

Table 9: Comparisons of the measurements of the astragalus of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

| | Arrisdrift AD 619'94 | Arrisdrift PQ AD 1219 | <i>D. gr. pachygnathus/neumayri</i> | | | | | | |
|------------------|-------------------------|--------------------------|-------------------------------------|-------|------|------|----------|-------------|--|
| | n | | n | mean | min. | max. | éc.-type | coeff. var. | |
| DT | 101 | 100 | 7 | 98,57 | 94 | 104 | 3,645 | 3,70 | |
| Height | 95 | 96 | 6 | 87,17 | 84 | 92 | 3,545 | 4,07 | |
| DAP medial | 63,5 | 64,5 | 6 | 63,00 | 61 | 65 | 1,897 | 3,01 | |
| DT artic distal | 75 | 78 | 7 | 81,07 | 76,5 | 86 | 3,101 | 3,83 | |
| DAP artic distal | 55 | 53,5 | 7 | 50,86 | 45 | 53,5 | 3,326 | 6,54 | |
| DT trochlea | 72 | 77 | 6 | 69,83 | 61 | 77,5 | 5,768 | 8,26 | |
| DT distal | 80,5 | 85 | 5 | 84,90 | 82 | 90,5 | 3,471 | 4,09 | |

| | <i>D. schleiermacheri</i> | | | | <i>Brachypotherium snowi</i> | | | | | |
|------------------|---------------------------|-------|------|------|------------------------------|-------------|---|--------|------|-------|
| | n | mean | min. | max. | éc.-type | coeff. var. | n | mean | min. | max. |
| DT | 11 | 91,45 | 86,5 | 99 | 3,595 | 3,93 | 2 | 108,75 | 105 | 112,5 |
| Height | 13 | 85,35 | 78,5 | 93 | 4,719 | 5,53 | 1 | 82,00 | | |
| DAP medial | 12 | 61,79 | 55 | 70 | 4,126 | 6,68 | 2 | 59,00 | 58 | 60 |
| DT artic distal | 8 | 73,00 | 62 | 82 | 6,649 | 9,11 | 2 | 82,25 | 80 | 84,5 |
| DAP artic distal | 10 | 47,95 | 44,5 | 55 | 2,833 | 5,91 | | | | |
| DT trochlea | 12 | 66,62 | 61 | 75 | 3,730 | 5,60 | 1 | 51,00 | | |
| DT distal | 10 | 79,75 | 76 | 86 | 3,810 | 4,78 | 2 | 92,75 | 90,5 | 95 |

| | ACERATHERES | | | | <i>Chilotheridium pattersoni</i> | | | | | |
|------------------|-------------|-------|------|------|----------------------------------|-------------|---|-------|------|------|
| | n | mean | min. | max. | éc.-type | coeff. var. | n | mean | min. | max. |
| DT | 29 | 79,60 | 72 | 88,5 | 4,347 | 5,46 | 3 | 88,50 | 85,5 | 92 |
| Height | 30 | 70,07 | 62 | 81 | 4,584 | 6,54 | 3 | 70,17 | 68,5 | 71 |
| DAP medial | 26 | 52,44 | 45 | 59 | 3,593 | 6,85 | 3 | 53,67 | 52 | 55,5 |
| DT artic distal | 29 | 64,59 | 56,5 | 73 | 3,880 | 6,01 | 3 | 71,00 | 64 | 79 |
| DAP artic distal | 25 | 39,68 | 35 | 47 | 2,688 | 6,77 | 2 | 40,50 | 38 | 43 |
| DT trochlea | 31 | 52,39 | 46 | 65 | 5,228 | 9,98 | 3 | 55,33 | 52 | 58 |
| DT distal | 28 | 70,95 | 65 | 76,5 | 3,122 | 4,40 | 3 | 75,33 | 73 | 79 |

| | IDA | | | | | | | | | |
|------------------|-----|-------|------|------|----------|-------------|--|--|--|--|
| | n | mean | min. | max. | éc.-type | coeff. var. | | | | |
| DT | 8 | 80,62 | 75,5 | 84 | 3,410 | 4,23 | | | | |
| Height | 7 | 72,79 | 69 | 78,5 | 3,706 | 5,09 | | | | |
| DAP medial | 7 | 52,14 | 47,5 | 56 | 3,159 | 6,06 | | | | |
| DT artic distal | 8 | 68,00 | 65 | 74 | 3,024 | 4,45 | | | | |
| DAP artic distal | 6 | 38,83 | 33,5 | 43,5 | 3,804 | 9,79 | | | | |
| DT trochlea | 7 | 48,79 | 45 | 50 | 1,890 | 3,87 | | | | |
| DT distal | 8 | 73,81 | 70,5 | 78,5 | 3,093 | 4,19 | | | | |

it is nevertheless possible to measure its total length. As for the Mc III the tibia is slightly longer than the biggest known specimens of *Diceros gr. pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*, as well as being slimmer (Tabl. 8). The dimensions of a broken distal epiphysis of *Diceros cf. douariensis* from Baccinello V3 are identical to those of the tibia from Arrisdrift.

Astragalus. Three astragali were discovered, of which two are complete (Pl. 3, Fig. 2). The dimensions (Tabl. 9) and the proportions (Fig. 4) are close to those of *Diceros gr. pachygnathus-neumayri*, and slightly different from *Dicerorhinus schleiermacheri*. The astragalus of *Brachypotherium snowi* is wider but clearly lower; its width/length ratio is lower, as for the much smaller *Chilotheridium*. In the true aceratheres the dimensions are lower and the proportions different, and the same applies to the undifferentiated sample of *D. leakeyi-A. acutirostratum*, which are remarkably similar to the former.

Among the qualitative characters is the median position, well above the distal margin of the bone, of the tubercle of the inferior part of the medial surface. The individual variation of the three astragali of *D. australis* is clear, especially in the height of the neck, in the obliquity

of the medial margin of the distal articulation, and in the development towards the rear of the upper extremity of the medial lip of the pulley.

Calcaneum. There are four adult and one juvenile calcanea, of which three are complete (Pl. 3, Fig. 1). As for the astragalus, the dimensions (Tabl. 10) and proportions of the calcanea are close to *Diceros gr. pachygnathus-neumayri* and *D. schleiermacheri*, and have nothing to do with those of *Paradiceros*, *Chilotheridium* or the true aceratheres.

In posterior view the axis of the sustentaculum tali makes a right angle with the axis of the body of the bone; this is a Dicerotinae feature.

In lateral view, the summit of the tuberosity is located well behind the beak (which is the most anterior part of the bone); the anterior margin of the surface, which joins these two points, is oblique and slightly concave. The posterior margin of the lateral surface is globular in its superior two thirds and depressed in its lower third, particularly in specimen PQ AD 601 (in AD 353'00 the lower third is straight). The more or less globular outline of the lateral surface of the bone is another dicerotine character.

