larger-sized and higher-crowned populations during the early Pliocene (notably the Langebaanweg rhinocerotid sample). It appears thus to be closely related to the stock that eventually evolved into the highly specialized *Ceratotherium* lineage during the Pliocene.

Comparison with the Langebaanweg Sample

The abundant rhinoceros sample from the early Pliocene locality of Langebaanweg (Hooijer 1972) has been inaccurately associated with *"Ceratotherium praecox"* and has been used for many years as its flagship reference. Contrary to *Diceros praecox* from Kanapoi, the stratigraphically older Langebaanweg rhinoceros represents indeed a more advanced form with respect to all Miocene African Dicerotini and the Pliocene–extant black rhinoceros lineage. However, it still lacks several key apomorphic features of the true grazing Plio-Pleistocene-extant white rhinoceros, as Hooijer (1972: 153) correctly outlined. A comprehensive revision of the enriched Langebaanweg collection is necessary to further evaluate the variation within this population. In this section, we restrict our discussion to the most essential morphological characters. The age of the Langebaanweg fauna is biochronologically estimated at about 5 Ma (Hendey 1981).

Some of the cranial features cited by Hooijer in his introduction (1972) were reproduced from the descriptions of the Kanapoi and Ekora *Diceros* specimens. From Langebaanweg, however, only some partial skull fragments are recorded (Hooijer 1972). Two large nasofrontal fragments (SAM: L.2520, L.6658) show the typical Dicerotini features: frontal and nasal horn bosses with extensive vascular rugosities, wide and rounded rostral border of nasals, and frontals with strong supraorbital processes. A pair of premaxillaries (SAM: L.13747) shows the presence of rudimentary upper incisors (Hooijer 1972: Plate 28), which sometimes also occur in the extant species (Figure 14.2D). Thus, it is not a diagnostic feature. The occipital morphology can only be observed on the partially reassembled portion of a very fragmentary cranium (SAM: L.31747). It appears to be intermediate between the two extant species, as Hooijer (1972: 158, plate 26) indicated. Compared to the Kuseralee cranium and extant *Diceros,* the occiput seems to be more inclined and the nuchal crest thicker and somewhat more prominent, but still not to the extent achieved by late Pliocene grazing *Ceratotherium* specimens from eastern Africa, or the terminal specimens of the late Miocene extra-African *"D." neumayri*. Important mandibular features of the Langebaanweg rhinocerotid include a symphysis anteriorly abbreviated and narrow (resembling modern *Diceros* and not *Ceratotherium*), posteriorly extending beneath P_3, and a convex ventral border of the mandibular corpus without marked angulation at the mandibular angle (Hooijer 1972: plates 30–33).

The total length of the maxillary toothrows from Langebaanweg (Hooijer 1972: table 1) is greater than that of Kuseralee (Table 14.2). Two unworn M^3s (SAM: L.6696, L.6638) have a height/length index of 120 and 121, respectively (Hooijer 1972), and thus are somewhat larger than the M^3 of the Kuseralee cranium. The following features are similar between the Kuseralee and the Langebaanweg dentitions but are generally more primitive than Plio-Pleistocene *Ceratotherium* (the latter cited in parentheses in the following list): strong continuous cingulum in premolars (progressively reduced during Plio-Pleistocene);

TABLE 14.2 Measurements of the Upper and Lower Permanent Dentition of the Middle Awash Specimens from Kuseralee and Saitune Dora

	Kuseralee Upper Dentition		Saitune Dora Upper Dentition		Saitune Dora Lower Dentition	
	KUS-VP-1/20		STD-VP-2/1	STD-VP-2/12	STD-VP-2/12	STD-VP-2/12
	DEX.	SIN.	DEX.	SIN.	DEX.	SIN.
P1L				30.2		
Wd				30.5		
P2L	38.5	37.5		37.7	35.2	(35.5)
Wm	41.7	44.0		43.3	23.1	nm
Wd	46.1	47.6		44.5	24.7	nm
P3L	(45.7)	nm		44.6	44.8	43.3
Wm	nm	(62.3)		61.0	nm	27.5
Wd	nm	61.3		59.4	nm	34.1
P4L	47.8	47.8			48.2	(49.7)
Wm	69.9	72.2			32.5	32.3
Wd	65.4	66.1			36.7	39.5
M1L	58.8	56.1			(56.0)	nm
Wm	70.0	69.5			nm	nm
Wd	65.2	66.7			44.5	nm
M2L	nm	61.0			57.6	57.8
Wm	nm	69.2			nm	43.9
Wd	nm	(64.1)			37.1	36.2
M3Lb	63.1	63.4	63.4	nm	nm	54.5
Wm	60.2	60.6	63.9	nm	nm	35.4
La	52.3	54.7	(58.5)	nm	nm	34.0
P2–M3	nm	284.0			nm	ca. 285.0
P2–P4	136.1	134.8			nm	ca. 130.0
P3–P4	97.2	96.8			nm	nm
M1–M3	nm	156.8			nm	ca. 155.0

NOTE: All measurements are in mm. Values in parentheses are estimates; nm = the measurement was not possible.

marked mesial protocone groove in molars (frequently more marked); absence of distal protocone groove and antecrochet in molars and premolars (also absent); inequalities in enamel thickness (enamel thickness remains more equal over the entire tooth); metaloph of M^1 is perpendicular with respect to the ectoloph (progressively more oblique and finally bending distolingually like the protoloph).

The following dental characters, particularly in molars, are further accentuated in the Langebaanweg specimens with respect to the Kuseralee dentition but remain markedly less advanced than in Plio-Pleistocene *Ceratotherium* (the latter cited in parentheses): The teeth are somewhat more high-crowned (but functionally still not hypsodont); the occlusal surface becomes less concave (but not flat); the ectoloph mesowear profile is lower (but not flattened); the cement investment increases (but is still not abundant); the moderate paracone fold persists or weakens, and the wide mesostyle fold is now more evident (structure develops further and the paracone fold gradually disappears); the protoloph bends somewhat more distolingually (obliquity increases further); the lingual protocone groove

TABLE 14.3 Measurements of the Ectocuneiform of ASK-VP-3/202 from Asa Koma and Other
Dicerotini Specimens

	Asa Koma	Langebaanweg	Africa, Extant	Africa, Extant
	DICEROS SP. ASK-VP-3/202	DICEROTINI HOOIJER (1972)	D. BICORNIS GUÉRIN (1980A)	C. SIMUM GUÉRIN (1980A)
DT	62.0	53.0–60.0 $n = 8$ $\bar{x} = 56.3$	43.0–60.0 $n = 22$ $\bar{x} = 51.0$	51.5–62.0 $n = 11$ $\bar{x} = 55.9$
DAP	55.8	51.0–59.0 $n = 7$ $\bar{x} = 56.7$	39.0–48.5 $n = 22$ $\bar{x} = 43.7$	46.5–56.0 $n = 11$ $\bar{x} = 52.5$
H	(29.0)	27.0–33.0 $n = 8$ $\bar{x} = 30.0$	22.0–22.9 $n = 22$ $\bar{x} = 25.0$	25.5–29.5 $n = 9$ $\bar{x} = 27.4$

NOTE: All measurements are in mm. First row of each measurement shows either the value of single specimens or the range for the species. Second row presents the sample size for the species. Third row presents the mean value for the species. Data for extant *D. bicornis* and *C. simum* after Guérin (1980a); for the Langebaanweg sample after Hooijer (1972). Value in parentheses is an estimate.

becomes more evident (frequently present in late Pliocene *Ceratotherium,* but gradually disappearing later as bending of the protoloph increases and the protocone narrows); a small crista appears in some molars, but very rarely a closed medifossette, which occurs only in 3 out of 40 Langebaanweg teeth (a closed medifossette is very frequently present in Pliocene *Ceratotherium* and almost always present in Pleistocene and extant specimens).

