New carnivores from the basal Middle Miocene of Arrisdrift, Namibia.

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ABSTRACT

The early Middle Miocene locality at Arrisdrift, Namibia, has yielded seven species of carnivores, comprising a giant creodont, two amphicyonids, a mustelid, a stenoplesictid and two felids. The mustelid, stenoplesictid and felids belong to new genera and one of the amphicyonids is a new species, while the other forms are similar to species already known from East Africa and Europe.

Comparisons of the Namibian fossils with those from other parts of Africa and Europe suggest that Arrisdrift correlates with Faunal Set P IIIa of East Africa (Pickford 1981) and the early part of MN04 of the European mammal zonation (ca 17–17.5 Ma) (Mein 1990).

ZUSAMMENFASSUNG

Die früh-mitteleozäne Lokalität Arrisdrift, Namibia, lieferte sieben Spezies von Carnivoren, bestehend aus einem Riesen-Creodonten, zwei Amphicyoniden, einem Musteliden, einem Stenoplesictiden und zwei Feliden. Der Mustelide, Stenoplestictide und die Feliden gehören zu neuen Gattungen. Einer der Amphicyoniden ist eine Spezies, während die anderen Formen Arten ähnlich sind, die schon von Ostafrika und Europa bekannt sind.

Vergleiche der namibischen Fossilien mit solchen aus anderen Gebieten von Afrika und Europa weisen darauf hin, dass Arrisdrift mit «Faunal Set P IIIa» von Ostafrika (Pickford 1981) und dem frühen MN04 der europäischen Säugetier-Zonierung (ca 17–17,5 Ma) (Mein 1990) korrelierbar ist.

1. Introduction

The early Middle Miocene site at Arrisdrift, Namibia (fig. 1), which was discovered in 1976 during diamond prospecting activities, yielded a rich and diverse fauna (Corvinus & Hendey 1978; Harris 1977; Pickford 1987) including four species of Carnivora (Hendey 1978). Recently, palaeontological study of the site has continued thanks to the support and encouragement of Namdeb Diamond Corporation (Pty) Ltd. (formerly Consolidated Diamond Mines (CDM) (Pty) Ltd).

The fossiliferous sediments occur in a 14 metre wide channel carved into bedrock to a depth of 2 metres, located some 150 metres east of the main channel of the Proto-Orange River. The infilling of this lateral channel consists of conglomerates, sands, silts and clays with gypsum, deposited in a complex cut-and-fill sequence. The clay layers are thin and appear to be clay drapes of the sort that settle out of quiet water, while the cut-and-fill character of the succession indicates that the infilling was subjected to erosion from time to time, each episode of erosion being followed by deposition of new sediment.

It is most likely that the Arrisdrift channel only occasionally had water flowing through it, perhaps on a seasonal basis when the Proto-Orange overtopped its principal channel.

Fossils are scattered throughout the channel fill, the average grade of the deposit being 50 fossils per cubic metre. There is no obvious bone-bed or horizon at which the fossils occur. Many of the fossils have been reworked locally from a pre-existing deposit, while some of them are in their primary burial context. However, the reworked faunal elements consist of the same species as those in primary context, and consequently, there is not a great deal of time difference between the two assemblages. The surfaces of many of the fossils are cracked, suggesting that they were exposed to the sun prior to being buried, while several of the larger mammal bones have tooth marks of the sort made by crocodiles.

Some of the carnivores described here were collected in 1976–1978 by Corvinus (1978), while preliminary descriptions and interpretations were published by Hendey (1978). New

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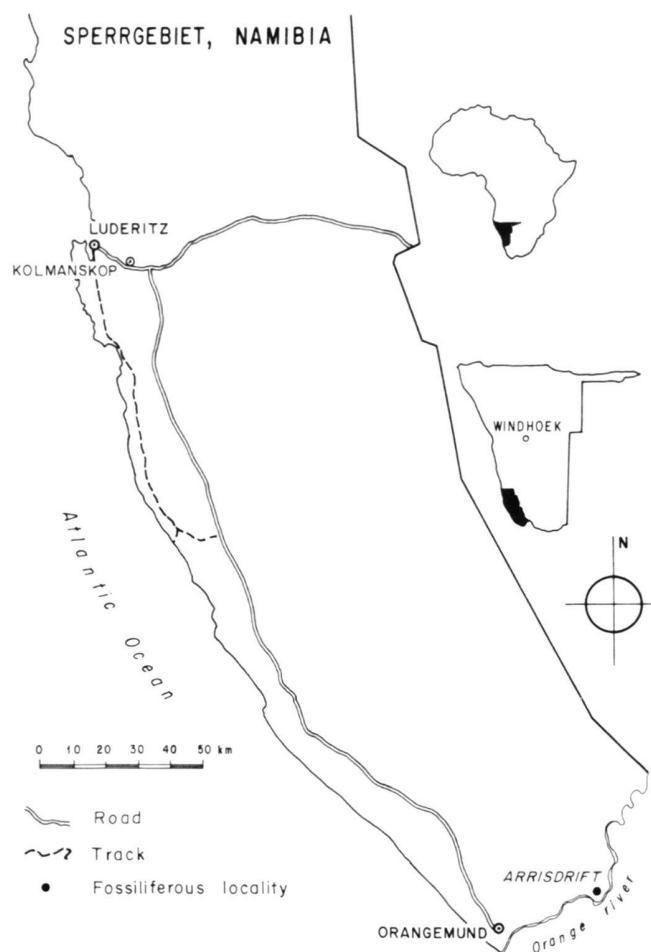
Fig. 1. Location of Arrisdrift, an early Middle Miocene site in Southern Namibia.

Fig. 2. AD 375'94, P^4, *Hyainailourus sulzeri*, A, lingual view. B, buccal view. C, occlusal view.

material, including the first creodont from the site, was unearthed by the Namibia Palaeontology Expedition in 1994 and 1995. The material studied is currently housed in the Museum of the Geological Survey of Namibia (Windhoek, Namibia).

2. Systematic palaeontology

Order Creodonta Cope 1875
Family Hyaenodontidae Leidy 1869
Genus *Hyainailourus* Biedermann 1863
Species *Hyainailourus sulzeri* Biedermann 1863

Material: AD 375'94, fragment of right maxilla with unworn M^1 (measurements: L(Length)=35.2 mm, W(Width)=23 mm), figure 2.

Description

M^1 with moderate parastyle, paracone high, wide and subdivided at its tip. Metastyle reduced, much smaller than the paracone. Protocone located anterior to the paracone, but slightly behind the parastyle, with the cusp in the shape of a horseshoe separated from the paracone by a valley. Cingulum only at the base of the parastyle.

Discussion

This tooth is extremely similar to its homologue in *Hyainailourus sulzeri* (Ginsburg 1980; Azanza et al. 1993) and to that of *Pterodon napakensis* (Savage 1965; Ginsburg 1980). Both these forms possess similar sized molars, especially if we take into account the fact that the creodonts display strong interspecific size variability in their dentition, which can reach values of nearly 100%.

Morphologically the differences between the above two species are minor, and it is possible that they belong to a single species. Nevertheless, the Arrisdrift M^1, as in *H. sulzeri*, possesses a protocone which is more individualised and located further to the rear than in the molar of *P. napakensis*, and its external wall, even though it is more rectilinear than in the European form, does not attain the almost flat profile seen in *P. napakensis*. In addition, the parastyle of the Arrisdrift molar is clearly more developed than in *P. napakensis*, a further feature that allies it with *H. sulzeri*.

Fig. 3. AD 133, holotype mandible of *Ysengrinia ginsburgi* sp. nov. A, buccal view. B, lingual view. C, occlusal view of cheek teeth.