The individual variation occurs most obviously at the level of the proximal part of the bone, in rear view: the

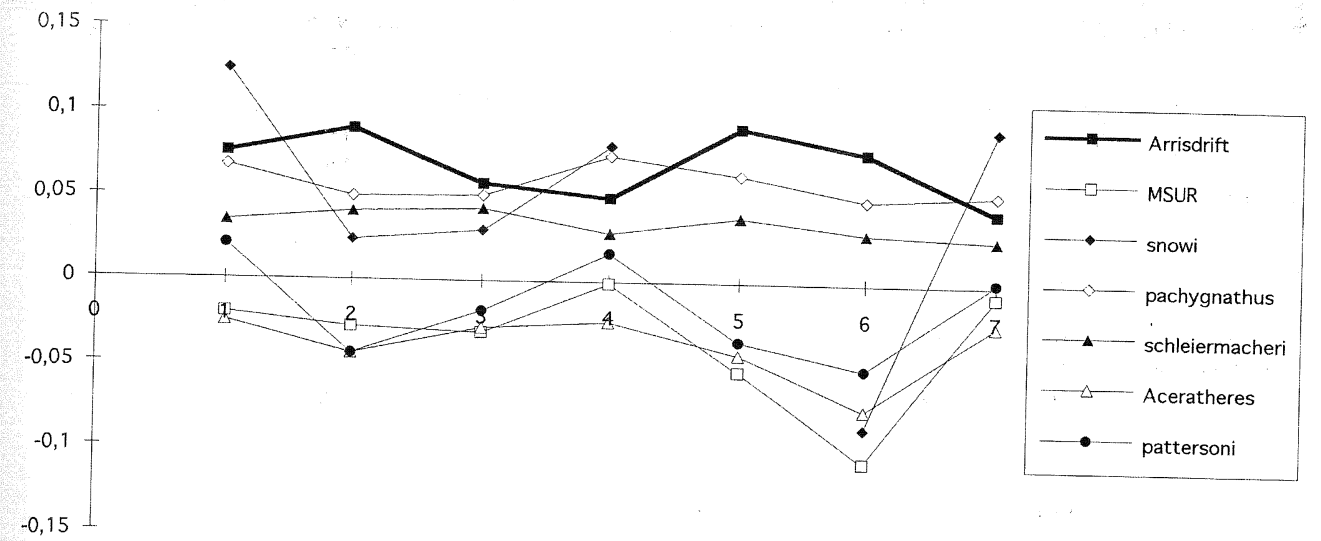


Figure 4: *Diceros australis*: Simpson diagram of the astragalus compared with other Miocene rhinos. The reference is *Diceros bicornis*. 1: DT; 2: Height; 3: DAP medial; 4: DT articular distal; 5: DAP articular distal; 6: proximal width of the trochlea; 7: DT maximal distal.

summit is an inverted V in calcaneum PQ AD 601 and AD 353'00, whereas it is flat in AD 50'97.

Other tarsals. The cuboid is very large: its total length is 77 mm, its maximum height is 61 mm, and the greatest width is 52.5 mm. The anterior surface is higher than wide (respectively 53 and 41.5 mm), and its lateral border is longer than the medial one.

Two naviculars were collected (AD 920'97 and PQ AD 1841); the first is not completely free of matrix on its external edge and the second is rolled; they are wider than

long: respectively 67 x 56.5 mm for a height of 40 mm and 78 x 56.5 mm for a height of 38 mm.

A small cuneiform (AD 16'00) is 38 mm long, for a width of 22 mm and a height of 20.5 mm.

The external cuneiform AD 399'00 is 66 mm high for a transverse diameter of 30 mm and an anteroposterior diameter of 39 mm; it has a projecting transverse tuberosity in the middle of its medial surface.

Metatarsal II. Four Mt II were discovered of which two are complete or subcomplete (they were broken during

Table 10: Comparisons of the measurements of the calcaneum of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

| | ARRISDRIFT | | | | | | <i>Paradiceros</i> | | IDA | |
|------------------|------------|-----------|-----------|-----------|--|--|--------------------|--|-------|--|
| | AD 50'97 | PQ AD 601 | AD 530'95 | AD 353'00 | | | Kisegi | | | |
| Height | 158,5 | 153 | 153 | 162,5 | | | 92,5 | | 130,5 | |
| DP head | 58 | 55 | 64 | 56 | | | 36 | | 52,5 | |
| DAP head | 77 | 67 | | 76,5 | | | 50 | | 54 | |
| DT middle | 41,5 | 40 | | | | | 33 | | 43 | |
| DT sustentaculum | 77,5 | 79 | 77 | | | | 50 | | 81 | |
| DT max | 81 | 81 | 80 | 76* | | | 55,5 | | 85,5 | |
| DAP max | 84 | 75,5 | ca 75 | 80 | | | 63 | | 63 | |
| | | | | | | | 50 | | 60 | |

| | <i>D. gr. pachygnathus/neumayri</i> | | | <i>Chilotheridium pattersoni</i> | | | | | | | | |
|------------------|-------------------------------------|--------|------|----------------------------------|----------|-------------|---|--------|------|------|----------|-------------|
| | n | mean | min. | max. | éc.-type | coeff. var. | n | mean | min. | max. | éc.-type | coeff. var. |
| Height | 7 | 143,36 | 132 | 151,5 | 6,296 | 4,39 | 3 | 120,83 | 113 | 132 | 9,929 | 8,22 |
| DP head | 6 | 58,42 | 54 | 63 | 3,639 | 6,23 | 3 | 44,33 | 42 | 48,5 | 3,617 | 8,16 |
| DAP head | 7 | 75,07 | 65 | 82 | 5,762 | 7,68 | 3 | 67,67 | 60 | 74 | 7,095 | 10,48 |
| DT middle | 2 | 46,50 | 45 | 48 | 2,121 | 4,56 | | | | | | |
| DT sustentaculum | 7 | 82,07 | 74 | 87,5 | 4,641 | 5,65 | 2 | 70,00 | 70 | 70 | 0,000 | 0,00 |
| DT max | | | | | | | | | | | | |
| DAP max | 5 | 77,90 | 72 | 83 | 5,030 | 6,46 | 3 | 59,17 | 57 | 62 | 2,566 | 4,34 |

| | <i>D. schleiermacheri</i> | | | ACERATHERES | | | | | | | | |
|------------------|---------------------------|--------|------|-------------|----------|-------------|----|--------|------|-------|----------|-------------|
| | n | mean | min. | max. | éc.-type | coeff. var. | n | mean | min. | max. | éc.-type | coeff. var. |
| Height | 5 | 142,10 | 134 | 149 | 6,712 | 4,72 | 20 | 108,82 | 98,5 | 123,5 | 6,660 | 6,12 |
| DP head | 6 | 53,17 | 50,5 | 55 | 1,780 | 3,35 | 20 | 42,97 | 35 | 49 | 3,925 | 9,13 |
| DAP head | 6 | 72,67 | 68,5 | 79,5 | 5,965 | 9,01 | 19 | 61,03 | 49,5 | 79 | 6,550 | 10,73 |
| DT middle | 4 | 40,12 | 37 | 43,5 | 2,780 | 6,93 | 6 | 33,75 | 26 | 41 | 6,031 | 17,87 |
| DT sustentaculum | 5 | 80,90 | 72,5 | 88 | 6,368 | 7,87 | 15 | 70,33 | 61 | 78,5 | 4,139 | 5,88 |
| DT max | | | | | | | | | | | | |
| DAP max | 6 | 74,50 | 69 | 86 | 6,716 | 9,01 | 20 | 59,58 | 51 | 70 | 5,095 | 8,55 |

Table 11: Comparisons of the measurements of the Mt II of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

| | Arrisdraft | | | | <i>Chilotheridium pattersoni</i> | | IDA |
|-----------------|------------|-----------|-----------|-----------|----------------------------------|---------|--------|
| | AD 744'97 | PQ AD 251 | AD 442'97 | AD 348'95 | Loperot | Loperot | Kiboko |
| Length | 182,5 | 181 | | | 129 | 115 | 153 |
| DT prox. | 30 | 31 | 32 | 31 | env. 36 | 30 | 27 |
| DAP prox. | 51 | 47 | 57 | 51 | | 37,5 | 34,5 |
| DT dia. | 31 | 30 | 31,5 | | | 23 | 19,5 |
| DAP dia. | 30 | 25,5 | 29 | | | 21 | 18,5 |
| DT max. dist. | 40,5 | 39 | | | 42 | 35 | 29 |
| DT artic. dist. | 38,5 | 37,5 | | | 38,5 | 32,5 | 28 |
| DAP dist. | 46 | 40 | | | 43 | 36,5 | 30 |