A very important feature of the Langebaanweg rhinocerotid is the great length of its relatively slender limb bones, which in most cases significantly exceeds the maximum values recorded in the two extant species (for comparisons of the ectocuneiforms and third metatarsal, see Tables 14.3 and 14.4). Guérin (1979, 1980b, 1987b) analyzed the available postcranial material from the Rift Valley and demonstrated that similar size and proportions to the Langebaanweg limb bones were sustained by the late Pliocene *Cerato-therium* from Hadar-SH and Laetoli (which he referred to as *Ceratotherium praecox,* but the name *C. efficax* might be appropriate). During the early-middle Pleistocene, Guérin (1979, 1980b) recorded a shift toward more massive limb bones in the Olduvai sequence (referred to as *C. simum germanoafricanum*), which was then followed by a size reduction to that of the extant *C. simum* during the middle-late Pleistocene. However, northern African Pleistocene populations (for which the name *Ceratotherium mauritanicum* is available) seem to retain the long and relatively slender metapodials (personal observation: MNHN: 1956-12-109 from Ternifine; MNHN: 1953-21-58 from Ain Hanech). A similar pattern for the Plio-Pleistocene *Ceratotherium* limb bones was suggested by Geraads (2005: 455, figure 4), but using different species names. It is consistent with the cranio-dental evidence (Hooijer 1969; Groves 1975; Harris 1976a; Hooijer 1978; Guérin 1980b; Harris 1983a; Guérin 1985; Geraads 1987; Guérin 1987b; Likius 2002; Geraads 2005).

TABLE 14.4 Measurements of STD-VP-1/19 (Third Metatarsal) from Saitune Dora and Comparisons with Other Dicerotini Specimens

	Saituna Dora	Fort Ternan	Bou Hanifa	Arrisidrift	Langebaanweg	Hadar	E. Mediterranean	Africa, Extant	Africa, Extant
	DICEROS SP. STD-VP-1/19	P. MUKIRII HOOIJER (1968)	D. PRIMAEVUS MNHN: 1951-9/242 9/144	D. AUSTRALIS GUÉRIN (2003)	DICEROTINI HOOIJER (1972)	CERATOTH. SP. NME: AL.382-5Y	"D". NEUMAYRI GIAOURTSAKIS (IN PREP.)	D. BICORNIS GUÉRIN (1980a)	C. SIMUM GUÉRIN (1980a)
L	188.0	115.0[a] 132.0[a]	161.0 164.0	178.0–190.5 $n = 4$ $\bar{x} = 188.3$	171.0–198.0[a] $n = 20$ $\bar{x} = 183.8$[a]	201.0	160.0–181.0 $n = 16$ $\bar{x} = 170.2$	141.5–178.0 $n = 33$ $\bar{x} = 157.1$	157.0–180.0 $n = 12$ $\bar{x} = 168.4$
DT ep. prox.	(68.0)	43.0 45.0	52.2	54.0–61.0 $n = 3$ $\bar{x} = 57.5$	55.0–70.0 $n = 20$ $\bar{x} = 60.8$	57.3	55.1–67.7 $n = 14$ $\bar{x} = 59.3$	43.5–58.5 $n = 33$ $\bar{x} = 48.9$	51.5–64.5 $n = 12$ $\bar{x} = 55.8$
DAP ep. prox.	(60.0)	36.0 41.0	46.2 48.3	49.0–52.0 $n = 2$ $\bar{x} = 50.5$	51.0–61.0 $n = 16$ $\bar{x} = 55.0$	55.4	49.1–60.5 $n = 15$ $\bar{x} = 52.7$	40.0–56.5 $n = 32$ $\bar{x} = 48.4$	46.0–53.0 $n = 11$ $\bar{x} = 49.4$
DT dia.	(59.5)	31.0 45.0	46.8 41.8	44.0–52.5 $n = 4$ $\bar{x} = 49.5$	47.0–62.0 $n =$ $\bar{x} = 53.5$	49.3	46.7–57.6 $n = 16$ $\bar{x} = 50.2$	37.5–48.0 $n = 33$ $\bar{x} = 42.5$	43.0–52.5 $n = 12$ $\bar{x} = 47.3$
DAP dia.	29.2	20.0 19.0	23.6 23.2	25.5–26.0 $n = 3$ $\bar{x} = 25.7$	25.0–35.0 $n =$ $\bar{x} = 29.3$	25.3	23.7–30.2 $n = 18$ $\bar{x} = 25.7$	17.0–25.5 $n = 30$ $\bar{x} = 21.2$	23.0–28.5 $n = 11$ $\bar{x} = 25.2$
DT max. dist.	77.6	40.0 53.0	59.1 52.3	55.5–61.5 $n = 4$ $\bar{x} = 56.7$	58.0–82.0 $n = 16$ $\bar{x} = 69.1$	69.8	62.0–76.5 $n = 15$ $\bar{x} = 66.2$	50.5–64.0 $n = 33$ $\bar{x} = 56.1$	59.0–72.0 $n = 12$ $\bar{x} = 64.0$
DT ep. dist.	59.8	37.0 42.0	50.3 48.5	51.0–57.0 $n = 4$ $\bar{x} = 53.4$	53.0–69.0 $n = 18$ $\bar{x} = 57.5$	56.8	50.9–61.5 $n = 16$ $\bar{x} = 53.8$	40.0–55.5 $n = 33$ $\bar{x} = 47.3$	48.5–60.0 $n = 12$ $\bar{x} = 52.8$
DAP ep. dist.	53.6	33.0 36.0	42.7 44.3	42.0–47.5 $n = 4$ $\bar{x} = 44.4$	46.0–58.0 $n = 20$ $\bar{x} = 50.8$	41.3	44.2–51.2 $n = 14$ $\bar{x} = 46.2$	32.0–43.5 $n = 27$ $\bar{x} = 40.1$	40.0–49.0 $n = 10$ $\bar{x} = 45.5$

NOTE: All measurements are in mm. Values in parentheses are estimates. First row of each measurement shows either the value of single specimens or the range for the species. Second row presents the sample size for the species. Third row presents the mean value for the species. Data for extant D. bicornis and C. simum after Guérin (1980a); for D. australis after Guérin (2003); for P. mukirii after Hooijer (1968); for the Langebaanweg sample after Hooijer (1972). Measurements follow Guérin (1980a).

[a] Hooijer (1968, 1972) provides the median length rather than the total length of the bone. In the case of 3rd metatarsals, this usually results in ca. 2–4 percent smaller values.

The size and proportions of the third metatarsal from Saitune Dora (STD-VP-1/19) corresponds well to the Langebaanweg sample, indicating close relationships. Postcranial elements of *D. douariensis* are still not securely associated, since only fragments have been recovered from the type locality (Guérin 1966).

The Langebaanweg rhinocerotid probably originated from large-sized, high-crowned late Miocene populations similar to the Douaria and Kuseralee rhinocerotids. Its particular morphology shows that it is closely related to the lineage that evolved into the true grazing *Ceratotherium* during the Pliocene, as Hooijer (1972) suggested. This scheme does not imply any concrete migrational evolutionary patterns between northern, eastern, or southern Africa, but rather reflects the inadequate fossil material presently available. The intermediate character of the Langebaanweg rhinocerotid is explained by dietary requirements related to local seasonal environmental conditions.

Comparison with Diceros douariensis

The presence of a fossil rhinoceros in Douaria, Tunisia, was first mentioned by Roman and Solignac (1934) in a "Pontian" fauna list as *Rhinoceros pachygnathus*. The rhinocerotid material was reexamined in detail by Guérin (1966), who assigned all remains to the new species *Diceros douariensis*. The holotype is a partial adult cranium (FSL: 16749), missing the nasal and occipital regions, associated with a fairly complete mandible (FSL: 16750). Guérin (2003) biochronologically estimates the age of the site of Douaria at 9.5 Ma, but based on the associated fauna a younger age cannot be excluded. Some dental remains and an astragalus have been described as cf. *Diceros douariensis* from the Miocene locality of Djebel Krechem el Artsouma, central Tunisia (Geraads 1989). The referred occurrence of the species in Baccinello V3, Italy (Guérin 1980b, 2000) is doubtful.