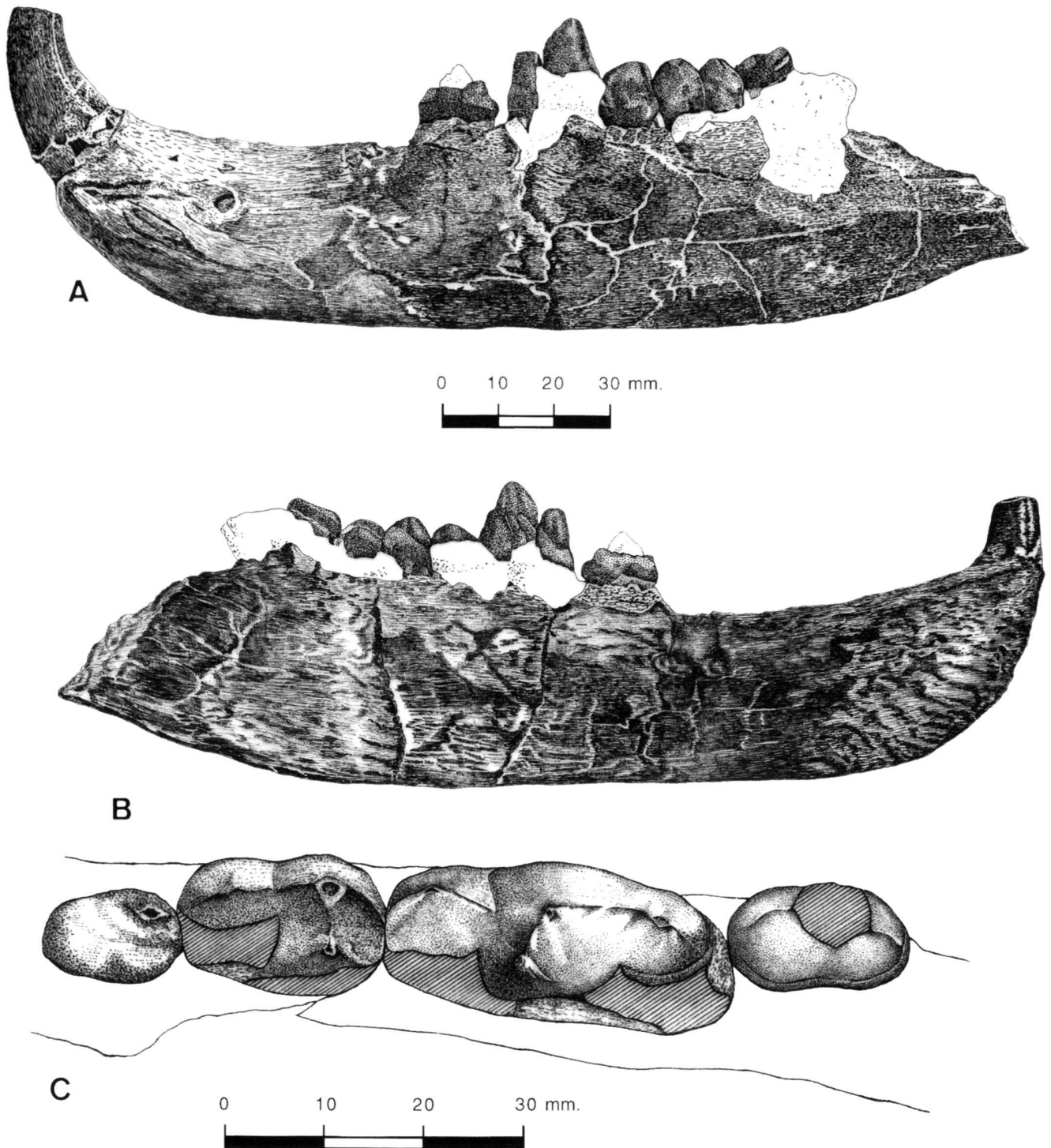Suborder Fissipeda Blumenbach 1791
Family Amphicyonidae Trouessart 1885
Genus *Ysengrinia* Ginsburg 1966a
Species *Ysengrinia ginsburgi* sp. nov.

Previous identification: *Amphicyon* cf. *steinheimensis* (Hendey 1978)

Holotype: AD 133, left mandible, figure 3.

Type locality: Arrisdrift, Namibia.

Age: Basal Middle Miocene, Faunal Set P IIIa (Pickford 1981) (= MN04a, Mein 1990).

Derivatio nominis: In honour of Dr Leonard Ginsburg.

Diagnosis

Ysengrinia of large size; M_1 larger than M_2; metaconid of M_1 reduced; Paraconid of M_2 lost; Protocone of P^4 reduced.

Differential diagnosis: *Y. ginsburgi* differs from *Y. gerandiana* (Viret 1929; Kuss 1965; Ginsburg 1966a) and from *Y. valentiana* (Belinchon & Morales 1989) by its larger size. It differs from *Y. gerandiana*, which is better known than *Y. valentiana* by the greater reduction of the M_1, the loss of the paraconid of M_2, and the larger size of M_1 with respect to M_2.

Description

AD 604'94 is a right maxilla with P^3–M^1 and a single alveolus for the anterior root of M^2 (Fig. 4). A small diastema occurs between P^3 and P^4. The infraorbital foramen is located above the gap between P^3 and P^4.

P^3 (L=11.5 mm, W=6.1 mm) very reduced, formed of a single, relatively low cusp.

P^4 (L=25.5 mm, W=13 mm) has no parastyle. The protocone is greatly reduced, being barely a bump with no sign of a definite cusp. The internal cingulum is strong. The paracone is very voluminous, with a clearly defined anterior crest which is interrupted at mid height by an incision. The metastyle is short. There is a horizontal wear facet on the paracone and a vertical one on the interior face of the metastyle.

M^1 (L=21.7 mm, W=26.5 mm) has a strong external cingulum at the base of the metacone, less strong at the base of the paracone. The paracone is larger than the metacone. The metastyle is high and well marked, whereas the parastyle is weaker. The paraconule and metaconule are similar in size, each backing onto a dune-shaped protocone. The central valley of the trigon is deep. The protocone is separated from the well developed internal cingulum by a deep slit. Wear facets are horizontal on the paracone and metacone, and vertical on the antero-internal face of the paracone and internal surface of the metacone.

AD 606'94 is an edentulous right maxilla with the alveoli of C-M^2. In terms of size this specimen is very similar to the one described above. The anterior margin of the alveolus of the canine is damaged, so measurements cannot be taken. P^1 (L= 5.5 mm); P^2 (L= 9.2 mm); P^3 (L= 11 mm); P^4 (L= 26.5 mm); M^1
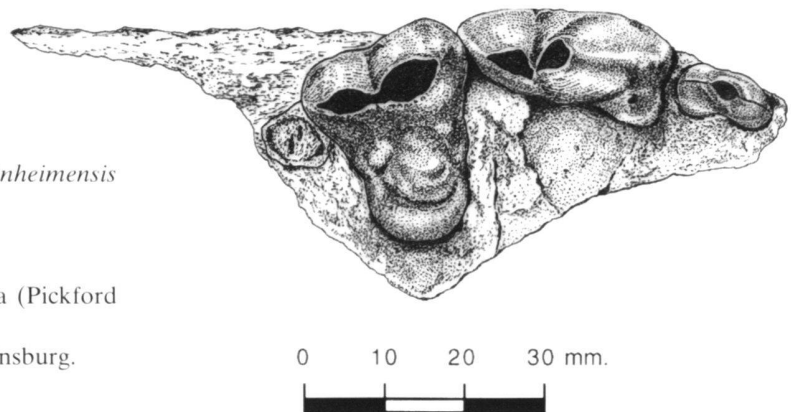

Fig. 4. AD 604'94, maxilla with P^3 – M^1 of *Ysengrinia ginsburgi*, sp. nov. Occlusal view.

(L=20.5 mm, W=29 mm); M^2 (L=14 mm, W=26 mm). This specimen enables us to infer than the M^2 is rather large.

Holotype AD 133 (fig. 3 a–c) is a left mandible with broken ascending ramus. The symphysis is extensive with a rugose surface. The horizontal ramus is high (the height at the anterior margin of P_3 is 32 mm and below M_1 is 38.5 mm). Two foramina occur in the mandible, one level with the gap between P_1 and P_2, the other below the P_3.