| | <i>D. schleiermacheri</i> | | | | | |
|-----------------|---------------------------|--------|------|----------|-------------|-------------|
| | Mean | min. | max. | éc.-type | coeff. var. | coeff. var. |
| Length | 3 | 153,33 | 150 | 156 | 3,055 | 1,99 |
| DT prox. | 3 | 33,83 | 27 | 40,5 | 6,752 | 19,96 |
| DAP prox. | 3 | 45,67 | 43 | 50,5 | 4,193 | 9,18 |
| DT dia. | 2 | 27,00 | 26 | 28 | 1,414 | 5,24 |
| DAP dia. | 2 | 27,75 | 27 | 28,5 | 1,061 | 3,82 |
| DT max. dist. | 3 | 37,17 | 35,5 | 39 | 1,756 | 4,72 |
| DT artic. dist. | 3 | 35,00 | 33 | 37 | 2,000 | 5,71 |
| DAP dist. | 3 | 39,17 | 37 | 40,5 | 1,893 | 4,83 |

| | <i>D. gr. pachygnathus/neumayri</i> | | | | | |
|-----------------|-------------------------------------|--------|-------|----------|-------------|-------------|
| | Mean | min. | max. | éc.-type | coeff. var. | coeff. var. |
| Length | 5 | 153,70 | 147,5 | 157,5 | 4,040 | 2,63 |
| DT prox. | 5 | 33,60 | 30,5 | 37 | 3,029 | 9,01 |
| DAP prox. | 5 | 45,70 | 42,5 | 49 | 2,729 | 5,97 |
| DT dia. | 5 | 34,80 | 32 | 37,5 | 2,080 | 5,98 |
| DAP dia. | 5 | 25,20 | 23,5 | 27 | 1,483 | 5,89 |
| DT max. dist. | 4 | 43,50 | 40 | 45 | 2,380 | 5,47 |
| DT artic. dist. | 5 | 39,30 | 36,5 | 41 | 1,754 | 4,46 |
| DAP dist. | 5 | 43,50 | 39 | 47 | 2,958 | 6,80 |

| | ACERATHERES | | | | | |
|-----------------|-------------|--------|-------|----------|-------------|-------------|
| | Mean | min. | max. | éc.-type | coeff. var. | coeff. var. |
| Length | 8 | 137,06 | 117,5 | 165,5 | 14,374 | 10,49 |
| DT prox. | 9 | 28,00 | 25,5 | 31 | 1,696 | 6,06 |
| DAP prox. | 9 | 39,17 | 35 | 41,5 | 2,264 | 5,78 |
| DT dia. | 7 | 26,57 | 23,5 | 32 | 2,992 | 11,26 |
| DAP dia. | 7 | 21,93 | 19 | 25 | 2,130 | 9,71 |
| DT max. dist. | 7 | 36,07 | 31 | 40 | 3,181 | 8,82 |
| DT artic. dist. | 8 | 32,88 | 26 | 40 | 4,604 | 14,00 |
| DAP dist. | 7 | 36,50 | 33 | 40,5 | 2,799 | 7,67 |

fossilisation, but recemented in place). They are much longer but slimmer than the largest specimens known of *Diceros gr. pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*. The Mt II of *Chilotheridium* is very short and relatively more stocky, and that of true aceratheres is shorter with different overall proportions (Tabl. 11).

The lateral surface of the proximal epiphysis has two clearly separated articular facets, both with elliptical outlines that are higher than wide. In specimen n° AD 542'97 the posterior part of the proximal epiphysis is more strongly developed towards the rear than the others; the

lateral articular facets are the widest and there are two well separated articular facets on the medial surface, that are also visible on AD 744'97.

The transverse section of the diaphysis is a rounded trapezoid, which is wider on its posterior margin and with a sharp anterior angle, especially in the superior third of the bone.

Metatarsal III. Arrisdraft has yielded four Mt III, of which two are well preserved (Pl. 2, Figs 1 and 2), one was broken in two but recemented in place and another has an incomplete proximal epiphysis which has been attacked by

Table 12: Comparisons of the measurements of the Mt III of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

| | Arrisdraft | | | | <i>C. pattersoni</i> | |
|-----------------|------------|-----------|------------|-----------|----------------------|--|
| | AD 618'94 | PQ AD 249 | PQ AD 1190 | PQ AD 183 | Loperot | |
| Length | 197,5 | 197 | ca 180 | ca 178 | 128 | |
| DT prox. | 57,5 | 61 | | 54 | 43,5 | |
| DAP prox. | 52 | | | 49 | 40 | |
| DT dia. | 50 | 51,5 | 52,5 | 44 | 36 | |
| DAP dia. | 26 | 25,5 | | 25,5 | 18,5 | |
| DT max. dist. | 61,5 | 60,5 | 57,5 | 55,5 | 48 | |
| DT artic. dist. | 53 | 57 | 52,5 | 51 | 43 | |
| DAP dist. | 46 | 47,5 | 42 | 42 | 35 | |

| | <i>D. schleiermacheri</i> | | | | | |
|-----------------|---------------------------|--------|-------|------|----------|-------------|
| | n | Mean | min. | max. | éc.-type | coeff. var. |
| Length | 2 | 173,25 | 171,5 | 175 | 2,475 | 1,43 |
| DT prox. | 1 | 48,00 | | | | |
| DAP prox. | 1 | 40,00 | | | | |
| DT dia. | 2 | 45,00 | 43,5 | 46,5 | 2,121 | 4,71 |
| DAP dia. | 2 | 23,25 | 23 | 23,5 | 0,354 | 1,52 |
| DT max. dist. | 2 | 55,50 | 53,5 | 57,5 | 2,828 | 5,10 |
| DT artic. dist. | 2 | 47,75 | 46 | 49,5 | 2,475 | 5,18 |
| DAP dist. | 2 | 39,00 | 33 | 45 | 8,485 | 21,76 |

| | <i>D. gr. pachygnathus/neumayri</i> | | | | | |
|-----------------|-------------------------------------|--------|------|-------|----------|-------------|
| | n | Mean | min. | max. | éc.-type | coeff. var. |
| Length | 9 | 174,56 | 165 | 194,5 | 8,557 | 4,90 |
| DT prox. | 8 | 60,06 | 57 | 64,5 | 2,321 | 3,86 |
| DAP prox. | 8 | 50,88 | 45 | 57,5 | 4,955 | 9,74 |
| DT dia. | 9 | 53,22 | 51,5 | 55 | 1,228 | 2,31 |
| DAP dia. | 9 | 25,33 | 22,5 | 28,5 | 1,969 | 7,77 |
| DT max. dist. | 7 | 66,93 | 60,5 | 71,5 | 3,758 | 5,61 |
| DT artic. dist. | 8 | 54,50 | 49,5 | 60,5 | 3,645 | 6,69 |
| DAP dist. | 8 | 46,50 | 41,5 | 49 | 2,405 | 5,17 |

| | ACERATHERES | | | | | |
|-----------------|-------------|--------|------|------|----------|-------------|
| | n | Mean | min. | max. | éc.-type | coeff. var. |
| Length | 11 | 150,36 | 130 | 166 | 11,437 | 7,61 |
| DT prox. | 10 | 46,25 | 40 | 53,5 | 4,626 | 10,00 |
| DAP prox. | 10 | 41,90 | 38 | 46 | 2,757 | 6,58 |
| DT dia. | 11 | 41,32 | 37,5 | 46,5 | 2,704 | 6,55 |
| DAP dia. | 10 | 19,90 | 16,5 | 24,5 | 2,757 | 13,85 |
| DT max. dist. | 11 | 52,45 | 47 | 60,5 | 4,120 | 7,85 |
| DT artic. dist. | 11 | 45,45 | 40,5 | 51,5 | 3,228 | 7,10 |
| DAP dist. | 11 | 37,82 | 32 | 42,5 | 3,466 | 9,17 |