A partial juvenile cranium (FSL: 16752) was also used by Guérin (1966: figures 2, 6) to complement the hypodigm of *D. douariensis*. The presence of a complete protocone constriction by a mesial and distal protocone groove and a well-developed antecrochet in the M^1 and M^2 of the juvenile skull are atypical for Dicerotini. Dicerotini molars usually have only a mesial (anterior) protocone groove, without a distal (posterior) one. Thus there is no true (complete) protocone constriction and no prominent antecrochet developed, exactly as in the adult skull from Douaria. Moreover, the hypocones of the juvenile specimen also appear to be constricted, at least by a mesial groove. The juvenile specimen represents clearly a different species, probably an acerathere or brachypothere, and is excluded from the comparisons.

The available morphology of the holotype adult cranium (FSL: 16749) is described and illustrated in detail by Guérin (1966). It displays characteristic features of the Dicerotini, including the presence of well-developed nasal and frontal horn bosses, the strong supraorbital process, the laterally sloping lower border of the orbit, and the short edentulous premaxillary bone. Unfortunately, the incomplete condition of the neurocranium obstructs the evaluation of important features related to the development of the posterior cranial region. The associated mandible (FSL: 16750) is also characteristic: The ventral border of the mandibular corpus is convex without marked angulation at mandibular angle; the anterior border of the mandibular symphysis is abbreviated, edentulous, and

rather narrow; and the posterior border extends below the level of P_3. One of the diagnostic characters reported by Guérin (1966) is the particularly large size of the skull with respect to extant *D. bicornis*. Because of the incompleteness, the most important measurements had to be estimated. The basal length of the skull is estimated by Guérin (1966) to be about 605 mm, thus larger than the majority of the extant subspecies and comparable only with *D. b. bicornis*. The zygomatic breadth of 260 mm is probably underestimated, because this region is incomplete and apparently distorted (Guérin 1966: figure 5). The length of the dentition (P^2–M^3) measures 264 mm (Guérin 1966: table 1) and is thus somewhat smaller than in the Kuseralee cranium (KUS-VP-1/20).

The teeth of the adult skull were described as high-crowned and, although somewhat worn, the illustrations seem to support this assessment (Guérin 1966: figures 1, 3). However, the hypsodonty indices provided by Guérin (1966) were based on the unworn M^1 and M^2 of the dubious juvenile skull. Hooijer (1973) questioned the "hypsodonty" of *D. douariensis* and recalculated these indices based on greatest ectoloph lengths, concluding that the molars of the juvenile skull are rather lower-crowned compared to the extant *Diceros*. In any case, neither calculation should be considered as applicable for the crown height of the adult skull. The dental morphology of *D. douariensis* follows the unspecialized *Diceros* pattern. The premolars have a strong, continuous crenellated cingulum; a crochet is present, and the crista is absent. Guérin (1966) mentions the presence of a weak antecrochet on P^2–P^3. A paracone fold is developed on the ectoloph. A weak metacone fold is reported on the P^3. The molars, although high-crowned, are functionally brachyodont with concave occlusal surfaces, unequal enamel thickness, and sharp paracone and metacone buccal apices. Cement is present. A crochet is present but no crista or medifossette. The mesial protocone groove appears to be marked, but a distal groove is not developed. The ectoloph bears a paracone fold; a weak mesostyle bulge is apparently also developed (Guérin 1966: figures 5, 8). The M^3 has a continuous ectometaloph. In these morphological features the skull from Douaria is similar to the Kuseralee cranium, as well as to the extant *D. bicornis* (although some subspecies of the latter have secondarily developed a crista or a bifid crochet on premolars [Rookmaaker and Groves 1978; Guérin 1980b; personal observation]).

Besides the reported large size and the apparent high-crowned teeth, some derived dental features also signify a closer relationship between the Douaria and Kusarelee rhinocerotids and distinguish them from Plio-Pleistocene and extant *D. bicornis*. The first one is the obliquity of the protoloph of M^1 reported by Guérin (1966: 30): "Le protolophe est fortement convexe vers l'avant, quelle que soit l'age de l'inividu." The second one is the development of a lingual protocone groove (on the lingual side of the protoloph): "Son extremité linguale est . . . deprimée verticalement en son milieu." This lingual protocone groove is also clearly indicated on the line-drawing illustration (Guérin 1966: figure 8). It is the same feature seen on the M^2 from Lothagam, the molars of the Langebaanweg sample, and the Pliocene true *Ceratotherium*. Some differences can be observed between the Douaria and Kuseralee dentitions. The lingual protocone groove is very marked on the M^1 of the Douaria dentition, and a faint antecrochet seems to be present. Contrarily, the distolingual bending of the protoloph is more conspicuous in the Kuseralee M^1 and the

paracone fold weaker. More material is thus nessesary to appreciate the variation of both populations.

Guérin (1966) considered *D. douariensis* as a circum-Mediterranean species showing a mixture of progressive and primitive features with respect to the eastern Mediterranean *"D." neumayri*, a well-established species at the time. Hooijer and Patterson (1972: figure 11) considered *D. douariensis* as a possible ancestor of both extant African lineages. Hooijer (1978: figure 19.1) later deemed its position to be close to the split, on the side of *Diceros*. Heissig (1989) also suggested a placement near the split but on the *Ceratotherium* side. Geraads (2005) considered *D. douariensis* as potentially conspecific with *"D." neumayri* and the latter as the common ancestor of the extant species (all other authors regarded *"D." neumayri* as a separate lineage). The morphological similarities between the Kuseralee cranium and *D. douariensis* support the assignment of the former to the same species/lineage with a position close to the ancestral stock of the *Ceratotherium* clade, as Heissig (1989) suggested. Based on the available material, their precursor could have originated from the earlier *D. primaevus* or *D. australis*.

Comparison with Diceros primaevus

The rhinoceros material from the early late Miocene locality of Bou Hanifia (Oued el Hammam), Algeria, was originally described as *Dicerorhinus primaevus* by Arambourg (1959) and was later allocated to *Diceros* by Geraads (1986b). The Bou Hanifia Tuff, found below the mammal horizon, has provided a radiometric date of 12.18 ± 1.03 Ma (Ameur et al. 1976). The type specimen of *Diceros primaevus* is a partial juvenile cranium with erupting M^1 (MNHN: 1951-9/222; Arambourg 1959: Plate 6, figure 1-3). The rest of the recovered dental material consists of juvenile maxillae and hemimandibles with deciduous dentition. The cranial morphology of the partial juvenile skull displays the typical characters of the tribe Dicerotini: strong nasal and frontal horn boss, laterally sloping lower border of the orbit, well-developed supraorbital process (although broken), and absence of a postorbital process (contra Arambourg 1959). The nasals are mediolaterally crushed and compressed; therefore, the characteristically wide and rounded rostral border is not apparent in Arambourg's illustrations.

The unworn M^1 and M^2 of a juvenile maxilla (MNHN: 1951-9-219) are morphologically identical to extant *Diceros* but somewhat less high-crowned. All deciduous dentitions (five specimens) show some primitive features, such as a weak or absent crista in D^3 and D^4, which are retained by some subspecies of extant *Diceros*. This apparently primitive morphology as well as a misleading comparison with the eastern Mediterranean species *Diceros pachygnathus* (here: *"Diceros" neumayri*) and *Dicerorhinus orientalis (recte: Dihoplus pikermiensis)* have contributed to the initial assignment of the Bou Hanifia rhinocerotid to the genus *Dicerorhinus* by Arambourg (1959). Arambourg (1959: figures 33a, 33b) misidentified and swapped the juvenile maxillae of the two Eastern Mediterranean species from Pikermi and incorrectly associated the Bou Hanifia maxillae with the *"Dicerorhinus"* morphology. Deciduous dentitions of the synchronic and partly sympatric species *"Diceros" neumayri* and *Dihoplus pikermiensis* from the eastern Mediterranean can be easily distinguished based on

several unambiguous morphological features (Giaourtsakis et al. 2006: table 3; Geraads 1988).

