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ELEVEN BONES: MORE FOSSIL REMAINS OF CAVE LIONS AND CAVE HYAENAS FROM THE NORTH SEA AREA

by

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SUMMARY

Six fossil Cave Lion bones and five fossil Cave Hyaena bones are described. One lion bone and one hyaena bone were dredged from the Westerschelde (= Western Scheldt, southwestern part of the Netherlands). The other specimens were recovered from the bottom of the North Sea, in the area West and Southwest of the Brown Ridge (or Brown Bank), about 80 km West of IJmuiden on the Dutch coast.

RÉSUMÉ

Description de six pièces du squelette du Lion des Cavernes et de cinq os de l'Hyène des Cavernes. Un os de lion et un autre d'hyène ont été dragués du Westerschelde (= l'Escaut occidental, partie sud-ouest des Pays-Bas). Les autres pièces ont été pêchées à la drague du fond de la Mer du Nord, dans une zone située à l'ouest et au sud-ouest du "Brown Ridge" (ou "Brown Bank"), à 80 km environ à l'ouest d'IJmuiden sur la côte hollandaise.

INTRODUCTION

Remains of large carnivores are always a rarity in collections of fossils. The body weight ratio between a predator and its prey constitutes one of the reasons for this fact. Another reason is formed by the chance of becoming fossil; an estimation such as the very general one suggested by Kurtén (1971: 15-16) leaves only very few top carnivores in the end. Solitary habits, typical of many of the big cats, result in even more disadvantageous circumstances for fossilization than in the case of animals living in packs or bands, the usual way of life among hyaenas. But nothing definite is known about the habits of Cave Lions or Cave Hyaenas. Cave Lions may well have operated in prides, as do recent lions, while Cave Hyaenas may just as well have roamed their territories (if they were territorial) singly, or in pairs only. Any description of hitherto undescribed fossil carnivore remains may be considered a contribution, albeit a small one, to the knowledge on their kind.

Of the eleven specimens on which the present paper is based, six can be ascribed to the genus *Panthera* and five to the genus *Crocuta*. The collections containing this material are those of the Zoological Museum of the University of Amsterdam (ZMA), of the Zoological Museum of Utrecht University (Plompetorengracht 9, Utrecht) (ZMU), and of the Dutch amateur collectors Mr. D. J. Mol (de Tuger 141, 's-Heerenberg), Drs. J. Mulder (Goudenregenstraat 21, Nieuwleusen), and Ds. C. F. H. van Tuyll van Serooskerken (Molenweg 36, Oostkapelle).

Nine of the eleven fossils were collected by fishermen in the general area West and Southwest of the Brown Ridge (also called the Brown Bank) in the North Sea, some 80 km due West of the Dutch coast near IJmuiden. A more exact position within this area is recorded for five specimens, all in the collection of Mr. Mol. These five came from 52°N 02°40'E. Of the other specimens it is only known that one, now in the ZMU collection, and another, belonging to the Van Tuyll van Serooskerken collection, have been collected by the same person, Mr. P. van Es of Stellendam, owner of the fishing vessel GO 27, who also collected the fossils belonging to Mr. Mol.

Louwe Kooijmans (1972), citing Jelgersma (1961), Houbolt (1968) and Oele (1969, 1971), amongst others, has given a very useful survey

of the geographical and geological circumstances prevailing in the area around the Brown Ridge (following Houbolt I prefer that name to the frequently used one of Brown Bank). Most of the recovered fossil mammal bones seem to derive from the Brown Ridge Beds, a clay deposited in a large Early Weichselian freshwater lake (fig. 1). These beds are exposed in the floors of gullies in the otherwise sandy bottom of the North Sea. The recorded place of finding of an earlier described mandibular fragment of a Cave Lion (see Bosscha Erdbrink, 1981) is situated in just such a gully at 52°45'N 02°50'E. Fossil animal remains of a much older, probably Villafranchian nature are known from still deeper deposits, only exposed in the deepest and most westerly depressions of the area. They usually have a very dark colour and they are heavily mineralized, as has been recorded by Kortenbout van der Sluys (1972).

The two specimens in the ZMA collection have been collected in 1953 and 1954 from the Westerschelde (Western Scheldt) around Ellewoudsdijk (Zuid-Beveland, province of Zeeland) during dredging operations. This is a well-known locality for Pleistocene mammal bones (see, amongst others, Hooijer, 1960, and Kruizinga, 1958).