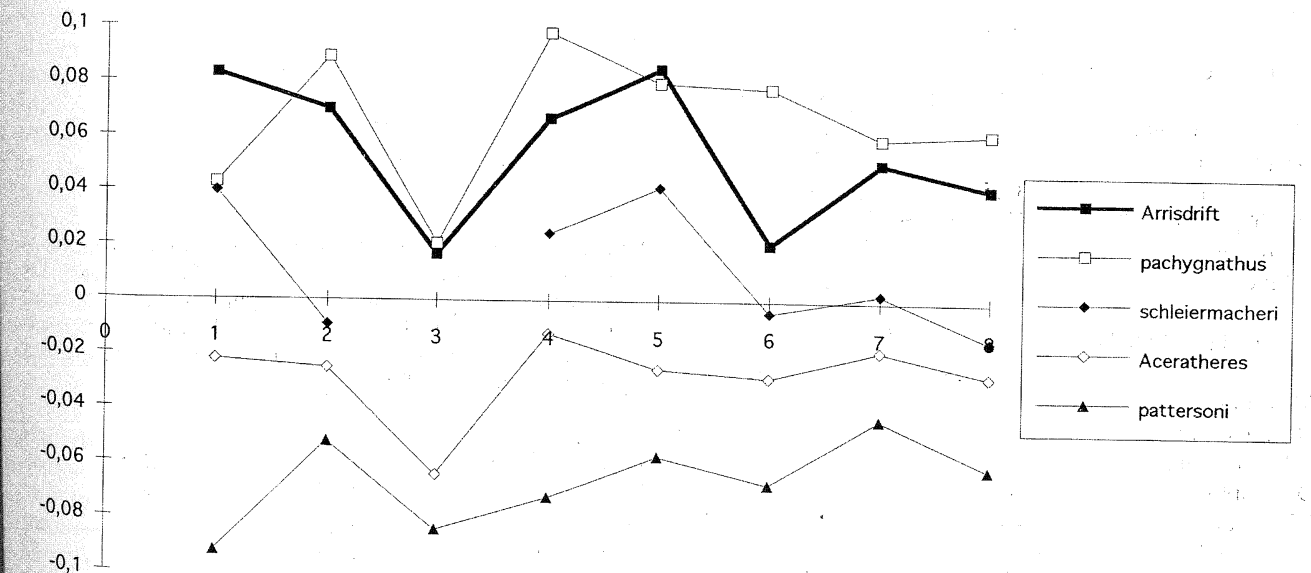


Figure 5: *Diceros australis*: Simpson diagram of the Mt III compared with other Miocene rhinos. The reference is *Diceros bicornis*. 1: Length; 2: DT proximal; 3: DAP proximal; 4: DT diaphysis; 5: DAP diaphysis; 6: DT maximal distal; 7: DT articular distal; 8: DAP distal.

The bone is about as long as the longest specimen known *Diceros gr. pachygnathus-neumayri* and has the same proportions, save for the sub-articular distal transverse diameter. It is significantly longer than that of *Dicerorhinus schleiermacheri*. The Mt III of *Chilotheridium* is much shorter and relatively more solidly built. In the true aceratheres the bone is smaller and its proportions are different (Tabl. 12, Fig. 5).

The proximal articulation is very wide, triangular with a convex anterior margin of which the point of inflexion is offset laterally; the antero-lateral angle is pointed; the medial border is convex in its anterior part, then weakly depressed towards the rear, and once more becomes convex in the posteriormost part. The lateral surface of the proximal epiphysis has two articular facets; the anterior one is positioned higher than the posterior one, of which the outline is an elongated ellipse.

The median transverse section of the diaphysis is trapezoidal with a convex anterior border and a concave posterior one; the lateral margin is straight and the medial one slightly convex.

Individual variation concerns mainly the more or less triangular outline of the anterior articular facet on the lateral surface of the proximal epiphysis, as well as the convexity and concavity of the anterior and posterior edges respectively of the transverse section of the diaphysis.

Metatarsal IV. Only one specimen was found, and it is poorly preserved. As for the Mt II, it is much longer than the biggest known specimens of *Diceros gr. pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*, but without being much more gracile. The Mt IV of *Chilotheridium* is very short, and that of true aceratheres is relatively shorter with different proportions (Tabl. 13).

Phalanges. There are 6 incomplete or uncleaned phalanges and 5 in good condition:

Table 13: Comparisons of the measurements of the Mt IV of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T = transversal.

| | Arrisdrift PQ AD 253 | | <i>Chilotheridium pattersoni</i> Loperot | |
|-----------------|-------------------------|--|---|---------|
| | | | Loperot | Loperot |
| Length | ca 182 | | 111 | 113 |
| DT prox. | 44 | | 41 | 40,5 |
| DAP prox. | 42 | | 40 | ca 38,5 |
| DT dia. | 35,5 | | 22,5 | 22,5 |
| DAP dia. | 22,5 | | 20,5 | 20 |
| DT max. dist. | 42 | | 33 | 30,5 |
| DT artic. dist. | 41 | | 34,5 | 32 |
| DAP dist. | ca 36 | | 35,5 | 34,5 |

| | <i>D. schleiermacheri</i> | | min. | max. |
|-----------------|---------------------------|--------|------|------|
| | n | mean | | |
| Length | 2 | 153,50 | 152 | 155 |
| DT prox. | 2 | 42,25 | 37 | 47,5 |
| DAP prox. | 1 | 50,00 | 50 | 50 |
| DT dia. | 2 | 27,75 | 26,5 | 29 |
| DAP dia. | 2 | 29,25 | 28 | 30,5 |
| DT max. dist. | 2 | 36,00 | 35,5 | 36,5 |
| DT artic. dist. | 2 | 36,50 | 35 | 38 |
| DAP dist. | 2 | 42,50 | 42 | 43 |

| | <i>D. gr. pachygnathus/neumayri</i> | | min. | max. | éc.-type | coeff. var. |
|-----------------|-------------------------------------|--------|-------|-------|----------|-------------|
| | n | mean | | | | |
| Length | 8 | 148,31 | 138,5 | 166,5 | 9,047 | 6,10 |
| DT prox. | 8 | 48,62 | 43 | 53 | 3,148 | 6,47 |
| DAP prox. | 8 | 46,88 | 42,5 | 51 | 2,900 | 6,19 |
| DT dia. | 8 | 32,12 | 30 | 35 | 1,642 | 5,11 |
| DAP dia. | 8 | 29,00 | 24,5 | 32 | 2,790 | 9,62 |
| DT max. dist. | 8 | 41,12 | 37 | 45 | 2,615 | 6,36 |
| DT artic. dist. | 8 | 39,75 | 35,5 | 43 | 2,777 | 6,99 |
| DAP dist. | 8 | 42,75 | 40 | 45 | 1,927 | 4,51 |

| | ACERATHERES | | min. | max. | éc.-type | coeff. var. |
|-----------------|-------------|--------|-------|------|----------|-------------|
| | n | mean | | | | |
| Length | 10 | 131,40 | 117,5 | 144 | 9,021 | 6,87 |
| DT prox. | 11 | 40,95 | 37 | 44,5 | 2,079 | 5,08 |
| DAP prox. | 11 | 38,09 | 32,5 | 42,5 | 3,590 | 9,43 |
| DT dia. | 10 | 26,85 | 23 | 30 | 2,082 | 7,76 |
| DAP dia. | 10 | 24,85 | 21 | 28 | 2,212 | 8,90 |
| DT max. dist. | 9 | 31,56 | 29 | 34,5 | 1,976 | 6,26 |
| DT artic. dist. | 8 | 30,25 | 27,5 | 35,5 | 2,866 | 9,47 |
| DAP dist. | 10 | 35,15 | 31 | 37,5 | 2,484 | 7,07 |

Two central phalanges I:

| | AD 85'98 | AD 225'99 |
|-----------------|----------|-----------|
| Maximum height: | 51.5 | 51.5 |
| DT proximal: | 61 | 61 |
| DAP proximal: | 37.5 | 39.5 |
| DT diaphysis: | 52 | 52.5 |
| DT distal: | 53 | 53.5 |
| DAP distal: | 24.5 | 26 |

One lateral phalanx I:

| | AD 744'00 |
|-----------------|-----------|
| Maximum height: | 55 |
| DT proximal: | 44 |
| DAP proximal: | 39 |
| DT diaphysis: | 40 |
| DT distal: | 41 |
| DAP distal: | 29 |

Two abaxial phalanges II:

| | PQ AD 1836 | AD579'98 |
|-----------------|------------|----------|
| Maximum height: | 40 | 33.5 |
| DT proximal: | 61 | 58 |