The postcranial elements found in Bou Hanifia are generally slender for Dicerotini. Their size and morphology fall perfectly within the range and variation documented for the extant *D. bicornis* (Guérin 1980b; personal observation). Compared to the third metatarsal from Saitune Dora, the early Pliocene sample from Lagebaanweg, and the Pliocene *Ceratotherium,* they are significantly shorter (Table 14.4). Compared to the extra-African *"D." neumayri,* they are more slender. A fragmentary atlas (Arambourg 1959: figure 25), showing the presence of an alar incisure lateral to the articular surface of the occipital condyle, does not belong to a rhinoceros but represents probably a short-necked giraffid. This feature has also contributed to the initial assignment to *Dicerorhinus* (in Dicerotini an alar foramen is present instead of an incisure).

D. primaevus preserves an ancestral morphology that essentially persists, with relatively few modifications, in the extant black rhinoceros. Populations similar to *D. primaevus* could have migrated outside Africa, around the middle-late Miocene boundary, and evolved to *"Diceros" neumayri*. In addition, the conservative morphology of *D. primaevus* does not exclude a placement of this species before the split between the extant black and white rhinoceros lineages. This depends, however, on the affinities of the recently discovered early middle Miocene Arrisdrift rhinoceros from Namibia, considered next.

Comparison with Diceros australis

Guérin (2000) described the new species *Diceros australis* based on material discovered at the locality of Arrisdrift in the Orange River Valley of Namibia. A slightly extended version including some additional specimens was presented by Guérin (2003). According to Pickford and Senut (2003), the age of the Arrisdrift fauna is estimated at about 17.5–17 Ma. Besides a small occipital and a few mandibular fragments, the rhinocerotid material from Arrisdrift assigned to *D. australis* comprises several isolated dental and postcranial elements.

The morphology of the upper permanent cheek teeth follows the unspecialized Dicerotini pattern, similar to the extant *Diceros*. Compared to the younger *D. primaevus* from Bou Hanifia, the most notable difference is the size. Guérin (2003) points out a closer resemblance of *D. australis* with the younger (by 8 million years) *D. douariensis,* which shows very similar dimensions. Both still fall within the dental size variation observed in extant *Diceros bicornis* ssp. (Guérin 1980b: table 5), but *D. australis* lacks the few advanced features of *D. douariensis* and the Kuseralee dentition described earlier.

The most prominent feature of *D. australis* (~17 Ma), however, is the significant size of its postcranial elements. The holotype specimen itself is a left third metacarpal (GSN: AD-52'97). The recovered limb bones of *D. australis,* especially the metapodials, are considerably larger than the maximum values recorded for the two extant species, as well as the early late Miocene *D. primaevus* (~12 Ma) and the side branch of the extra-African *"D." neumayri* (Table 14.4). A similar size and morphology can be found in a fourth metatarsal from the much younger Mpesida beds of Kenya (~6.2–6.9 Ma), originally referred to *Ceratotherium praecox* by Hooijer (1973), in the third metatarsal from Saitune Dora (~5.6 Ma) described in this chapter, and in the abundant material from the early

Pliocene of Langebaanweg (~5 Ma) documented by Hooijer (1972). As discussed earlier, this pattern continued thereafter by the true *Ceratotherium* lineage during the Pliocene and early Pleistocene and was followed by a significant size reduction and modification of the osteometric proportions during the middle and late Pleistocene leading to the extant white rhinoceros (Guérin 1979, 1980b, 1987b).

The puzzling discovery of the large *D. australis* as the oldest known representative of the tribe Dicerotini raises important issues regarding the early radiation of the tribe and further perplexes the search for 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 smaller sized *D. primaevus*. Further fossil evidence is required to shed light on the early evolution of the tribe in Africa.

Revision of Paradiceros mukirii

Hooijer (1968) described the new genus and species *Paradiceros mukirii* from the middle Miocene Fort Ternan Beds in Kenya. Recently, Pickford et al. (2006) refined the age of the Fort Ternan fossiliferous sediments to ca. 13.7 ± 0.3 Ma. Hooijer (1968) originally portrayed *P. mukirii* as a primitive collateral species of the ancestral *Diceros* stock, differing from *Diceros* in a combination of primitive and progressive features. However, our comparisons indicate that the majority of the material, if not all, may belong to the dicerorhine *"Dicerorhinus" leakeyi* Hooijer, 1969. The ascription of the latter species to the genus of the extant Sumatra rhinoceros might be incorrect but shall provisionally be retained, because a more comprehensive comparison with the Eurasian Miocene dicerorhines (*sensu* Guérin 1989) would be required.

There are casts of three important specimens from Fort Ternan in the collections of the BMNH: the juvenile holotype cranium (BMNH: M.29929; original KNM-FT-1962-3113; Hooijer 1968: plate 1), the incomplete adult cranium (BMNH: M.29930; original KNM-FT-1962-3376; Hooijer 1968: plate 2, figures 2, 3) and one mandible (BMNH: M.29931; original KNM-FT-1962-3209). The holotype of *P. mukirii* is a well-preserved juvenile cranium missing the nasal, basioccipital, and premaxillary bones due to incomplete ossification. The available cranial morphology is lacking several important Dicerotini features: The lower border of the orbit is not sloping laterally downwards; the frontal horn boss is developed as a prominent but restricted swelling in the middle of the frontals; and the frontals are only slightly convex at the level of the the supraorbital processes. In contrast, even in juvenile Dicerotini, the supraorbital process is strong; a postorbital process is generally absent, or only faintly developed; the frontal horn boss is more extensive with marked vascular impressions; and the frontals are very convex between the supraorbital processes. In addition, the nasals of the incomplete adult cranium are rather long (length between nasal tip and nasal incision) and do not terminate abruptly rostrally (see also Hooijer 1968: plate 2, figure 3). All these features observed in the Fort Ternan crania are typical of Dicerorhinini (Guérin 1980a; Heissig 1981; Groves 1983; Geraads 1988; Giaourtsakis et al. 2006).

The deciduous dentition of the holotype is markedly smaller than in all fossil and extant Dicerotini examined. Hooijer (1968) describes seven features that distinguish the

Fort Ternan deciduous dentition from extant *D. bicornis*. Although some of them may be variable in Dicerotini (presence and strength of crista, strength of paracone fold, strength of crochet), the combination of all of them is typical Dicerorhinini and characterizes the extant *Dicerorhinus sumatrensis,* as well as *"Dicerorhinus" leakeyi*. In particular, the constriction of the protocone by mesial and distal grooves, the presence of a weak but conspicuous antecrochet, the absent or faint crista on D^3–D^4, and the absence of lingual cingula or cingular pillars in the entrance of the medisinus are distinctive. We can also add the presence of a metacone fold on the ectoloph of D^3–D^4. The deciduous dentition of a juvenile maxilla (BMNH: M.32946) from Rusinga, the type locality of *"Dicerorhinus" leakeyi,* bears the same features and is indistinguishable from the Fort Ternan holotype. The permanent teeth of the Fort Ternan rhinocerotid are very low-crowned brachyodont, and they are also smaller with respect to all fossil and extant Dicerotini examined. The premolars of the partial adult skull do not have a lingual cingulum, which is always well-developed in Dicerotini (except Pleistocene and extant *Ceratotherium*). Hooijer (1968) notes, in some of the isolated permanent teeth, the presence of a weak but conspicuous protocone constriction by a mesial and distal protocone groove, as well as of an antecrochet. A metacone fold appears also to be present (Hooijer 1968: plate 2). These features are more markedly expressed in Miocene dicerorhines but are usually absent or dimly expressed in dicerotines.

The strongest argument of Hooijer was the absence of permanent tusk-like second lower incisors in two mandibles recovered at Fort Ternan. Hooijer (1968: 84) describes the mandible FT-1962-3209 as having "the symphyseal portion complete" and being "edentulous, showing milk incisor alveoli but no traces of permanent canines and incisors" [*sic*]. This mandible was not figured. Our observations of the mandible cast (BMNH: M.29931) suggest that the anterior part of the symphysis is fragmentarily preserved, probably dorsoventrally compressed, and incomplete. The symphysis could have extended further anteriorly, and the "milk incisor alveoli" reported by Hooijer may only represent the distal impression of the roots of the permanent incisors and not the complete alveoli. If the specimen belonged to a female individual, the permanent incisors could have been rather small and their alveoli faded out in front of, and not below, the P_2. For the second mandible (FT-1962-3503; Hooijer 1968: plate 2, figure 1) a close examination of the specimen would be necessary.