The sketch map of fig. 1 shows the position of the Brown Ridge area localities and that of Ellewoudsdijk.

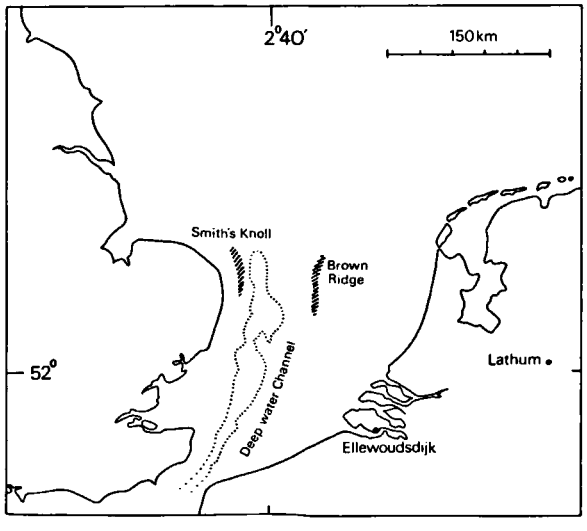

Fig. 1. Sketch map of the North Sea area between the Dutch and British coasts, with the position of Lathum and Ellewoudsdijk.

DESCRIPTION

Carnivora: Fissipedia: Felidae

Six specimens belong to this family. The most complete one is a left humerus without its proximal epiphysis, uniformly light yellowish brown coloured and shiny polished in parts (ZMA no. Mamm. 2574). It is labelled: "Felis spelaea (Goldfuss), det. Kortenbout van der Sluijs, don. C. Naaktgeboren, Westerschelde — 1953". In view of its colour and its state of preservation it may confidently be assumed that the fossil has been collected at or near Ellewoudsdijk.

The materia spongiosa at the plane of fracture, which closely follows the limits between the proximal epiphysis and the diaphysis, has the same light brown colour displayed by the rest of the bone. The aspect of this fracture probably implies that the specimen was not yet quite adult at the time of death. The diaphysis shows a number of fine diverging striae near its proximal end on the surface of the compacta. A rather curious minor feature consists of two series of three horizontal striae each (varying between 25 and 8 mm in length) on the surface of the compacta on the lateral posterior side, at the level of the distal end of the very robust deltoid ridge. Four very small horizontal scratches appear at the same place on the back of the diaphysis. The distal epiphysis is completely synostosed to the diaphysis. The area of fusion is no longer visible. The entepicondylar foramen is well developed. Evidently this bone belonged to a healthy, strong, perhaps subadult animal.

Next comes another left humerus, or rather a 25 cm long fragment of such a bone, now in the Van Tuyll van Serooskerken collection, but acquired from Mr. Mol and collected in the Brown Ridge area by Mr. Van Es in March 1981. It has also lost its proximal articulation; in addition about half of the capitulum and of the lateral epicondyle have broken off. While

the highly irregularly striated materia compacta of the specimen is shiny black with some dark brown spots (especially in the striae), the spongiosa is reddish brown at the fractures. Most of the materia spongiosa at the proximal fracture is lost, indicating transport or at least the influence of sand-laden water. The entepicondylar foramen is well developed. The nutrient foramen on the anteromedial surface of the diaphysis (known in human anatomy too), at about one third of its height from below and opening upwards, is much smaller in this specimen than in that from the Westerschelde. Some bryozoan colonies occur higher up on the same side.

A third specimen, belonging to the Mulder collection, is a very dark brown, almost black, shiny, complete fourth metatarsal bone of the left side. Its measurements (see table I) indicate that it has belonged to a large and robust animal, as is also attested by the well-developed areas for muscular attachment. The groove for the lateral articulation with metatarsal V is distinct, as is the process fitting into the groove of metatarsal III. The half-spherical trochlea is provided with a high, thin medial crest. According to Schlosser (1924: 21) this is a feline feature.

The fourth felid specimen is morphologically connected to the third. It is a third metatarsal bone of the left side, inscribed as no. 924 in Mr. Mol's collection and acquired from Mr. Van Es in September 1981. It almost fits to the fourth metatarsal bone in the Mulder collection and as it displays an identical colour and state of fossilization, one is tempted to assume that the two bones may have belonged to the same strongly developed individual. The bone is complete and its measurements can be found in table I, while it is represented, with all the other felid specimens, in fig. 2.