The canine (L=15.7 mm, W=10 mm) possesses a clearly feloid outline, with two well marked crests, one posterior, the other lingual.

All the premolars are separated from each other by diastemata. The anterior ones are more developed than the posterior ones. Only the alveoli of P_1 and P_2 are preserved. They are small, uniradiculate in P_1 and two-rooted in P_2. The P_3 is broken and only the roots are preserved in the alveoli.

P_4 (L=14.5 mm, W=8 mm) has its main cusp broken. There is a low anterior accessory cusplet and a slightly higher posterior accessory cusplet. The two cusplets are similar to each other in appearance. The internal cingulum is strong.

M_1 (L=27.2 mm, W=12 mm; L trigonid=17.5 mm, 64% of the total length, protoconid height = 18.5 mm) is a relatively short tooth, with high trigonid and talonid. The paraconid is almost vertical and narrow, the protoconid is very high and is also narrow. The metaconid is close to the protoconid and is relatively small. The talonid is rather eroded in the region of the entoconid, so that all that can be said is that it is dominated by the high, narrow, hypoconid which occupies almost all the talonid. There are three wear facets, all of which are vertical, located on the posterior surface of the paraconid, the anterior face of the protoconid and the anterior aspect of the hypoconid.

M_2 (L=17 mm, W=11.5 mm; L trigonid= 8.9 mm, 52% of the total length; height of the protoconid = 11 mm) is a relatively small tooth compared with M1. The external wall is high
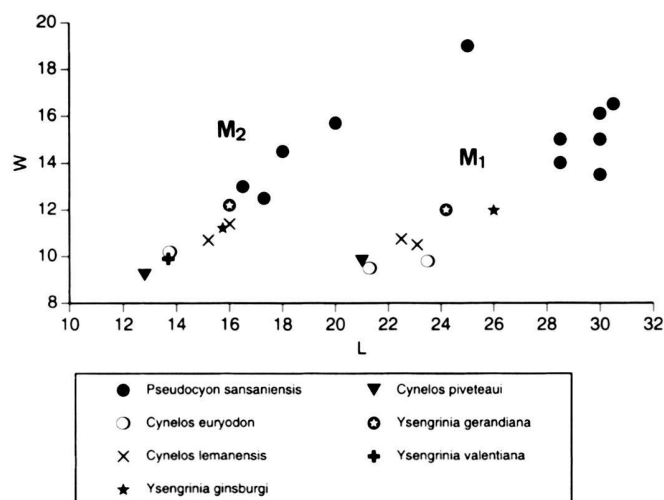
Fig. 5. Length-Width plot of M_1 and M_2 of various amphicyonids. Measurements: *Pseudocyon sansaniensis* and *Cynelos lemanensis*, Kuss (1965); *Cynelos euryodon*, Savage (1965) and Schmidt-Kittler (1987); *Cynelos piveteaui*, Ginsburg (1966b); *Ysengrinia valentiana*, Belinchón & Morales (1989).

Fig. 6. Proportion plot of length of M_1 – length M_2 for various amphicyonids. Measurements: *Pseudocyon sansaniensis* and *Cynelos lemanensis*, Kuss (1965); *Cynelos euryodon*, Savage (1965) and Schmidt-Kittler (1987); *Cynelos piveteaui*, Ginsburg (1966b).

and vertical while the lingual one is lower. The trigonid has no paraconid and is dominated by a large, high protoconid located in front of the metaconid. There is a low antero-internal valley in the anterior part of the trigonid. As in M_1, the region of the entoconid is eroded, but it is possible to observe that the talonid is comprised predominantly of an enormous hypoconid. The posterior margin of the talonid is narrow. There is a small horizontal wear facet at the tip of the protoconid and a vertical one on the external border of the hypoconid.

M_3 (L=10.6 mm, W=8 mm) has low relief, is relatively small and quite wide.

Discussion

The genus *Ysengrinia* was created by Ginsburg (1966a) for the species from Saint-Gérand-le-Puy previously identified as *Pseudocyon gerandianus* by Viret (1929), and which Kuss (1965) had included in *Pseudocyonopsis landesquei. Y. ginsburgi* differs from the species of the genus *Cynelos (C. lemanensis, C. euryodon)* by is greater size, the better developed hypoconid in the lower molars, the weaker metaconid of M_1, reduction of the paraconid of M_2 (very reduced in some specimens of *C. lemanensis* from Saint-Gérand-le-Puy), greater size of the M^1 compared to M^2 and the protocone of P^4 more reduced (Figs 5, 6).

There is no doubt that some of the characters that differentiate *Y. ginsburgi* from *Cynelos* occur in the genus *Pseudocyon*. For example, the reduction of the metaconid in M_1, reduction of the protocone of P^4 or the presence of a well developed hypoconid in the talonid of M_1 and M_2, occur in *Pseudocyon*

sansaniensis from Saint-Gérand-le-Puy (Viret 1929, pl. 3, fig. 1–6). However, the dentition of *Y. ginsburgi* is more gracile, and because of that is more sectorial. The P_4 is less reduced and the external wall of the protoconid of M_2 is vertical, not expanded towards the exterior as in *Pseudocyon*. In summary, *Ysengrinia* possesses a more hypercarnivorous dentition than *Pseudocyon*, which is clearly observed in the new species from Arrisdrift.

Genus *Amphicyon* Lartet 1836
Species *Amphicyon giganteus* (Schinz) 1825

Previous identification: Amphicyonidae gen. et sp. indet. Hendey (1978)
Material available: AD 1520, right mandible with P_4–M_2, figure 7.

Description

This mandible was described by Hendey (1978). The horizontal ramus is robust and there is no premasseteric fossa. The as-

Fig. 7. AD 1520, mandible of *Amphicyon giganteus*, A, buccal view. B, occlusal view to show heavy wear and abrasion of the cheek teeth.

cending ramus is very long antero-posteriorly, with a deep and vast masseteric fossa. Despite the large size of the premolars, in particular the P_3 and P_4, there is an alveolus for a single-rooted P_1 separated by a diastema from P_2, whereas there are no gaps between the rest of the dental series. The P_4 (L=21.3 mm, W=14.3 mm) is a large tooth with a robust main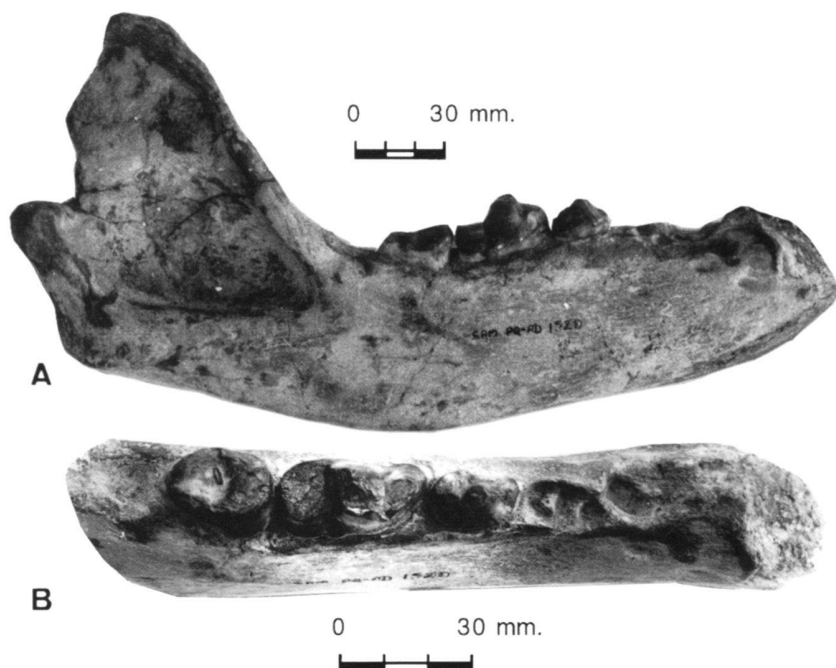 cusp, behind which is an appreciable posterior accessory cusplet. The two molars – M_1 (L=35.5 mm, W=19 mm), M_2 (L=26.5 mm, W=21.5 mm) – which, as in the fourth premolar, have been heavily worn, are robust teeth. In the M_2 it is possible to observe that the labial wall is expanded towards the external side. There is a large alvelous for M_3.