The postcranial skeleton also supports an ascription of the Fort Ternan fossils to Dicerorhinini. Hooijer describes an atlas (KNM-FT-1963-3497) and underlines the presence of an alar incisure lateral to the articular surface of the occipital condyle. As Hooijer correctly notes, this is a feature seen in extant *Dicerorhinus* and not in Dicerotini, fossil or extant, where an alar foramen is developed instead (personal observation of ca. 20 skeletons). Detailed description of the Fort Ternan limb bones is not provided by Hooijer (1968). However, their size is significantly smaller than all known Dicerotini (for the third metatarsal comparison, see Table 14.4). To the contrary, it corresponds perfectly to the size reported for the *"Dicerorhinus" leakeyi–Turkanatherium acutirostratum* specimens from Rusinga (Hooijer 1966; Guérin 2003). Hooijer (1966) stated that it was not possible to distinguish the limb bones of these two species, which have similar dimensions, but we agree with Guérin (2003) that revision of the abundant remains preserved in the KNM collection should permit a resolution of this problem.

Rhinoceros findings identified as *Paradiceros mukirii* were reported at Maralal (Hooijer 1968), the Samburu Hills (Nakaya et al. 1984; Tsujikawa 2005) and the Ngorora Formation (Pickford et al. 2006) in Kenya, as well as the Kisegi Formation in Uganda (Guérin 1994) and at Beni Mellal in Morocco (Guérin 1976). The available material from these localities is rather scant, and each case must be revised separately.

Comparison with Diceros neumayri *and Biogeographic Remarks*

"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 common element of the *Hipparion* faunas of the sub-Paratethyan mammalian province (Bernor 1984) and has been documented in numerous localities from Greece (Gaudry 1862–1867; Weber 1904; Arambourg and Piveteau 1929; Geraads 1988; Geraads and Koufos 1990; Giaourtskis 2003; Giaourtskis et al. 2006) and Turkey (Heissig 1975; Geraads 1994b; Kaya 1994; Heissig 1996; Fortelius et al. 2003a; Antoine and Saraç 2005), as well as from the locality of Maragheh in Iran (Osborn 1900; Thenius 1955) and Eldari-2 in the Caucasus (Tsiskarishvili 1987). The referred occurrence of the species in the Vienna Basin (Thenius 1956) was confirmed as a *Brachypotherium* (Giaourtsakis et al. 2006). Some specimens from Spain reported as *Diceros pachygnathus* by Guérin (1980b) were assigned to *Dihoplus schleiermacheri* (Cerdeño 1989). Specimens referred to as *Rhinoceros pachygnathus* from Mont Léberon, France (Gaudry 1873), and Baltavar, Hungary (Pethő 1884), belong also to *Dihoplus schleiermacheri* (personal observations at MNHN and MAFI). A much worn P^2 from Sahabi, Lybia, reported as *Diceros neumayri* by Bernor et al. (1987: figure 15), can equally belong to *D. douariensis* or another unknown Dicerotini, as it does not bear any diagnostic features.

Although craniodentally very distinct, *"D." neumayri* has been frequently confused and misidentified with the synchronic and partly sympatric *Dihoplus pikermiensis,* a large Dicerorhinini (Heissig 1975; Geraads 1988; Giaourtsakis et al. 2006). Because of its dental similarities with the extant *Diceros,* the taxon has been commonly assigned to this genus (Ringström 1924; Thenius 1955; Hooijer 1972; Heissig 1975; Hooijer 1978; Guérin 1980b, 1982; Tsiskarishvili 1987; Heissig 1989). Geraads (1988) pointed out cranial similarities with *Ceratotherium.* These cranial similarities represent, however, early convergences. Following Geraads (1988), the "common usage" has uncritically changed to *Ceratotherium neumayri* (Geraads and Koufos 1990; Kaya 1994; Heissig 1996; Fortelius et al. 2003a; Giaourtsakis 2003; Antoine and Saraç 2005), although some reservations regarding the preliminary taxonomic status were retained (Guérin 2000, 2003; Giaourtsakis et al. 2006). Because an extensive revision of the taxon is currently in preparation, nomenclatural issues will not be treated further here, but the generic allocation for "common usage" is reconsidered, because it has been used to imply biogeographic, evolutionary, and ecological patterns. The Kuseralee cranium offers new data, in particular because the occipital morphology of Miocene African Dicerotini was practically unknown until now.

The early dispersal and migrational pattern of the Dicerotini outside Africa is not yet well-established. Thomas et al. (1978) described as *Dicerorhinus* cf. *primaevus* an unworn right M^2 from the middle Miocene locality Al Jadidah of the Hofuf Formation in the

eastern Province of the Kingdom of Saudi Arabia. A cast of the tooth is housed in the collections of MNHN and is indeed morphologically and metrically very similar with the unworn M^2 of the juvenile specimens from Bou Hanifia (MNHN: 1951-9/219). It bears typical Dicerotini features, such as the absence of a distal protocone constriction and antecrochet. It also has a well-developed paracone fold, a rather prominent crochet, and no crista. It is best referable to as *Diceros* cf. *primaevus* until further material is made available. The oldest occurrence of Dicerotini in the eastern Mediterranean is not yet well-documented. The referred occurrence of a primitive Dicerotini in the middle Miocene of Chios (Heissig 1989) is doubtful, because it has not been followed by evidence. In the well-calibrated Sinap sequence, the lineage of *"Diceros" neumayri* is reported to have a range of ~11.0–6.0 Ma (Fortelius et al. 2003a), and, within this range, its distribution falls more or less in other localities of Turkey (Heissig 1975, 1996), as well as in Greece (Giaourtsakis 2003) and Iran (Bernor et al. 1996d). Practically, this means that the Kuseralee cranium is stratigraphically younger than most specimens of this species.

Cranially, *"D." neumayri* is undoubtedly more specialized than the Kuseralee rhinocerotid, with convergent derived features similar to Pliocene *Ceratotherium,* but expressed to a lesser degree: The skull is usually longer and more dolichocephalic; the anterior border of the orbit is placed either at the same level as in the the Kuseralee cranium (in front of the middle of M^2) or in most specimens more retracted (behind the middle of M^2); the occiput inclines more posterodorsally, and the strong nuchal crest extends in many specimens beyond the level of occipital condyles; the occipital notch of the nuchal crest is deeply concave or forked.

Dentally, *"D." neumayri* follows a different pattern than the Douaria, Kuseralee, and Langebaanweg rhinocerotids. This pattern appears to evolve spatiotemporarily several times during its radiation in the eastern Mediterranean and is probably affected by migrational activities, population exchange, or regional adaptations (Heissig 1975; Fortelius et al. 2003a; personal observation). Increase in size and crown height, development of cristae in premolars and molars (very frequent in Turolian specimens), cingulum reduction, obliquity of the protoloph associated with broadening of the protocone, strengthening of the mesostyle bulge, and broadening or narrowing of the medisinus valley are general trends. Heissig (1975) and Fortelius et al. (2003a) argue that the changes seen (including body size) are of a magnitude that would justify recognition of separate morphospecies or geographic variations. This idea was first put forward by Thenius (1955), but the material he studied was too limited to establish unambiguous characters. Tsiskarishvili (1987) has described the species *Diceros gabuniae* as being a regional variant in the Caucasus, but detailed comparisons are lacking. Our observations (revision in preparation) confirm the radiation of several morphotypes and indicate an evolutionary pattern similar to the numerous, locally adapted extant *Diceros* subspecies. Contrary to the pattern seen in Eurasia, the development of cristae appears to be delayed in Africa, and even in the Langebaanweg sample they are only occasionally developed (less than 40 percent). Instead, the distolingual bending of the protoloph, the fading of the paracone fold, and the flattening of the occlusal surface is favored. The development of a lingual protocone groove, which is so conspicuous in the molars of Douaria, Lothagam (KNM-LT89), Langebaanweg, and Pliocene *Ceratotherium,* is never observed in *"D." neumayri*. The functional interpretation of this groove is not clear,

but it might be a structure to gradually enhance the distal curvature of the lingual wall of the protoloph, as Hooijer and Patterson (1972) have suggested.