A fifth specimen, inscribed in Mr. Mol's collection as no. 933 and acquired in January 1982 from Mr. Van Es, who collected it at a locality given as 52°N 02°40'E, is a very dark brown, nearly complete left radius. It displays numerous irregular shallow scratches all over its surface, as if plant roots corroded the surface of the bone everywhere. The styloid process has broken off; dark brown spongiosa is apparent at the break. Bryozoan colonies are encountered in several places, notably all around the lower edge of the caput, showing that the fossil must have lain free on the bottom for some time. As in recent lions, the radial tuberosity is strongly developed. Approximately 3 cm below this feature a large foramen nutricium is displayed, opening downwards, almost on the lateral edge of the pronounced interosseous border. The distinct ulnar notch at the distal extremity of the bone bears a slightly concave, oblique facet with a semicircular form, measuring roughly 17 by 9 mm. Although this bone is not particularly large in size, its crests and ridges are strong and it unquestionably belongs to a lion, as comparison with a recent skeleton in the ZMU collection showed. The several radii of recent leopards in the same collection displayed a much more slender build, with less pronounced crests.

The sixth specimen consists of part of a left parietal bone of the skull, with the auditory meatus and the posterior part of the zygomatic arch. The relatively large, 28 mm vertically protruding postglenoid tubercle, having the form of an orange segment, has remained intact. The specimen was collected to the West of the Brown Ridge by Mr. Van Es. At present it is inscribed in the ZMU collection as Mamm. no. 353. It was acquired from the amateur collector Mr. A. Hamer of Roosendaal in 1981, in whose collection it bore no. 35. The fossil is coloured intensely black all over; so is its materia spongiosa, visible on the planes of fracture. There are some lighter coloured bryozoan colonies (see fig. 2) in sheltered places, so that this specimen must also have lain uncovered on the bottom of the sea for some time. A stretch of the sagittal crest has been preserved; so has part of the braincase over the left ear. When the specimen is held in its natural position, the approximate vertical distance from a horizontal line through the auditory meatus from the left to that of the right ear, towards the top of the sagittal crest, is 120 mm. The distance from the exit of the left auditory meatus along the above-


A
B
C
D
E
5cm
5cm
5
cm
F
G
H
I
J
5cm
5cm
K
L

TABLE I

Measurements (in mm) of the described fossil felid specimens compared with data taken from Ballesio (1980) and Terzea (1965).

Humeri	ZMA no. 2574	Coll. Van Tuyll van Serooskerken	Ballesio: petite forme no. 300834	300835	300836
Total length	>315	>260	326	324	—
Mid-shaft, transverse width	29	27	28	28	—
Mid-shaft, ant.-post. width	52	46	—	—	—
Mid-shaft, circumference	129	122	—	—	—
Distal articulation, transverse width	88	>75	83	83	88.5
Distal articulation, ant.-post. width	58	47	—	—	—

Radii	Coll. Mol no. 933	Ballesio: petite forme no. 300837	300838	300922	300923	grande forme 300996	300997
Total length	256	297.5	—	299	296	—	—
Prox. articulation, transverse width	27	40.5	41	43	42.5	49	—
Prox. articulation, ant.-post. width	39.5	—	—	—	—	—	—
Mid-shaft, transverse width	18	30	31	33.5	34	—	—
Mid-shaft, ant.-post. width	32	—	—	—	—	—	—
Mid-shaft, circumference	86	—	—	—	—	—	—
Distal articulation, transverse width	30	61	—	60	61.5	—	76
Distal articulation, ant.-post. width	>50	—	—	—	—	—	—