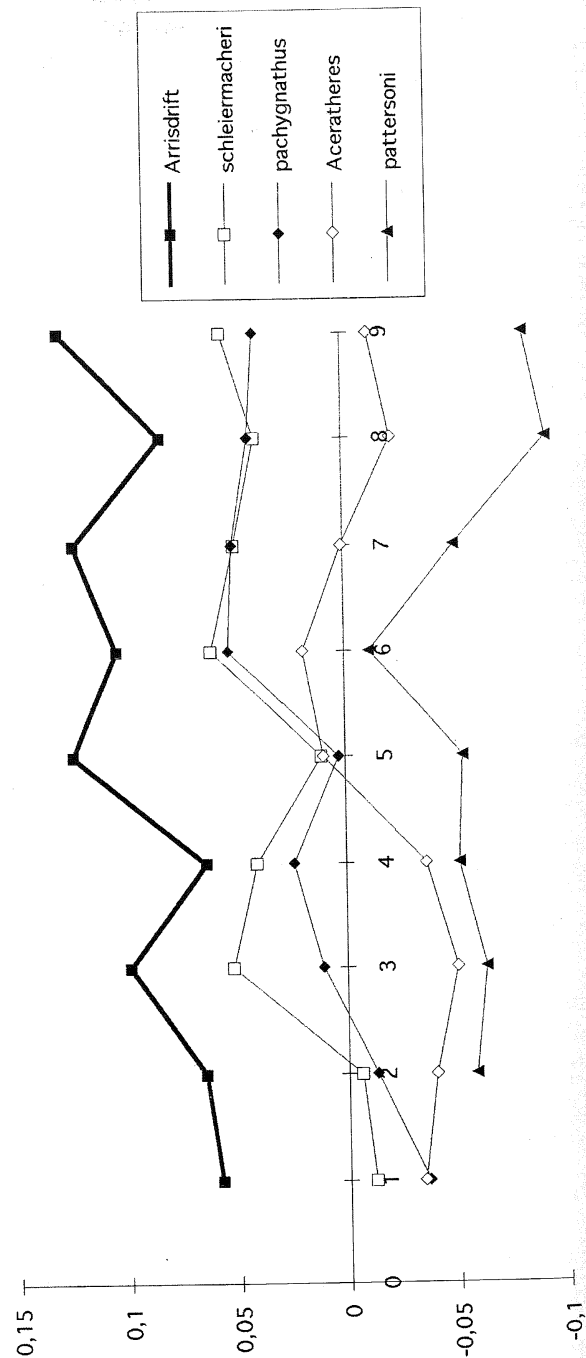


Figure 6: *Diceros australis*: Simpson diagram of the segments of the limbs compared with those of other Miocene rhinos. The reference is *Diceros bicornis*. 1: length of the ulna; 2: length of the radius; 3: length of Mc II; 4: length of Mc III; 5: length of Mc IV; 6: length of the tibia; 7: length of Mt II; 8: length of Mt III; 9: length of Mt IV.

| | | |
|---------------|------|------|
| DAP proximal: | 27 | 26.5 |
| DT diaphysis: | 49.5 | 48 |
| DT distal: | 51.5 | 46.5 |
| DAP distal: | 20.5 | 19 |

Other material. A patella (AD 580'98) is 115 mm high for a transverse diameter of 101.5 mm and an antero-posterior diameter of 54 mm.

Three sesamoids are preserved, as well as a dozen

vertebrae in poor condition or incompletely cleaned, which in their present state can only be identified to family.

Relations of the limb segments. A Simpson diagram of the limb segments (Fig. 6) shows once again many similarities with *Dicerorhinus schleiermacheri* and *Diceros gr. pachygnathus-neumayri*, with, in addition, a remarkable peculiarity: a much greater relative length of the abaxial metapodials with respect to the axial ones.

Affinities of *Diceros australis*

111 out of the 112 identifiable remains of rhinocerotids from Arrisdrift constitute a homogeneous sample which allowed the definition of *Diceros australis*. In comparison with the other rhinos from the Miocene of Africa, this species is characterised by the following:

- with the possible exception of *Kenyatherium*, of which the teeth are completely different, it is the largest of all;
- the size and proportions of the metapodials and long bones show clear similarities with *Diceros gr. pachygnathus-neumayri* of the Upper Miocene of the Near East, and to a lesser extent to *Dicerorhinus schleiermacheri* of the Upper Miocene of Western Europe;
- The morphology of the upper cheek teeth, notably P4/, is typical of Dicerotinae; these upper cheek teeth have great morphological and biometric resemblances to *Diceros douariensis* from the early Late Miocene of the Maghreb and Italy, the post-cranial skeleton of which is practically unknown.

- the morphology of the mandible has strong similarities to those of Dicerotinae, among others, the probable brevity of the symphyseal region. The same applies to other anatomical parts, such as, for example, the radius, calcaneum, etc...

- the i/2 which is very reduced could correspond to an evolutionary stage before the total loss of the anterior dentition.

It was the combination of these features that led me in 2000 to attribute the remains of the large rhinoceros from Arrisdrift to a new species of *Diceros*. In the present state of our knowledge it is the oldest known species of Dicerotinae; hitherto it was *Paradiceros mukirii*, of the latter part of the Middle Miocene of East Africa, which is a Dicerotinae but on a side branch. A hiatus of more than 7 Ma thus occurs between *Diceros australis*, of the basal Middle Miocene and *Diceros douariensis*, of the basal Late Miocene; it would be surprising if new discoveries don't fill this void.

Sub-family Chilotheriinae
Genus *Chilotheridium* Hooijer, 1971
Species *C. pattersoni* Hooijer, 1971

Diagnosis (the same for the genus and the species, after Hooijer, 1971) : Single small nasal horn in both sexes; weak premaxillae, no upper incisors; frontals and parietals pneumatized; the orbit is further from the skull roof than in *Chilotherium*; skull and occiput narrow; parietal crests not far from each other; pseudo-auditive meatus opens ventrally; symphyseal part of the mandible narrow, widening slightly anteriorly. Very hypsodont cheek teeth, as in *Chilotherium*, and with the same kind of construction: uppers with the paracone fold disappearing towards the

base, and the posterior part of the ectoloph flattened; protocone flattened on its internal side; anterior fold of the metaloph underlining the hypocone; anticrochet prominent at its base, recurving towards the interior at the entrance of the medisinus; crochet usually well developed, crista weak or absent; swelling of the metacone at the base of the M3/; strong anterior cingulum, weak lingual cingulum usually forming relief at the entrance of the medisinus. Lower tusk with subtriangular section, depressed dorsoventrally, with trenchant internal margin and with outer margin rounded below and keeled above. Scapula low and wide; limb bones very shortened; radius and ulna, as well as the tibia and fibula not fused; radius with a facet for the pyramidal; semilunar lacking radial facet; metacarpal V present and attaining 3/5 of the length of Mc IV; lateral metapodials slightly divergent towards the rear; small third trochanter in the femur; calcaneum lacking the tibial facet; navicular almost rectangular; cuboid wider than high; metatarsal III with a small cuboid facet.

Locus typicus and Stratum typicum: Loperot, volcano-sedimentary formation of Turkana Grit, Turkana District, Kenya; 17 Ma.

Other localities: Kirimum (15 Ma), Ngorora (12 to 11 Ma), Ombo (16 Ma) and Rusinga (18 Ma) in Kenya, and Bukwa (ca 17.5 Ma) in Uganda.

Holotype: Skull 2 (70-64K, B 12), fig. in D.A. Hooijer (1971) pl. 1.

Other specimens: The hypodigm corresponds to at least 8 individuals, the detailed list of which is given as an annex (p. 390-392) in D.A. Hooijer (1971).

Conservation: The material was collected by a team from the Harvard Museum of Comparative Zoology. It is currently in the National Museum, Nairobi, Kenya.

Material studied: A magnum AD 618'97 collected at Arrisdrift.

Description: By its morphology (Pl. 3, Fig 3), its size and proportions, this magnum is completely different from the one collected in the same locality and attributed to *Diceros australis*.