The postcranial elements of *"D." neumayri* also follow a different specialization pattern than the Langebaanweg sample (which is similar in dimensions to the late Miocene Mpesida and Saitune Dora metapods) and the Pliocene *Ceratotherium*. The Vallesian specimens retain the length of *D. primaevus* but become more robust (personal observations), or "graviportal" as Guérin (1980b, 1982) notes. During the Turolian, several populations increase their size and robustness, but the exact pattern seems to constitute a complicated cline, as other populations retain the smaller dimensions (Heissig 1975; Kaya 1994; Fortelius et al. 2003a; personal observation). In any case, the maximum length values seldom reach the minimum values of the Langebaanweg population or the Mpesida and Saituna Dora metapods (Table 14.4), and the robustness is retained or accentuated. In addition, *"D." neumayri* displays some autapomorphic features. For example, although the proximal epiphysis of the third metacarpal widens, the articular facet for the second metacarpal is shifted more laterally with respect to the medial border of the diaphysis. In this way, the lateral border becomes markedly concave, and the minimum width is shifted closer to the middle of the diaphysis rather than the proximal epiphysis. The anteroposterior diameter of the proximal and distal epiphyses of the bone also increases.

Because of its unique combination of cranial, dental, and postcranial features, *"D." neumayri* has been regarded by the majority of authors as a separate lineage evolving independently from African Dicerotini (Hooijer and Patterson 1972; Heissig 1975; Hooijer 1978; Guérin 1980b, 1982; Heissig 1989).

Geraads (2005) deemed *"Diceros" neumayri* (which he calls *Ceratotherium neumayri*) as the common ancestor of both living species, arguing that it is morphologically and ecologically intermediate between them. In this context, the Miocene African *P. mukirii* and *D. primaevus* were considered as being related to *"D." neumayri,* and *D. douariensis* as potentially conspecific with *"D." neumayri*. However, no arguments were provided to support this grouping. Whereas an ancestry of *D. primaevus* for both *D. douariensis* and the extra-African *"D." neumayri* cannot be excluded (and is, in fact, a feasible option), a lineage of *D. primaevus* – *"D." neumayri* (= *D. douariensis*) splitting then into Pliocene *Diceros praecox* and *Ceratotherium mauritanicum* is inappropriate. Geraads (2005: 455) defines *Diceros praecox* as having "the following apomorphic features with respect to its likely ancestor *C. neumayri*: orbit more anterior to tooth row; skull profile more concave; occipital plane more vertical; nuchal crest less extended posteriorly [*sic*]." Apart from the more concave profile (which we agree is accentuated in Pliocene *Diceros* but not derived from *"D." neumayri*), all other cranial features cited are plesiomorphic (Antoine 2002) with respect to *"D." neumayri*, as they are with respect to the Plio-Pleistocene and the extant *Ceratotherium*. In these cranial features (plus the straight or only slightly indented nuchal crest), the Kuseralee cranium is also more primitive with respect to *"D." neumayri*. Even the occipital morphology of the stratigraphically younger Langebaanweg rhinocerotid (SAM: L-13747) is more conservative than that of Turolian specimens of the extra-African late Miocene *"D." neumayri* (SMNK: Ma 2/15; AMPG: PA 4721/91; MNHN: PIK-971; AUBLA: 18.ÇO-553; MTA: AK4-212; see also Antoine and Saraç 2005: figure 1). An occipital morphology similar to that of the eastern Mediterranean specimens

is independently achieved and further developed in Africa during the late Pliocene, by the descendants of the Kuseralee and Langebaanweg populations, that is, the *Ceratotherium* (*sensu stricto*) lineage: Hadar, NME: A.L. 129-25, A.L. 269-4, A.L. 235-3; Dikika, NME: DIK-1-10; Laetoli, LAET-49.

Geraads (2005) 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*). The Kuseralee cranium confirms, however, the scenario that the split of the two extant lineages took place in Africa before the Miocene-Pliocene boundary and that *"D." neumayri* represents a convergent extra-African monophyletic lineage (Hooijer and Patterson 1972; Hooijer 1978; Guérin 1980b, 1982; Heissig 1989). The Kuseralee cranium preserves a cranial morphology more primitive than stratigraphically older skulls of *"D." neumayri* but demonstrates a dentition that develops a different specialization pattern traceable from the late Miocene (Douaria, Lothagam-Nawata) to the Mio-Pliocene boundary (Langebaanweg) before it adapts to an exclusively C_4 grass diet during the course of the Pliocene (*Ceratotherium* sp.). In addition, the dietary inferences of the Kuseralee rhinocerotid show that not only the common ancestor of the two extant lineages should have been a browser, but also that the ancestral stock of the *Ceratotherium* lineage must have favored a browsing diet for as long as available habitats could supply it.

The dispersal of some dicerotine populations outside Africa during the late Miocene was concomitant with the gradual establishment of a unique combination of primitive and derived craniodental features, as well as some autapomorphies, notably in the postcranial elements. Their spatiotemporal expansion in the eastern Mediterranean and adjacent regions must have followed an evolutionary pattern comparable to the numerous, locally adapted, modern *Diceros* subspecies. A separate generic assignment for this monophyletic extra-African Dicerotini lineage is appropriate, an option also considered by Geraads (2005) but in a different phylogenetic context. However, keeping in mind the existing complicated nomenclatural issues concerning the eastern Mediterranean horned rhinoceroses (Heissig 1975; Geraads 1988; Giaourtsakis 2003), which also affect the availability of the generic name *Pliodiceros* Kretzoi, 1945, we suggest that this taxon be preliminarily referred to as *"Diceros" neumayri*.

Paleoecology and Functional Morphology

Inferences about habitat and dietary preferences in fossil mammals are often influenced by the ecological preferences of their extant relatives. However, caution is required, because significant differences may often occur (Solounias and Dawson-Saunders 1988; Solounias et al. 2000). Morphological features that are adapted for particular dietary functions must be carefully compared and evaluated in order to assess accurately the dietary preferences in fossil rhinocerotids (Zeuner 1934; Fortelius 1985; Fortelius and Solounias 2000). Stable isotope analysis of enamel carbonate is another useful tool for understanding the ecology of fossil mammals and the evolution of their habitats during the past (Zazzo et al. 2000 Franz-Odendaal et al. 2002; ; Lee-Thorp and Sponheimer 2005). Microwear dental analysis is also an important method for paleodiet reconstruction (Solounias et al. 2000) but

has not yet been sufficiently applied to fossil rhinoceroses and remains a promising source of information for future studies.

Since several misleading interpretations have been uncritically accepted in the past, a brief summary on the ecological and dietary preferences of the two extant species is essential.