Discussion

The identification of this jaw as *Amphicyon giganteus* is based on the following considerations; it differs from large Hemicyoninae such as *Hemicyon-Dinocyon* by the absence of premasseteric fossa a feacture typical of these genera (Colbert 1939). It differs from *Amphicyon major* of the Middle Miocene of Europe, which is of similar size, by the greater size of the premolars and the absence of diastemata between them. The tendency towards reduction of the premolars and the development of diastemata between them seems to have been a general trend in all the Amphicyonidae and Ursidae during the Middle Miocene.

The combination of an amphicyonid dentition with absence of premolar reduction, absence of diastemata between the three posterior premolars and large size, occurs in *Amphicyon giganteus,* and for this reason we feel confident in identifying the Arrisdrift fossil as this species.

Family Mustelidae Swainson 1835
Subfamily Mustelinae Fischer 1817
Genus *Namibictis* gen. nov.
Species *Namibictis senuti* sp. nov.

Previous identification: *?Ischyrictis* sp. Hendey (1978).
Holotype: AD 614, right mandible, figure 8.
Type locality: Arrisdrift, Namibia.
Age: Basal Middle Miocene, Faunal Set P IIIa (Pickford 1981) (= MN04a Mein 1990).
Derivatio nominis: In honour of Dr Brigitte Senut.

Diagnosis

Mustelinae with hypercarnivorous dentition. Lower canine with very high crown, lower premolars and M_1 mediolaterally compressed, and as such rather sectorial, P_4 with high crown. M_1 with a vertical paraconid, a residual metaconid, a small talonid comprised of a bevelled hypoconid.

Differential diagnosis: *Namibictis* differs from *Ischyrictis, Hoplictis* and *Iberictis,* the more hypercarnivorous members of the family Mustelidae, by the greater height of the P_4 and of the protoconid of the M_1, and by the construction of the talonid in M_1 which is bevelled and sectorial.

Description

The canine is partly destroyed, but has a high crown with an anterior crest and a smooth basal cingulum. The alveolus for P_1 is uniradiculate (L=2 mm). P_2 (L=5.8 mm, W=3 mm) and P_3 (L=6.7 mm, W= 3.3 mm) are similar in size and morphology,
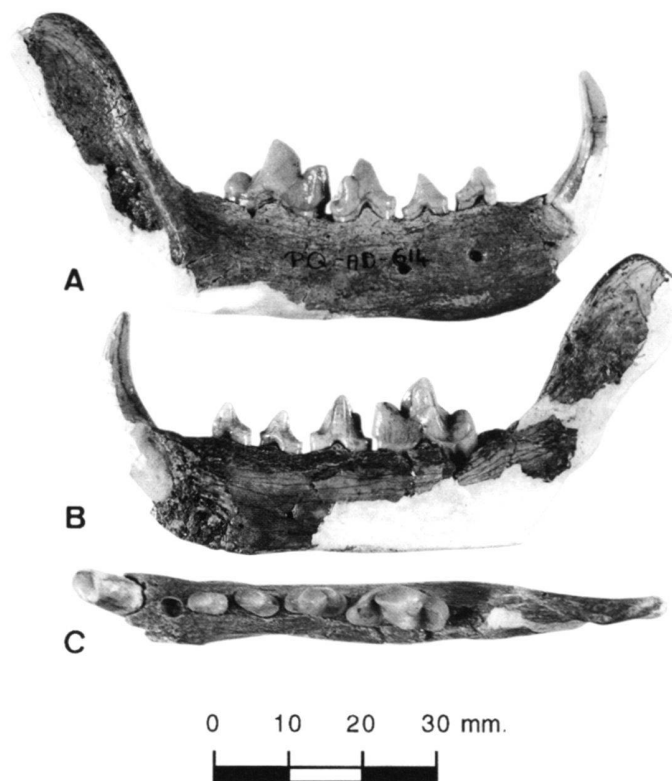
Fig. 8. AD 614, mandible of *Namibictis senuti* gen. et sp. nov. A, buccal view. B, lingual view. C, occlusal view.

Fig. 9. Comparison of right M_1s of a) *Iberictis buloti*, b) *Ischyrictis bezianensis* and c) AD 614, *Namibictis senuti* gen. et sp. nov. Occlusal view.

and possess a single, relatively low cusp and an enlarged posterior talonid without, however, any accessory cusplets. P_4 (L=9.2 mm, W=4.1 mm) has a high and narrow main cusp, with a posterior accessory cusp and a rather elevated talonid, while there is a smooth lingual cingulum. M_1 (L=14.6 mm, W=6.1 mm) has an almost vertical paraconid, its protoconid is very high, and it has a reduced metaconid. The talonid is comprised only of a hypoconid located close to the labial margin of the tooth and which descends as a bevel towards the centre of the talonid. There is no entoconid. Indeed where this cusp is usually situated there is a low valley open lingually.

Discussion

This form was identified by Hendey (1978) as being close to *Ischyrictis*. However, detailed examination reveals that the similarities between the two genera are superficial (dental formula, small, uniradiculate P_1, P_2 and P_3 small in comparison with P_4, sectorial, elongated, M_1 with a short and sectorial talonid), and the same could be said of genera close to *Ischyrictis* such as *Iberictis* and *Hoplictis* (Fig. 9). From all these, the Arrisdrift species differs by its more sectorial dentition, which is particularly expressed in P_4–M_1, both of which have high narrow cusps.

The construction of the talonid of M_1 in *Namibictis* is completely different from that observed in all these other genera, in which the talonid is always wider with a well defined, conical, hypoconulid and a crest-like entoconid. The same can be said for the height and morphology of the P_4, which in the above genera is always lower with a reduced anterior cuspid, differences which were noted by Hendey (1978) who considered that these characters of the Arrisdrift mustelid were primitive. Forms such as *Paragale huerzeleri* of the Lower Miocene of Saint-Gérand-le-Puy (Petter 1967), despite the differences in size, show a construction of the P_4 and M_1 which is relatively close to that of the Arrisdrift mustelid. *P. huerzeleri* possesses a high P_4 with a well developed anterior cuspid and its M_1 has a high protocone and a vertical paraconid, all characters found in the Arrisdrift species. However, the talonid is formed of an isolated hypoconid, surrounded by a high posterior cingulum,

Fig. 10. AD 1791, maxilla with P³ – M¹, holotype of *Africanictis meini* gen. et sp. nov. A, occlusal view (stereopar). B, buccal view.