The dimensions are as follows:

| | |
|-----------------------|---------|
| Total length: | 91 mm |
| Anterior breadth: | 50 mm |
| Anterior height: | 27 mm |
| Maximum height: | 54.5 mm |
| Sub-articular height: | 52.5 mm |

Low and very wide, with an anterior surface that is flat and oblique, it has a width/height ratio (Fig. 2) opposite to that of *D. australis*, which reveals that we are in the presence of a small to medium sized species with short, strong feet, probably *Chilotheridium*, of which the type site is about the same age as Arrisdrift.

For 10 incomplete specimens of *C. pattersoni* from Loperot (Hooijer, 1971, Tabl. 14) the anterior height is slightly greater (30 to 33 mm) but the anterior breadth is slightly less (44 to 49 mm); these differences are not very significant, because they could result from geographic

variation, but more likely to a difference in measuring technique; whatever the case, they are the same order of magnitude.

Affinities: *Chilotheridium* is a monospecific genus and is the only Chilotheriinae known up to now in Africa. Its discovery at Arrisdrift increases its geographic range a great deal, hitherto being restricted to Kenya and Uganda. From the point of view of its stratigraphic distribution, it was limited to the Middle Miocene (it was known to occur between 18 and 11 Ma) but the recent discovery of a left Mc IV at Grillental (20 to 21 Ma) shows that the species also occurs in the lower Miocene.

Unidentifiable Rhinocerotidae from Auchas Mine

At Auchas Mine an atlas vertebra, still in its matrix, and a small fragment of mandible with several cheek teeth still covered in sediment were found during the excursion which followed the congress of the PSSA at Windhoek in 1998. As far as I can tell, the mandible appears to be close to the genus *Brachypotherium*.

Conclusions

Two of the Miocene vertebrate sites, Arrisdrift and Auchas Mine, excavated since 1991 by the Namibia Palaeontology Expedition are located in the Orange River Valley and have yielded remains of Rhinocerotidae.

The more important of the two is Arrisdrift, which is aged about 17 Ma and where 112 specimens of rhinos were collected, of which 111 constitute a homogeneous sample corresponding to a large cursorial Dicerotinae that I described in 2000 as *Diceros australis* nov. sp. This one, perhaps the largest species of rhino known up to now in Africa, is represented by teeth, mandibles, and all the elements of the postcranial skeleton, only the skull remaining unknown. The teeth, the mandible and the limb skeleton possess all the features of the sub-family; they show close morphological and biometric similarities with two species from the Late Miocene, *Diceros douariensis* from the Maghreb and Italy, and *Diceros* gr. *pachygnathus-neumayri* from the Near-East. *D. australis*, which is known only from the type locality, is at present the oldest known representative of the sub-family of Dicerotinae. Within this sub-family, it provides evidence of an evolutionary stage before that of species from the Late Miocene: lower tusks are still present but are vestigial and the limbs are not yet graviportal.

The only specimen from Arrisdrift which is not attributed to *D. australis* is a magnum corresponding in its morphology, size and proportions to a small to medium sized species with short legs. It is most likely to be a Chilotheriinae *Chilotheridium pattersoni*, first defined at Loperot in Kenya, which is similar in age to Arrisdrift, and known in five other East African sites and also recently discovered in the Sperrgebiet at Grillental, the latter specimen being the earliest known record of the species.

At Auchas Mine an atlas and a fragment of mandible were discovered; but being covered in sediment they cannot yet be identified.

From the point of view of the Rhinocerotidae, the works of the Namibia Palaeontology Expedition have thus led to the discovery of two localities in the Orange River

Valley of which the richest, Arrisdrift, has yielded abundant well preserved remains of a new species, *Diceros australis*. This is the oldest known representative of the sub-family of Dicerotinae, which is of considerable interest for understanding the history and evolution of the entire family Rhinocerotidae.

Acknowledgements

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References

- Aguirre, E., & Guérin, C., 1974 - Première découverte d'un Iranotheriinae (Mammalia, Perissodactyla, Rhinocerotidae) en Afrique: *Kenyatherium bishopi* nov. gen. nov. sp. de la formation vallésienne (Miocène supérieur) de Nakali (Kénya). *Estudios geológicos*. Madrid, **30**: 229-233.
- Geraads, D., 1986 - Sur les relations phylétiques de *Dicerorhinus primaevus* Arambourg, 1959, rhinocéros du Vallésien d'Algérie. *Comptes rendus hebdomadaires des séances de l'Académie des Sciences de Paris*. II, **302 (13)**: 835-837.
- Geraads, D., 1989 - Vertébrés fossiles du Miocène supérieur du Djebel Krechem el Artsouma (Tunisie centrale). Comparaisons biostratigraphiques. *Geobios*. Lyon, **22 (6)**: 777-801.
- Guérin, C., 1966 - *Diceros douariensis* nov. sp., un rhinocéros du Mio-Pliocène de Tunisie du Nord. *Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon*. **16**: 1-50.
- Guérin, C., 1976 - Les restes de rhinocéros du gisement miocène de Béni-Mellal, Maroc. *Géologie méditerranéenne*. Marseille, **3 (2)**: 105-108.
- Guérin, C., 1980a. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles. *Documents des Laboratoires de Géologie de Lyon*. **79 (1-3)**: 1-1185.
- Guérin, C., 1980b. A propos des rhinocéros (Mammalia, Perissodactyla) néogènes et quaternaires d'Afrique: essai de synthèse sur les espèces et sur les gisements. *Proceedings of the 8th. PanAfrican Congress of Prehistory and Quaternary Studies*. Nairobi, September, 1977, TILLMIAP edit., Nairobi, 58-63.
- Guérin, C., 1989 - La famille des Rhinocerotidae (Mammalia, Perissodactyla): systématique, histoire, évolution, paléocologie. *Cranium*. Rotterdam, **6(2)**: 3-14.
- Guérin, C., 1994 - Les Rhinocéros (Mammalia, Perissodactyla) du Néogène de l'Ouganda. In: B. Senut

& M. Pickford (eds), *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire*, vol. II: Palaeobiology, *CIFEG occasional publication* **29**: 263-279. Orléans.

- Guérin, C., (1999) - Chapitre 5: l'évolution des faunes, p. 143-198, biblio p. 381-385, 24 fig., in A. Gallay (ed.), *Comment l'homme? A la découverte des premiers Hominidés d'Afrique de l'Est*. Errance édit., Paris, 408 p.
- Guérin, C., 2000 - The Neogene Rhinoceroses of Namibia. *Palaeontologia africana*. **36**: 119-138, 9 fig., 13 Tabl.
- Guérin, C., & Demathieu, G., 1993 - Empreintes et pistes de Rhinocerotidae (Mammalia, Perissodactyla) du gisement pliocène terminal de Laetoli (Tanzanie). *Geobios*. Lyon, **26 (4)**: 497-513.
- Guérin, C., & Pickford, M., 2003 - *Ougandatherium napakense* nov. gen. nov. sp. Le plus ancien Rhinocerotidae Iranotheriinae d'Afrique. *Ann. Paléont.* **89(1)**: 1-35.
- Hamilton, W.R., 1973 - North African Lower Miocene Rhinoceroses. *Bulletin of the British Museum (Natural History)*. London, **24 (6)**: 351-395.
- Hamilton, W.R., & Van Couvering, J.A., 1977 - Lower Miocene Mammals from South West Africa. *Bulletin of the Desert Ecological Research Unit*. Oct. 1977: 9-11.
- Heinz, R., 1933 - Ein vorzeitlicher Tränkplatz in der Namibwüste bei Lüderitzbucht (Deutsch-Südwestafrika). *Mitteilungen der Geographischen Gesellschaft in Hamburg*. **XLIII**: 267-302.
- Heissig, K., 1971 - *Brachypotherium* aus dem Miozän von Südwestafrika. *Mitteilungen der Bayerische Staatssammlung für Paläontologie und historische Geologie*. München, **11**: 125-128.
- Hooijer, D.A., 1966 - Miocene rhinoceroses of East Africa. *Bulletin of the British Museum (Natural History)*. London, **13 (2)**: 119-190.
- Hooijer, D.A., 1968 - A rhinoceros from the late Miocene of Fort Ternan, Kenya. *Zoologische Mededelingen*. Leiden, **43 (6)**: 77-92.
- Hooijer, D.A., 1971 - A new rhinoceros from the late Miocene of Loperot, Turkana District, Kenya. *Bulletin of the Museum of Comparative Zoology*. Cambridge

(Mass.), **142 (3)**: 339-392.