The extant *Diceros bicornis* is found in a very wide range of habitats, from montane forest and lowland marginal forest through savanna woodland, bush and thicket, mixed grassland and woodland, scattered tree grassland, to semi-desert and arid desert (Hillmann-Smith and Groves 1994). Distribution ranges from sea level to at least 1,500 m in southern and southeastern Africa, up to 3,000 m in eastern Africa (Guggisberg 1966; Kingdon 1979). Although they are able to deal with patchy vegetation, black rhinoceroses always show a preference for areas with denser cover, especially during the day. In mixed habitats, a direct relationship between the density of black rhinoceroses and the density of habitat has been documented (Hitchins 1969; Mukinya 1973; Goddard 1967). Black rhinoceroses are selective browsers on woody shrubs, young trees, and certain forbs, rejecting generally dry plant material. They are extremely flexible, shifting their food preferences according to circumstances and availability; they are even able to utilize plants that have heavy morphological and chemical defenses against most other herbivores (Hall-Martin et al. 1982; Loutit et al. 1987; ; Oloo et al. 1994). Black rhinoceroses are able to feed on a wide variety of plant species. Goddard (1968, 1970) reported 191 species of plants in Ngorongoro (Tanzania) and 102 in Tsavo (Kenya) browsed by black rhinoceroses, while Leader-Williams (1985) reported 220 species in Luangwa Valley (Zambia) and Hall-Martin et al. (1982) recorded 111 species in Addo (South Africa). Even in the extremely arid Darmaland in Northern Namibia, the desert black rhinoceros utilized 74 out of the 103 plant species encountered (Loutit et al. 1987). Depending on the region and availability, they prefer several *Acacia* species and their relatives, as well as *Grewia similis, Spirostachys* sp., *Phyllanthus fischeri, Euphorbia* sp., and *Hibiscus* spp. Small quantities of grass are taken during the wet season, or together with succulent plants in dry periods when other resources become unavailable (Mukinya 1977; Hall-Martin et al. 1982; Oloo et al. 1994). In very dry seasons, however, excessive consumption of forage with low nutritional value may lead to substantial death rates from malnutrition (Dunham 1985, 1994).

In contrast, the extant *Ceratotherium simum* is a very specialized animal. It does not favor closed forests and mountainous areas and avoids high altitudes. Steep country is only traversed, and relatively flat terrain is preferred. In South Africa, white rhinoceroses occupy open savannas with scattered trees across the open Bushveldt zone. In the Nile region, they inhabit open *Combretum* forest with grassland (Guggisberg 1966; Groves 1972). In both cases, density is of secondary interest because they use the available trees only to provide shade during the hottest parts of the day. White rhinoceroses are entirely grazers, with a preference of feeding on high-quality short grasses. *Panicum maximum, P. coloratum, Urochloa mozambicensis,* and *Digitaria* sp. constitute the bulk of their diet. These grasses occur mostly in shady areas of *Themada triandra* grasslands. However, climax *Themada triandra* is rarely eaten, except for the sprouting green grass regenerating after summer fires, which is an important supplementary food resource during the dry season. An additional 30 species of grasses can be consumed to a lesser extent. Sporadic geophagia, especially around termitaria, has been recorded, presumably to increase mineral content.

When grasses become rare, white rhinoceroses change region, sometimes on a seasonal basis (Foster 1960; Guggisberg 1966; Groves 1972; Owen-Smith 1973, 1988; Skinner and Smithers 1990; Shrader et al. 2006).

Zeuner (1934) and Loose (1975) have demonstrated a close relationship between skull shape and dietary adaptation in the two extant African species. The cranial morphology of the Kuserelee rhinocerotid more closely resembles the morphology of the extant *Diceros,* rather than *Ceratotherium.* In the Kuseralee cranium, as in extant *Diceros,* the occipital plane is nearly vertically oriented, the nuchal crest does not extend beyond the occipital condyles, and the cranial dorsal profile is clearly concave. As a result, the head is held rather horizontally, enabling the animal to browse twigs and leaves from trees and bushes (Mills and Hes 1997: 236, see figure). The skull of *Ceratotherium* is much longer and more dolichocephalic, the occiput inclines strongly backward (posterodorsally), the nuchal crest extends beyond the condyles, and the dorsal profile is only gently concave. As a result, the head is held at an angle close to the ground, enabling the animal to feed on short grasses (Mills and Hes 1997: 233, see figure).

The dental morphology of the Kuseralee cranium, as well as that of the incomplete holotype skull from Douaria, more closely resembles the dentition of extant *Diceros.* Functionally significant morphological similarities related to dietary preferences include the concave occlusal surface of the teeth; the saw-toothed ectoloph wear profile with sharp cusp apices and relatively high intermediate relief; the relatively thin enamel with irregular thickness; the presence of paracone folds that are stronger than the mesostyle folds; the occurrence of thin cement coverage; the presence of a strong, continuous lingual cingulum in the premolors; and the absence of crista and medifossette, particularly in the molars.

Fortelius (1982, 1985) has demonstrated that the concave occlusal surface is a result of two distinct chewing phases during the occlusal stroke: shearing and crushing. During the first phase, only the buccal edges of upper and lower teeth come in contact. The sharp paracone and metacone ridges of the adjacent teeth and the intermediate valleys form the main shearing blades. This configuration corresponds to the profile inducted by the mesowear method, where the buccal cusps are apically sharp with rather high intermediate relief (Fortelius and Solounias 2000). The presence of a paracone fold strengthens the shearing efficiency. During the second phase, the occlusal motion continues lingually and perpendicular to the masticatory force applied, following the inclined occlusal surface of the upper teeth. This results in a high-pressure, low-speed condition, which enables the crushing of the food. Differential wear regulates the shape of the occlusal surface by inequalities in enamel thickness, which is broader on the buccal and lingual sides. The combination of shearing and crushing is an adaptation to the comminution of bulky vegetation, such as soft plants, fruits, and twigs, that forms a typical browsing diet. On the other hand, *Ceratotherium* has a flat occlusal surface and a flat ectoloph mesowear profile. This corresponds to a one-phase, upward-inward, high-pressure occlusal stroke, an adaptation to the rapid comminution of fibrous, thin, and tough vegetation, such as grasses (Fortelius 1982, 1985). Because the occlusal pressure is more uniformly distributed over the entire surface, the enamel thickness remains more equal over the entire tooth. Further, the paracone fold is weakened, and the mesostyle fold is strengthened to maintain the ectoloph pattern.

On the Kuseralee cranium and modern *Diceros,* only a thin cement coat is developed. In fossil and extant *Ceratotherium,* the cement investment is thick and abundant, filling almost completely the inner valleys of the upper and lower dentition in the modern species. This is also an adaptation to a grassy diet, because the cement investment produces a wear-retarding and relief-enhancing structure (Fortelius 1985).

The occurrence of a well-developed, continuous lingual cingulum found in the Kuseralee and extant *Diceros* premolars is related with specific browsing capabilities. Its presence has been interpreted as an adaptation of lower-crowned teeth to protect the gums from injury by thorns and splinters. This necessity would decrease with increasing crown height and disappear with a shift to a diet free of such components, for example, a grassy diet (Fortelius 1982). Indeed, in Plio-Pleistocene *Ceratotherium* the lingual cingulum is gradually reduced, and in the extant species it is absent.

In the Kuseralee and extant *Diceros* molars, a crochet is the only secondary fold developed, the crista is rare, and a closed medifossette is absent. In fossil and extant *Ceratotherium* molars, a closed medifossette is always present, formed by the early junction of crista and crochet. This structure is associated with improved abrasion efficiency, because it increases the effective length (perpendicular to the occlusal motion) of the enamel ridges and may also support the growing demands for additional cement investment in the crown.

In summary, the functional analysis of the available cranial and dental material clearly indicates that the Kuseralee rhinocerotid was, first and foremost, a browser. As discussed, there are also a few advanced morphological features observed with respect to Miocene Dicerotini and Pliocene *Diceros* species, in particular the large size, the relatively higher-crowned teeth, and the tendency of the protoloph to bend distolingually in the molars. Increased crown height is associated with increased resistance to abrasion, resulting directly from the utilization or contamination with extraneous abrasive material, or indirectly from food requiring higher occlusal pressures for comminution (Fortelius 1985). Herbivores that shift to utilize more abrasive forage and exploit more open habitats are frequently larger than their ancestors. The gradual posterodistal deflection of the protoloph is a tendency to increase the effective length of the enamel ridges perpendicular to the occlusal motion (in *C. simum* both protoloph and metaloph are bending markedly distolingually). These features may reflect a slow but gradual adaptation to cope with more open or seasonal environments and their occasionally tougher and nutritionally inferior forage, equivalent to some extant black rhinoceros subspecies. The paleoenviromental reconstruction of the Kuseralee faunal community suggests a riverine woodland habitat with wet grassland (Su et al., Chapter 17) and is thus in accordance with the dietary inferences made here.