quite different from the single bevelled hypoconid in the Arrisdrift specimen, and in both forms there is no entoconid, the position of which is taken by a very low wall. Another species with an M_1 similar to that of *Paragale huerzeleri*, and thus closer to the Arrisdrift form, is *Mellalictis mellalensis* described by Ginsburg (1977)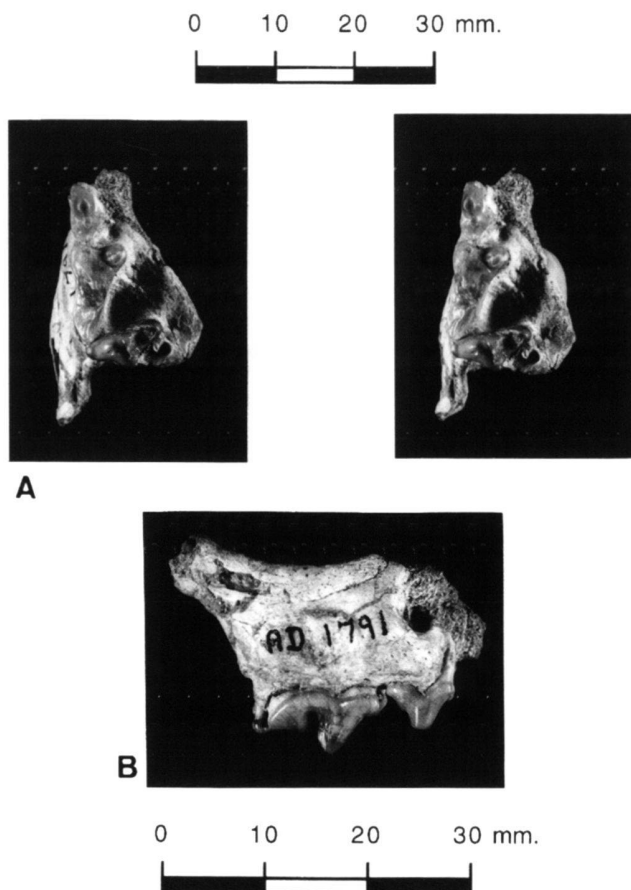 from Beni Mellal (Morocco), which is intermediate in size between the species from Saint-Gérand-le-Puy and Arrisdrift. The construction of the talonid of its M_1 is clearly similar to that of *P. huerzeleri*. Everything indicates that the simple, sectorial talonid is a character confined to the new genus, and that it was probably derived from forms closely related to *Paragale,* and that it represents an evolutionary convergence with felines.

Family Stenoplesictidae Schlosser 1923
Genus *Africanictis* gen. nov.

Type species: *Africanictis meini* sp. nov.
Other species: *Africanictis schmidtkittleri* sp. nov.

Diagnosis

Stenoplesictidae of the size of the primitive European Miocene hyaenid *Protictitherium crassum.* P_1 reduced, premolars high and narrow, M_1 with high trigonid and short talonid with a small hypoconid. P^4 narrow and elongate, with strong parastyle and conical protocone. M^2 small (unknown in *A. schmidtkittleri*). M^1 with well developed parastylar area, shortened in the type species.

Differential diagnosis: *Africanictis* differs from *Protictitherium* by the presence of higher and narrower premolars, and the trigonid of M_1 which in addition does not possess an entoconid in contrast to the strength of this cusplet in *P. crassum* and primitive species of the family Hyaenidae. In the upper dentition, it differs from the European genus by the strength of the parastyle and the pointed morphology of the protocone of P^4, and by the reduction of the M^2. It differs from *Semigenetta* by the retention of M^2 and the parastyle of P^4 better developed and simple. There is also a posterolingual expansion of the P^3 (present only in the most primitive species of *Semigenetta,* such as *S. laugnacensis*. It differs from *Stenoplesictis* by its narrower and longer P^4, with a more strongly developed parastyle and the tendency to shorten the M^1. It differs from the latter two genera by the larger size of the M_2.

Species *Africanictis meini* sp. nov.

Holotype: AD 1791, fragment of maxilla with P^3–M^1 and alveolus for the M^2 , figure 10.
Type locality: Arrisdrift, Namibia.
Age: Basal Middle Miocene, Faunal Set P IIIa (Pickford, 1981), (= MNO4a of Europe, Mein 1990).
Derivatio nominis: In honour of Dr Pierre Mein.

Diagnosis

Africanictis of large size. M^1 shortened.
Additional material: AD 100'95, left mandible with M_1; AD 100'95, right mandible with P_2–M_1 (figure 11).

Description

AD 1791 is a maxilla with P^3–M^1 and the alveolus for M^2. The P^3 (L=7.3 mm, W=3.9 mm) possesses an elevated main cusp, a small anterior cusplet and a slightly larger posterior cusplet, a weak posterior cingulum and a well marked posterolingual basal expansion. P^4 (L=12 mm, W=6.5 mm) is feloid in morphology; the parastyle is present, even though small; the protocone is moderate in size and conical in shape, and is located anterior to the parastyle. The M^1 (L=5 mm, W=9.5 mm) is subtriangular in occlusal outline, with a strong external projection of the parastylar area; the metacone and paracone are crest-like and the protocone is horseshoe shaped. The central valley is deep.
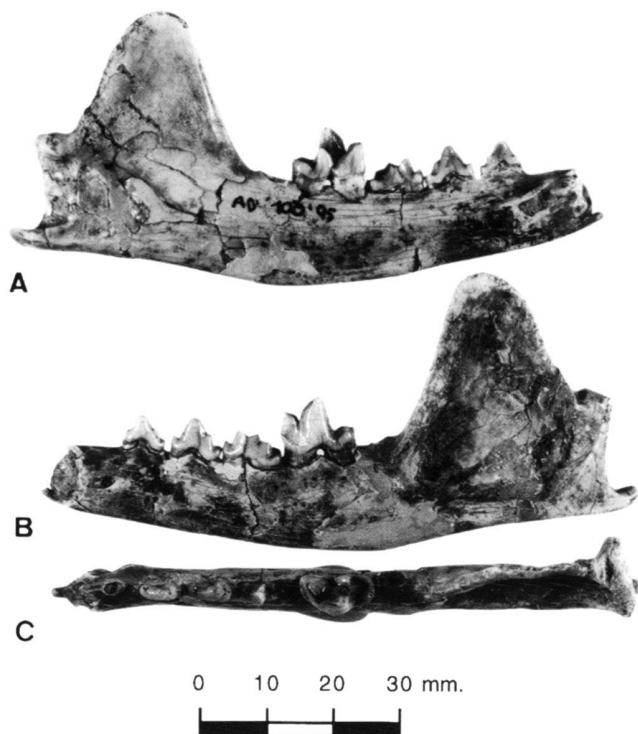
Fig. 11. AD 100'95, mandible of *Africanictis meini* gen. et sp. nov. A, lingual view. B, buccal view. C, occlusal view.

The P_1 of right mandible AD 100'95 is represented by a uniradicular alveolus. The P_2 (L=6.2 mm, W=2.5 mm) consists of a large, robust main cusp, a low, small anterior cusplet and a higher but small posterior cusplet, and a clearly defined posterior cingulum. The P_3 (L=7.5 mm, W= 3.1 mm) and P_4 (L=8.5 mm, W=4 mm) are larger versions of the P_2 but with the main cusp not as salient in comparison with the higher accessory cusplets and the better developed cingulum. In addition, in the lingual part of the cingulum of P_4 there is a small cuspid. The M_1 (L=11 mm, W=6 mm) possesses a high trigonid dominated by the protoconid which is notably higher than the paraconid and the metaconid is strong and is located at the base of the protoconid, without extending beyond it posteriorly, and forming with it a vertical plane which clearly separates the trigonid from the talonid. The talonid is short and consists of a very strong hypoconid which reaches posteriorly as a high posterolingual crest which possesses no signs of an entoconid.

The mandible is gracile in its anterior part, tending to thicken behind the P_4–M_1. The masseteric fossa is strongly developed and deep but does not extend anteriorly beyond the level of the alveolus of M_2.

The left mandible, AD 500'95 is slightly smaller than the specimen described above, but possesses the same morphology. The M_1 (L=10.5 mm, W=5.2 mm) is also slightly smaller than its counterpart in AD 100'95.

Species *Africanictis schmidtkittleri* sp. nov.

Previous identification: Viverridae nov. sp. (Schmitd-Kittler 1987).
Holotype: KNM CA 303, P4 described and figured by Schmidt-Kittler (1987, fig. 35).
Type locality: Chamtwara, Kenya
Age: Lower Miocene, Faunal Set P I (Pickford 1981), ca 20 Ma.
Derivatio nominis: In honour of Dr Norbert Schmidt-Kittler.

Diagnosis

Africanictis of small size with small parastyle in P^4 and a subtriangular M^1.
Differential diagnosis: *A. schmidtkittleri* differs from *A. meini* by being smaller overall, by the relatively smaller parastyle of its P^4 and its larger M^1, all characters that we consider to be primitive.