- Hooijer, D.A., 1973 - Additional Miocene to Pleistocene rhinoceroses of Africa. *Zoologische Mededelingen*. Leiden, **46 (11)**: 149-178.
- Hooijer, D.A., 1978 - Rhinocerotidae, In: V.J. Maglio & H. B.S. Cooke (eds), *Evolution of African Mammals*, pp. 371-378, Harvard University Press, Cambridge (Mass.).
- Nakaya, H., Pickford, M., Yasui, K., & Nakano, Y., 1999 (daté de 1987) - Additional large mammalian fauna from the Namurungule Formation, Samburu Hills, Northern Kenya. *Afr. Study Monogr. Suppl. Issue*. **5**: 79-130.
- Pickford, M., & Senut, B., 1999 - Geology and Palaeontology of the Namib Desert, Southwestern Africa. *Mem. Geol. Surv. Namibia*. **18**: 1-155.
- Pickford, M., Senut, B., & Hadoto, D., 1993 - Geology and palaeobiology of the Albertine Rift Valley, Uganda-Zaire, vol. I: Geology, *CIFEG édit.*, Orléans, occasional publication **24**: 1-190.
- Pickford, M., Senut, B., Mein, P., Morales, J., Soria, D., Nieto, M., Ward, J., & Bamford, M., 1995 - The discovery of lower and middle Miocene vertebrates at Auchas, southern Namibia. *Comptes rendus hebdomadaires des séances de l'Académie des Sciences de Paris*. II a, **322**: 901-906.
- Pickford, M., Senut, B., Mein, P., Gommery, D., Morales, J., Soria, D., Nieto, M. & Ward, J., 1995 - Preliminary results of new excavations at Arrisdrift, middle Miocene of southern Namibia. *Comptes rendus hebdomadaires des séances de l'Académie des Sciences de Paris*. II a, **322**: 991-996.
- Prothero, D.R., Guerin, C., & Manning, E., 1989 - The History of the Rhinocerotidae, In: D.R. Prothero & R. M. Schoch (eds), *The Evolution of Perissodactyls*, pp. 321-340, (IVth Theriological Congress, Edmonton, Alberta, 1985), Oxford Univ. Press, New York.
- Stromer, E., 1926 - Reste Land- und Süßwasserbewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. In: E. Kaiser (ed.), *Die Diamantenwüste Südwestafrikas*, **2**: 107-153, Dietrich Reimer (Ernst Vohsen) A.D. édit., Berlin.

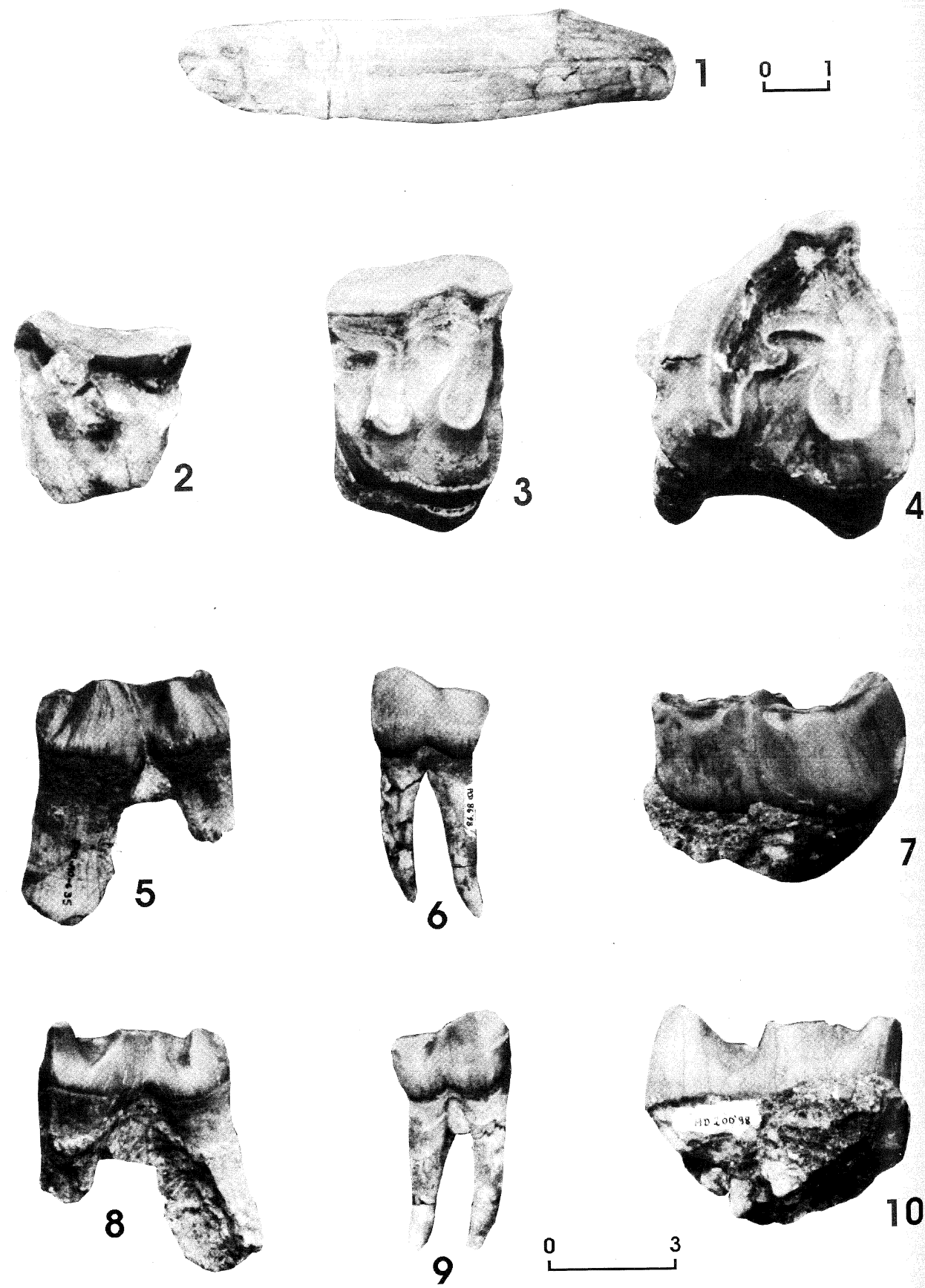


Plate 1: Isolated teeth of *Diceros australis* : lower tusk (i/2) AD 87'98 (photo V. Eisenmann); 2: left dm4/ AD 292'94; 3: right P4/ AD 578'98; 4: right M3/ PQ AD 339; 5 and 8: left dm3 PQ AD 635 (respectively in labial and lingual views); 6 and 9: left p2 AD 86'98 (respectively in labial and lingual views); 7 and 10: left m3 AD 200'98 (respectively in labial and lingual views). The scale is 1 cm for the tusk and 3 cm for the cheek teeth.



Plate 2: Axial metapodials of *Diceros australis* 1: Mt III AD 618'94, anterior view; 2: Mt III AD 618'94, posterior view; 3: Mc III AD 52'97, anterior view; 4: Mc III AD 52'97, posterior view. The scale is 3 cm.