In the rapidly changing landscape at the Miocene-Pliocene boundary (Cerling et al. 1997b), being able to adapt to increasingly open or seasonal habitats was an evolutionary advantage (Jernvall and Fortelius 2002). It is not a coincidence that none of the African Miocene rhinoceros lineages other than the dicerotines managed to survive successfully into the Pliocene. The few advanced morphological features observed in the Douaria and Kuseralee rhinocerotids are further accentuated by some large-sized populations at the beginning of the Pliocene. The most adequate and stratigraphically important material is the Langebaanweg sample from the Mio-Pliocene boundary. The teeth from Langebaanweg

are somewhat more high-crowned, the occlusal surface less concave (but not flat as in *Ceratotherium* sp.), the ectoloph mesowear profile markedly lower, the cement investment increased, and the lingual protocone groove more evident. The weak protocone fold persists, but the wide mesostyle fold becomes stronger. A small crista appears in some molars, but rarely a closed medifossette as in *Ceratotherium*. This intermediate morphology is in agreement with the stable isotope analyses of enamel carbonate, as well as with the particular local environmental circumstances documented for the locality. Franz-Odendaal et al. (2002) demonstrated that the terrestrial fauna of Langebaanweg existed in a local environment that remained C_3-dominated. The current local Mediterranean climate, controlled by latitudinal, seasonal movement of the South Atlantic high-pressure system, was already established in this region by the early Pliocene, preventing the expansion of C_4 grasses. This climate regime is characterized by wet, rainy winters and markedly arid summers. The rhinoceros of Langebaanweg was probably a mixed feeder, able to browse or graze on C_3 plants, depending on the seasonal conditions in the area.

Isotopic results were also reported for the rhinoceroses of Lothagam (Harris and Leakey 2003a; Cerling et al. 2003), which is geographically closer and temporally overlaps with the Middle Awash succession. All samples from the Lower Nawata (>6.5 Ma), including one referred to as *Ceratotherium praecox,* were C_3 browsers. A tooth from the younger Upper Nawata (>5 Ma) provided a C_4 signal. One sample from the Pliocene Apak Member was from a C_3 browser, and five were C_4 grazers. Harris and Leakey (2003a) tentatively assigned them to *Diceros* and *Ceratotherium,* respectively. Zazzo et al. (2000) applied stable isotope analyses in the Chadian fossil faunas and documented a shift in herbivore paleodiet related to paleoenvironmental changes during the Pliocene. In particular, rhinocerotid material referred to *Ceratotherium praecox* was recorded as a mixed feeder during the early Pliocene and as a pure grazer during the late Pliocene.

Overlooking some of the systematic assessments, which simply followed previously established concepts and might require refinement, these studies clearly indicate that during the late Miocene and early Pliocene some Dicerotini populations gradually increased the abrasive forage in their diet as a response to paleoenviromental changes, including increasing seasonality and expansion of open habitats. Ultimately, the establishment of open grasslands during the Pliocene accelerated the morphological adaptations required for an exclusive grass diet and contributed to the definitive morphogenetic evolutionary step of these populations toward the *Ceratotherium* condition. At the same time, less advanced populations of the *Diceros* lineage continued to survive in more temperate habitats and evolve independently, adapting to new spatiotemporal environmental challenges, probably following an evolutionary pattern analogous to the numerous locally adapted modern subspecies.

Appendix 14.1: Methods and Materials

The fossil rhinoceros material described here was collected by the Middle Awash project and is housed at the National Museum of Ethiopia, Addis Ababa. Skull measurements follow Guérin (1980b). Anatomical conventions follow Getty (1975) and Nickel et al. (1986). Dental measurements and terminology follow Peter (2002). Width measurements include the mesial (Wm) as well as the distal (Wd) width of each tooth. On the first upper and lower deciduous premo-

lar, only the maximal distal width (Wd) is measured. Measurements of M3 include the buccal length of the ectometaloph (Lb), the mesial width (Wm) and the lingual, anatomical length (La) comprising the distal cingular pillar, if present (Guérin 1980b; Peter 2002). Measurements ranging 0–150 mm were taken with a digital caliper to 0.01 mm and rounded to the nearest 0.1 mm. For larger measurements a linear caliper with a precision of 0.1 mm was applied. All measurements are given in millimeters (mm). The terms *low-* and *high-crowned* dentition refer to relative crown height, whereas the terms *brachyodont* and *hypsodont* refer to functionally different types, following Fortelius (1985).

Comparative studies with material from the Plio-Pleistocene localities of Hadar (Guérin 1980a; Geraads 2005) and Dikika (Geraads 2005) have been carried out at the NME; from the Omo Valley (Arambourg 1948; Hooijer 1969, 1972, 1973, 1975; Hooijer and Churcher 1985; Guérin 1985) at NME, RMNH, and MNHN. Pleistocene material from Olduvai Gorge, Laetoli, Kanjera, Kanam West, and Rawi (Hooijer 1969; Groves 1975) has been studied at BMNH. The Kohl-Larsen fossil collection from eastern Africa (Dietrich 1942b, 1945) has been studied at MNHB. Specimens from Bou Hanifia (Arambourg 1959; Geraads 1986b), Ternifine (Pomel 1895), and several Plio-Pleistocene North African localities (Arambourg 1970) have been examined at MNHN. Materials of *"Diceros" neumayri* from Greece (Pikermi, Samos, Axios Valley: Gaudry 1862–1867; Geraads 1988; Geraads and Koufos 1990; Giaourtskis 2003) have been studied at AMPG, LGPUT, MNHN, BMNH, NHMW, IPUW, MAFI, BSPG, SMF, and HLMD; those from Turkey (various localities: Heissig 1975, 1996; Geraads 1994b; Fortelius et al. 2003a) were studied at BSPG, SMNK, AUBLA, MTA and MNHN; and those from Iran (Maragheh: Osborn 1900; Thenius 1956) were examined at NHMW and MNHN. Casts of specimens from Fort Ternan (Hooijer 1968) and Langebaanweg (Hooijer 1972) have been examined at BMNH and BSPG, respectively. Digital images of the dentition of *Diceros douariensis* from Douaria (Guérin 1966) have been kindly provided by C. Guérin and A. Prieur, and of the holotype of *Diceros praecox* from Kanapoi (Hooijer and Patterson 1972) by M. Fortelius. Comparative studies with the extant species have been carried out at the zoological collections of NHMW, IPUW, RMNH, ZMA, SMNK, SMF, BMNH, MNHN, and USNM.

Institutional Abbreviations

AMPG	Athens Museum of Paleontology and Geology, University of Athens
AUABL	Ankara Üniversitesi, Antropoloji Bölümü Laboratuary, Ankara
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
HLMD	Hessisches Landesmuseum, Darmstadt
IPUW	Institut für Paläontologie der Universität, Wien
KNM	Kenya National Museum, Nairobi
LGPUT	Laboratory of Geology and Palaeontology, University of Thessaloniki
MAFI	Magyar Állami Földtani Intézet, Budapest
MNHB	Museum der Naturkunde für Humboldt Universität zu Berlin
MNHN	Muséum National d'Histoire Naturelle, Paris

MTA	Maden Tetkik ve Arama Museum, Ankara
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
USNM	United States National Museum (Smithsonian), Washington
ZMA	Zoological Museum, Amsterdam

Locality Abbreviations

KUS	Kuseralee
STD	Saitune Dora
ASK	Asa Koma
ALA	Alayla
VP	vertebrate paleontology locality (Middle Awash sample)
AL	Afar locality (Hadar sample)
SH	Sidi Hakoma Member (Hadar sample)
FT	Fort Ternan

Morphology Abbreviations

P, M, d	premolar, molar, deciduous (pre)molar
I, di	incisor, deciduous incisor
prmx.	premaxilla
nas.	nasal(s), nasal tip
nas.inc.	nasal incision
orb.	orbit anterior border
cond.	condyle
occ.	occipital
proc.	process(es)
MC	metacarpal
MT	metatarsal
dia.	diaphysis
ep.	epiphysis
prox.	proximal
dist.	distal
L	length
W	width
H	height
DT	transverse diameter
DAP	anteroposterior diameter

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