Discussion

Schmidt-Kittler (1987) identified this form as Viverridae nov. sp. on the basis of the peculiar association of characters that he observed in it. He considered that the M^1 and P^4 available to him belong to the same species, with which we concur. The morphology of the Chamtwara P^4, as well as that of the Arrisdrift specimen, separates this form as much from primitive hyaenids of the *Protictitherium* kind as from primitive viverrids, by the diminution of the height of the protocone and its more conical morphology, which, as was pointed out by Schmidt-Kittler (1987), could be considered a feloid specialisation. In contrast, the retention of M^1 with typical viverroid characters is not strange if one considers that it appears to be common in all the modern Feloidea (Felidae, Viverridae and Hyaenidae).

However, the size and general appearance of the mandibles approaches those of the primitive hyaenid of the Middle and Upper Miocene of Europe, *Protictitherium crassum.* Nevertheless, a detailed examination reveals that the differences between the Arrisdrift stenoplesictid and *Protictitherium* are marked. Thus the premolars are less robust in *Africanictis*, with lower main cusps. But, above all, the structure of the M_1 is very different, with the trigonid being very high with respect to the talonid, the metaconid less weakly developed and the absence of an entoconid, which in European hyaenids is almost the same size as the metaconid. This entoconid is present in the form described by Dehm (1950) as *Progenetta praecurrens* from the locality of Wintershof-West, belonging to the *Protictitherium* lineage, and in the more primitive *Herpestides antiquus* from Europe (Beaumont 1967) and *Herpestides aequatorialis* from Kenya (Schmidt-Kittler 1987). Thus, because many of the characters of the new African genus can be considered as primitive and would therefore be
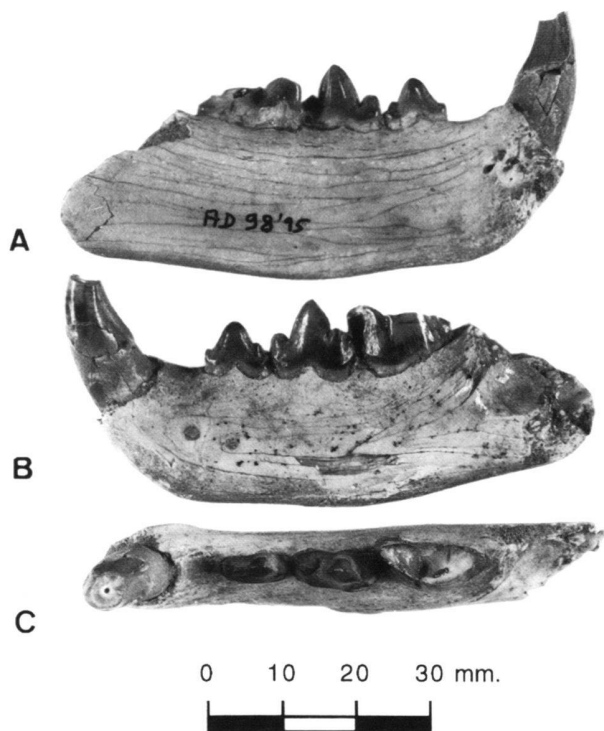
Fig. 12. AD 98'95, mandible with canine and cheek teeth, holotype of *Diamantofelis ferox* gen. et sp. nov. A, lingual view. B, buccal view. C, occlusal view.

0 10 20 30 mm.

dentition of *Percrocuta* shows a decided similarity to that of *Stenoplesictis* which is closer to the milk dentition of felids than it is to that of hyaenids.

As far as we can tell from available evidence, both stratigraphic and morphological, *Africanictis* occurs between the earliest known *Percrocuta* on the one hand, and forms related to or within the Stenoplesictidae on the other, a family which appears to be clearly identifiable as a well defined entity within the carnivores of aeluroid type.

Family Felidae Gray 1821
Genus *Diamantofelis* gen. nov.

Type species: *Diamantofelis ferox* sp. nov.
Other species: *Diamantofelis minor* sp. nov.
Derivatio nominis: Named for its discovery in Diamond Area 1 (Namibia).

Diagnosis

Medium to small Felidae with rounded mandibular symphysis, P_2 absent in the type species, short diastema, and because of this the mandible is also short, premolars narrow and high, M_1 with absent metaconid and reduced talonid.

Differential diagnosis: *Diamantofelis* differs from *Afrosmilus* by its rounded symphysis, its lower crowned lower canine the mandible and diastema much shorter. It differs from *Pseudaelurus* by its much shorter mandible and diastema, and by its much higher and narrower premolars and M_1.

common to the various primitive forms of the *Protictitherium* group, it appears clear that the separation between *Africanictis* on the one hand and the different species of *Protictitherium* on the other, occurred prior to the Lower Miocene.

The combination of dentitions with both feloid and typically viverroid characters is relatively rare, both among living forms and in the fossil record, especially when there is a tendency for the premolars to be relatively robust, at least among forms from the Middle Miocene attributed to *Protictitherium*.

Among the fossil groups that possess this combination are *Stenoplesictis* of the Oligocene of Europe, a genus also identified in the Lower Miocene of Africa (Schmidt-Kittler 1987) and *Semigenetta* of the Lower to Upper Miocene of Europe. These genera probably comprise a homogeneous unit related to the Felidae, whilst *Africanictis* deviates from the group by already possessing hyaenoid characteristics.

Africanictis provides additional evidence in favour of the polyphyletic origin of the family Hyaenidae argued by Schmidt-Kittler (1976); Chen Guanfang & Schmidt-Kittler (1983), and for this reason we here subdivide this heterogeneous family into two groups, the Hyaenidae *sensu stricto* (*Crocuta, Hyaena, Adcrocuta,* etc.) and the Stenoplesictidae (*Stenoplesictis, Africanictis, Percrocuta,* etc.). The deciduous

Species *Diamantofelis ferox* sp. nov.

Holotype: AD 98'95, left mandible with canine and cheek dentition (figure 12).
Type locality: Arrisdrift, Namibia.
Age: Base of the Middle Miocene, ca 17–17.5 Ma.
Derivatio nominis: ferox : latin for fierce.

Diagnosis

Diamantofelis slightly smaller than a cheetah *Acinonyx jubatus*, P_2 lost.

Description

The mandible is very robust, with a short horizontal ramus, the masseteric fossa not reaching the level of the talonid of M_1. The diastema is short, the symphysis is rounded and its articulation is strong and covered with heavy rugosities. The canine is sub-rounded in transverse section, the crown is relatively low with two sharp crests, one posterior and the other in an anterolingual position.

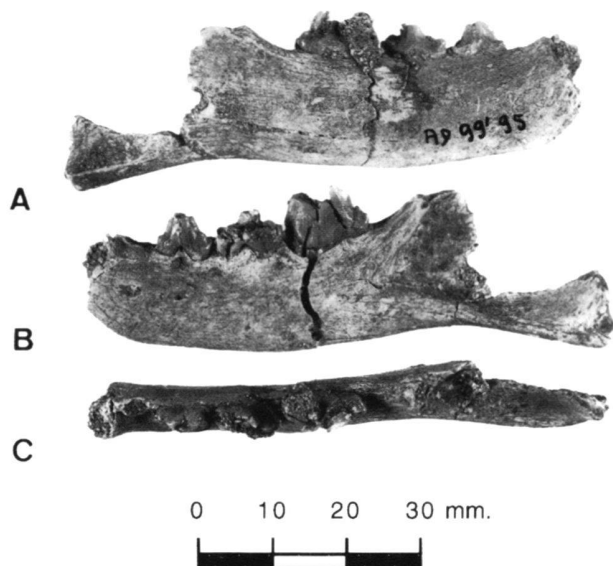The cheek dentition is very sectorial, both the premolars

Fig. 13. AD 99'95, mandible with cheek teeth, holotype of *Diamantofelis minor*, sp. nov. A, lingual view. B, buccal view. C, occlusal view.

and the carnassial being elongated and narrow. The P$_3$ (L=9.3 mm, W=4.1 mm) has three cuspids in line, the central main one being high while the anterior and posterior accessory cusplets are lower and smaller. The posterior accessory cusplet is bordered by a moderate posterior cingulum. The labial and lingual cingula are smooth.