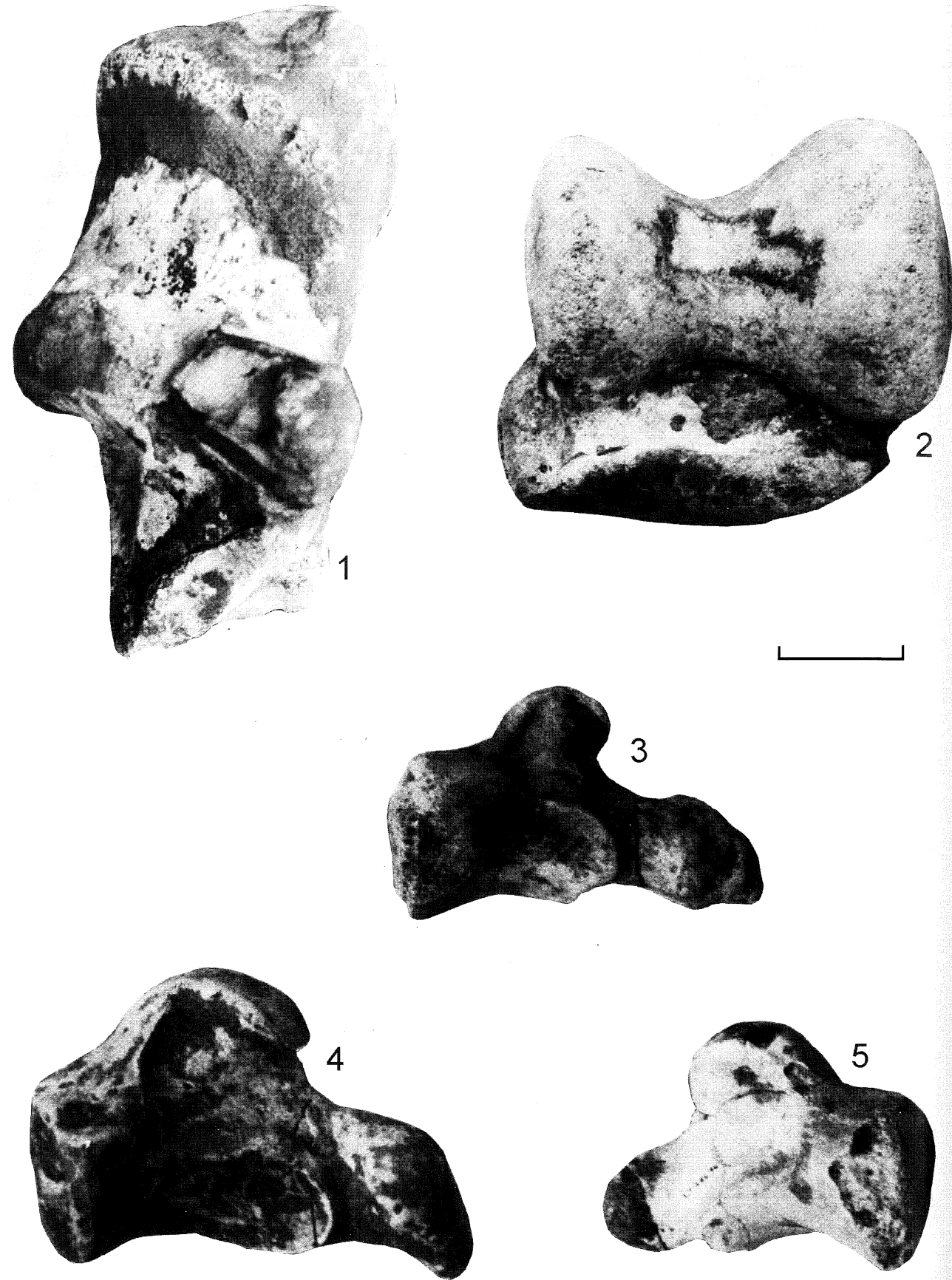


Plate 3: 1: right calcaneum (AD 50'97) of *Diceros australis*; 2: left astragalus (AD 619'94) of *Diceros australis*; 3-5: the three magnums of Miocene rhinos of Namibia: 3: cf. *Chilotheridium pattersoni* (AD 618'97), Arrisdrift, 4: *Diceros australis* (AD 638'97), Arrisdrift; 5: *Brachypotherium heinzlini* (LT 384'96), Langental. The scale is 3 cm.

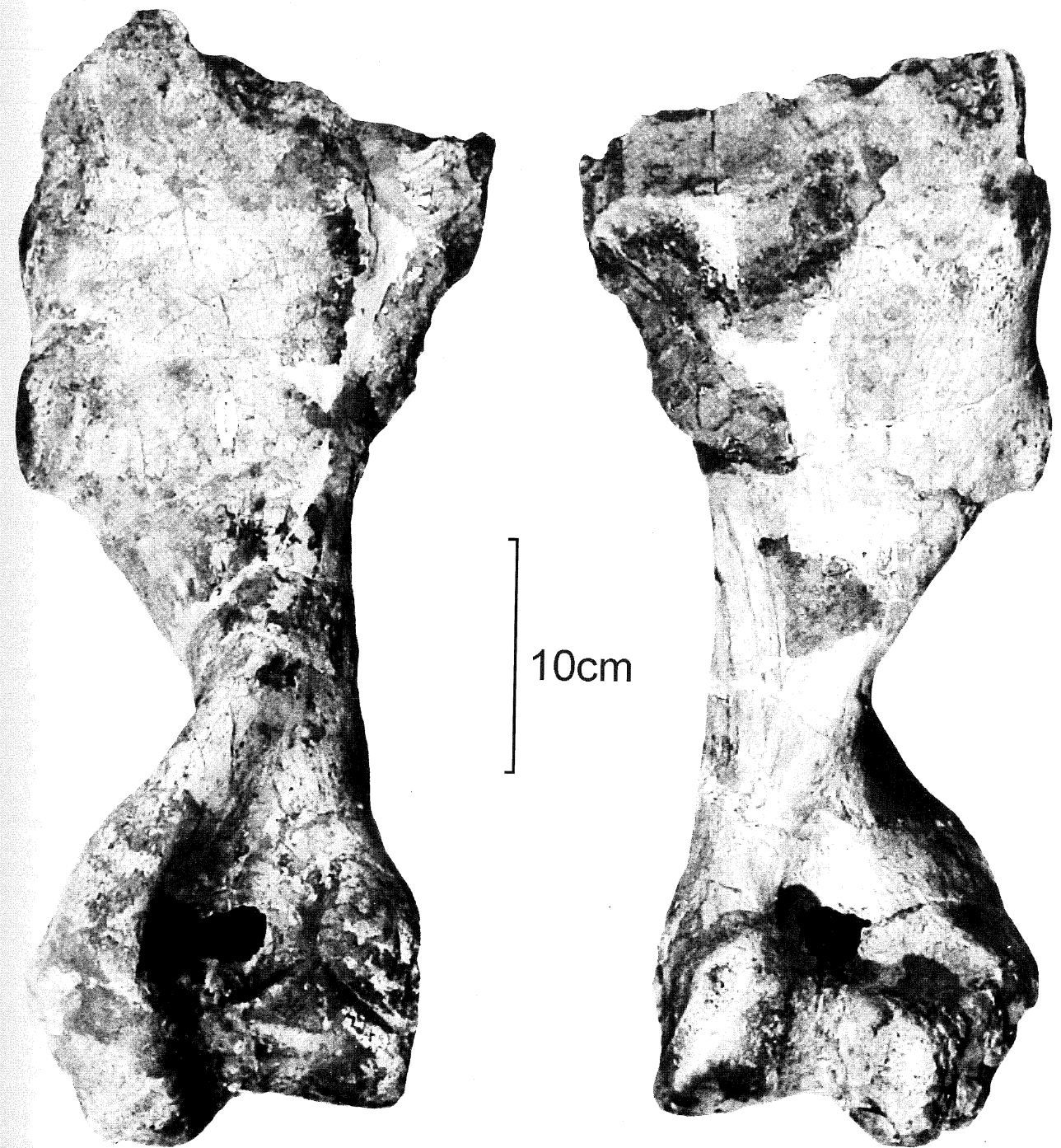


Plate 4: 1: left humerus (AD 736'00) of *Diceros australis*; anterior and posterior views.