The P$_4$ (L=12.6 mm, W=6 mm), like the P$_3$, is narrow, but is higher, and its anterior and posterior cusplets are higher. The lower first molar M$_1$ (L=15.2 mm, W=6.3 mm) lacks the tip of the paraconid and the lingual part of the protoconid, but despite the damage its morphology can be determined. The paraconid is quite high with a small anterobasal expansion. The talonid is very short and just anterior to it there is a low inflection in the buccal enamel surface corresponding to the base of a small metaconid.

Species *Diamantofelis minor* sp. nov.

Holotype: AD 99'95, left mandible with cheek dentition (figure 13).
Type locality: Arrisdrift Namibia.
Age: Base of the Middle Miocene, ca 17–17.5 Ma.
Derivatio nominis: minor on account of its small size.

Diagnosis

Diamantofelis of small size, approximately the size of a large wild cat *(Felis silvestris)* or a caracal *(Felis caracal);* P$_2$ present, mandible relatively longer than in *D. ferox.*

Description

The mandible is relatively gracile, with the masseteric fossa extending slightly anterior to the rear of M$_1$. There is an alveolus for the P$_2$ which occupies the entire space between the canine and the P$_3$ (L=7.7 mm, W=3.7 mm). The latter tooth is short with a rounded main cusp and small anterior and posterior accessory cusplets and a moderate posterolingual cingulum. The P$_4$ (L=9 mm, W=4.3 mm) is strongly corroded, but reveals morphology quite similar to that of P$_3$, but with a stronger main cusp, and a better developed posterolingual cingulum. The M$_1$ (L=11.5 mm, W=4.8 mm) is also poorly preserved, being corroded and fractured, but despite the damage its structure can be determined. The paraconid and protoconid are high, the talonid is short and there is a small metaconid in line with the talonid and protoconid.

Observations: Until now only felids of machairodontine type have been described from the lower and middle Miocene of Africa; *Syrtosmilus* Ginsburg, 1978, a form related to the European nimravids such as *Sansanosmilus,* and *Afrosmilus* (Kretzoi 1929) represented by two species, the type species *Afrosmilus africanus* described by Andrews (1914) from Karungu, and since then discovered at Rusinga (Savage 1965) and *Afrosmilus turkanae* described by Schmidt-Kittler (1987) from Moruorot and Songhor (Kenya).
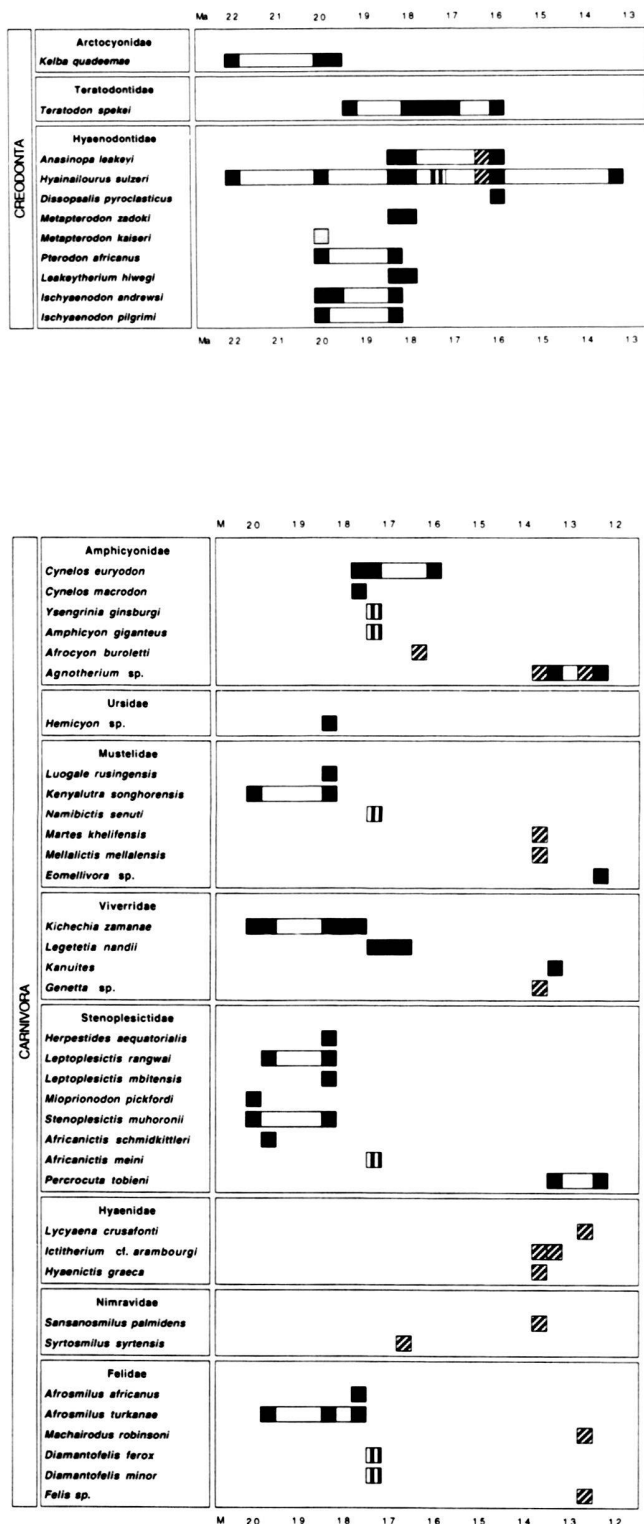
Thus the presence of these two felids at Arrisdrift represents a double novelty, on the one hand representing species hitherto unknown in Africa, and on the other comprising a feline morphotype not so far reported in Africa from this time period. We call attention to the close morphological similarities between the dentitions of the various species of *Afrosmilus* and *Diamantofelis,* in particular the height and narrowness of the lower premolars, which suggests to us a possible phylogenetic relation between the two genera.

The existence of two types of closely related felids during the lower and middle Miocene of Africa, which represent the two classical and repeated tendencies which characterise the felids (Felinae and Machairodontinae), probably indicate that these African felids had separated earlier than the Eurasiatic feloid lineages derived from the genus *Pseudaelurus.*

Conclusions and discussion

The seven species of carnivores recorded from Arrisdrift indicate that the site is most likely to be of basal Middle Miocene age, equivalent to Faunal Set P IIIa of East Africa (Pickford 1981) and Zone MN 04a of Europe (Mein 1990). This would indicate an age of about 17–17.5 Ma for the site (Pickford 1994).

The fact that the Arrisdrift stenoplesictid, mustelid and felids represent hitherto undescribed genera and species highlights the rarity of African carnivores in deposits of basal Middle Miocene age and the incompleteness of our knowledge about them. The fact that the Arrisdrift carnivores aged ca 17.5–17 Ma are so different from the lower Miocene faunas from East Africa (Schmidt-Kittler 1987) aged ca 20–17.8 Ma,

Tab. 1a — CREODONTA (Ma 22 21 20 19 18 17 16 15 14 13)

- Arctocyonidae
  - Kelba quadeemae
- Teratodontidae
  - Teratodon spekei
- Hyaenodontidae
  - Anasinopa leakeyi
  - Hyainailourus sulzeri
  - Dissopsalis pyroclasticus
  - Metapterodon zadoki
  - Metapterodon kaiseri
  - Pterodon africanus
  - Leakeytherium hiwegi
  - Ischyaenodon andrewsi
  - Ischyaenodon pilgrimi

Tab. 1b — CARNIVORA (M 20 19 18 17 16 15 14 13 12)

- Amphicyonidae
  - Cynelos euryodon
  - Cynelos macrodon
  - Ysengrinia ginsburgi
  - Amphicyon giganteus
  - Afrocyon buroletti
  - Agnotherium sp.
- Ursidae
  - Hemicyon sp.
- Mustelidae
  - Luogale rusingensis
  - Kenyalutra songhorensis
  - Namibictis senuti
  - Martes khelifensis
  - Mellalictis mellalensis
  - Eomellivora sp.
- Viverridae
  - Kichechia zamanae
  - Legetetia nandii
  - Kanuites
  - Genetta sp.
- Stenoplesictidae
  - Herpestides aequatorialis
  - Leptoplesictis rangwai
  - Leptoplesictis mbitensis
  - Mioprionodon pickfordi
  - Stenoplesictis muhoronii
  - Africanictis schmidkittleri
  - Africanictis meini
  - Percrocuta tobieni
- Hyaenidae
  - Lycyaena crusafonti
  - Ictitherium cf. arambourgi
  - Hyaenictis graeca
- Nimravidae
  - Sansanosmilus palmidens
  - Syrtosmilus syrtensis
- Felidae
  - Afrosmilus africanus
  - Afrosmilus turkanae
  - Machairodus robinsoni
  - Diamantofelis ferox
  - Diamantofelis minor
  - Felis sp.

Tab. 1. Records of Creodonts (1a) and Carnivora (1b) species in East Africa, North Africa and Namibia localities (Arrisdrift and Elisabethfeld). Black bar = East Africa. Striped bar = North Africa. Black and white bar = Arrisdrift locality. Grey bar = Elisabethfeld locality.

highlights the severity of the faunal turnover between Faunal Sets P II and IIIa already noted by Pickford (1981).

Although the representation of carnivores at the site is relatively good, there is little doubt that we have only obtained an incomplete picture of their true diversity. For example, the available fossil sample does not contain small creodonts and some of the fissipeds which one would expect to have lived in the region during the Middle Miocene, including Nimravidae and Viverridae have not been found there. In addition, in Europe and North Africa, the Lower and Middle Miocene was a period of major radiation among the mustelids. At least five genera have been recorded from North and East Africa, but there is only one species known from Arrisdrift.

The presence of the amphicyonid Ysengrinia ginsburgi at Arrisdrift is interesting in that the genus is widespread in Europe (Spain, France) and provides information concerning the age of the deposits of the Proto-Orange River. The same applies to the species Amphicyon giganteus and the giant creodont Hyainailourus sulzeri. Indeed carnivores, often being pandemic to cosmopolitan, have been the most useful group for intercontinental correlations, and in the case of Arrisdrift, this has certainly proven to be true, no other groups except the proboscideans and rhinocerotids being common to both southern Africa and Europe during this period.

The Arrisdrift amphicyonids differ from those known from localities in East and North Africa. The relationships of Afrocyon buroletti from Jebel Zelten (Arambourg 1961) are difficult to ascertain on account of the abraded condition of the only known specimen. However, it does not appear to be close to Ysengrinia ginsburgi, even though it is approximately the same size. The latter species shows incipient feloid tendencies in the upper carnassial, and it may well be ancestral to the late Middle Miocene amphicyonid Agnotherium, known from Beni Mellal (Morocco), Beglia (Tunisia) and Fort Ternan and Ngorora (Kenya) (Ginsburg 1978; Kurten 1976; Pickford 1986).

The dentition of the giant amphicyonid from Arrisdrift, Amphicyon giganteus, appears to have been adapted away from the feloid tendencies seen in Ysengrinia, the cheek dentition being more comparable to those of bone-crushing hyaenas. The heavy abrasion of the teeth suggests that its diet included durable items such as bones. It may well, therefore, have filled the hyaena niche in the early Middle Miocene of southern Africa.

The discovery of a medium-sized hypercarnivorous mustelid, Namibictis senuti, at Arrisdrift indicates that this family was already quite diversified and geographically widespread by the onset of the Middle Miocene. However, the record of the family in Africa is still poor.

The recovery of the Arrisdrift stenoplesictid, Africanictis meini, has enabled the authors to resolve the identity of a poorly known small East African carnivore previously identified as an unknown viverrid (Schmidt-Kittler 1987). The Chamtwara, Kenya, fossils represent a primitive species of the genus, Africanictis schmidtkittleri.

Africanictis possesses a lower dentition which foreshadows that seen in larger stenoplesictids such as *Percrocuta tobieni* from Fort Ternan and Ngorora in Kenya (Crusafont-Pairo & Aguirre 1971) and in other species of the genus from elsewhere in the Old World (Chen Guanfang & Schmidt-Kittler 1983).

The hypercarnivorous dentition of the Arrisdrift stenoplesictid has not yet evolved the classic „hyaena" specialisations for bone crushing seen in its possible descendant *Percrocuta tobieni*. Instead, at Arrisdrift the bone-crushing niche appears to have been occupied by the amphicyonids, especially *Amphicyon giganteus,* the dentition of which shows severe wear of the type seen in hyaena premolars.

No nimravids have yet been found at Arrisdrift, but they are known from late Middle Miocene sites in North Africa (Ginsburg 1978; Kurten 1976). Perhaps they entered Africa from Europe after the Arrisdrift deposits had accumulated.

Likewise, no true hyaenids have been found at Arrisdrift but they are known from late Middle Miocene sites in North Africa (Tab. 1) (Kurten 1976; Ginsburg 1978).

The Arrisdrift felids differ markedly from those known from other sites in East and North Africa by possessing feline symphyseal morphology rather than the down-turned machairodontine condition.

Possible predator/prey relationships

With the description of the Arrisdrift carnivores, possible predator/prey relationships can be postulated. The stenoplesictid, mustelid and felids were of hypercarnivorous feloid tendencies, suggesting that they specialised in eating the flesh of birds and small to medium-sized mammals such as the abundant macroscelidids, *Myohyrax,* the lagomorph *Australagomys,* rodents of diverse size such as the small sciurids and thryonomyids or the pedetid, *Megapedetes,* and they could perhaps have preyed on the young of the sheep-sized hyracoid *Prohyrax hendeyi,* fossils of which are extremely common at the site. The medium sized amphicyonid, *Ysengrinia ginsburgi,* possibly specialised on the medium sized mammals including the suids *Namachoerus moruoroti* and *Nguruwe kijivium,* small bovids, tragulids and climacoceratids, although adults of the latter may have been too large for them to handle. The gigantic amphicyonid, *Amphicyon giganteus* was about the size of a brown bear, and the heavy wear on its dentition suggests that it was probably chewing tough items including bones, thereby, to some extent occupying the classic hyaena niche. It could have been preying on the climacoceratids which are very common as fossils at Arrisdrift. The enormous hyaenodont, *Hyainailourus sulzeri* possibly preyed on rhinocerotids and may have included the occasional deinothere and gomphothere in its diet, the remains of which are well represented at the site, but its main prey item was probably the ubiquitous climacoceratids.

Although the known diversity of carnivores at Arrisdrift is low (7 species documented) it is evident that the fauna is dominated by fissipeds (6 fissipeds to 1 creodont), unlike the situation in the lower Miocene of East Africa in which creodonts are almost as diverse as fissipeds (10 creodont genera compared to 11 of fissipeds). In East Africa, the diversity of creodonts diminished abruptly at the end of the lower Miocene, in tune with the major faunal turnover pulse that characterised the transition between the Lower and Middle Miocene (tab. 1). At this time in East Africa about 80% of the lower Miocene mammal fauna disappeared to be replaced by lineages from Eurasia and other parts of Africa (Pickford 1981), and the creodonts were particularly badly affected (down from 10 genera to 4), their niches presumably being filled by fissipeds or disappearing entirely. The causes of this major faunal event have been discussed elsewhere, in particular by Morales et al. (1993) and Pickford & Morales (1994), in which a dramatic increase in the severity of seasonality, played a major role. This change not only affected the climate, but also the vegetation and the faunas dependent on it either directly (herbivores) or indirectly (carnivores).

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