Metatarsalia			Terzea La Adam	Taunton	Equi	l'Herm	Ballesio, petite forme no. 300876	300879	300959	300962
Total length	m.t III, Mol 924	135	136	137.1-150.8	122-145	140-162	—	125	128	—
	m.t. IV, Mulder	128	—	142.2	—	—	128	—	—	133
Prox. articulation, transverse width	m.t. III, Mol 924	29	29.8	26.6-32.2	27-33	30-33	—	—	27.5	—
	m.t. IV, Mulder	21.5	29.4	21.3	—	—	—	—	—	—
Prox. articulation, ant.-post. width	m.t. III, Mol 924	39.2	38	34.7-38.1	35-42.5	41-44	—	—	—	—
	m.t. IV, Mulder	35.5	32	40.6	—	—	—	—	—	—
Mid-shaft, transverse width	m.t. III, Mol 924	21	20	—	18.5-22.8	22-25	—	18.5	18.5	—
	m.t. IV, Mulder	16	18	—	—	—	17	—	—	17
Mid-shaft, ant.-post. width	m.t. III, Mol 924	19	18	—	15-19	18-20	—	—	—	—
	m.t. IV, Mulder	17	16.5	—	—	—	—	—	—	—
Distal articulation, transverse width	m.t. III, Mol 924	26.5	28	21-25.4	24-30	30-36	—	23.5	24.5	—
	m.t. IV, Mulder	22	—	—	—	—	21.5	—	—	23.6
Distal articulation, ant.-post. width	m.t. III, Mol 924	25	24	—	21-25.5	26-27	—	—	—	—
	m.t. IV, Mulder	23	—	—	—	—	—	—	—	—

Fig. 2. Fossil remains of Felidae.
A-C, Metatarsale III sin., Mulder coll., Brown Ridge area: A, posterior view; B, left lateral view; C, anterior view.
D-E, (Incomplete) humerus sin., ZMA coll. no. Mamm. 2574, Westerschelde 1935: D, posterior view; E, anterior view.
F, Radius sin., Mol coll. no. 933, Brown Ridge area 52°N 02°40'E, January 1982; anterior view.
G-H, Metatarsale IV sin., Mol coll. no. 924, Brown Ridge area 52°N 02°40'E, September 1981: G, left lateral view; H, posterior view.
I-J, (Incomplete) humerus sin., Van Tuyll van Serooskerken coll., Brown Ridge area, March 1981: I, posterior view; J, anterior view.
K-L, Skull fragment with auditory meatus sin., ZMU coll. Mamm. no. 353 (ex coll. Hamer no. 35, 1981), Brown Ridge area: K, anterior view; L, external side view.

mentioned horizontal line to below the sagittal crest (i.e. to the base of the mentioned vertical distance) is approximately 45 mm. The vertical height of the sagittal crest is measurable as well, because it is possible to look into a sinus between the bony roof of the braincase and the bone structure of the crest (fig. 2, K). This height is 27 mm. In the observed sinus a number of separate bladder-like bony compartments can be observed. The supramastoid crest follows an absolutely straight course and forms a flat platelike structure on its external side. This same feature was encountered by me in the skulls of recent lions, tigers and leopards, whereas in bears and dogs, and hyaenas, the crest is slightly curved up and does not form quite such a large plate externally. A small portion of the originally large tympanic bulla is still present too. The posterior line of fracture of the fossil specimen consists for about half of its distance of part of the oblique crista between the posterior end of the sagittal crest, and the ear region. The general size of the skull fragment is such, that one may safely conclude that it is larger than the corresponding part of the skull in a leopard. This is borne out by at least one measurement: the distance between the exits of the right and left auditory meatus. In a recent tiger's skull in the ZMU collection this is 92 mm, in the skull of a recent lion in the same collection 87 mm, and in five leopard skulls the range runs from 48 to 62 mm. Half the distance between the two earholes in the fossil has been estimated (see above) at 45 mm; thus the complete distance, roughly 90 mm, is in accordance with that of recent lions and tigers.

Measurements of the first five of these felid specimens are given in table I, while all have been pictured in fig. 2.

Carnivora: Fissipedia: Hyaenidae

Five specimens have to be attributed to this family. They have been illustrated in fig. 3, while some of their measurements are given in table II.

The first specimen is a complete right humerus in the ZMA collection. According to its label, which bears no number, it was donated by Mr. Guillonard in 1954, while it was collected at Ellewoudsdijk on the Westerschelde. Its uniform light brown colour, slightly darker on surfaces of joints such as the trochlea, is exactly identical to that of the incomplete lion humerus in the same collection which is described above. The bone is sturdily built and possesses a strong deltoid ridge, but otherwise it does not appreciably differ from the humerus of a recent *Crocuta crocuta* (Erxleben, 1777) (no. ZMA Mamm. 715).

The second specimen, also a right humerus, is incomplete; its proximal part is missing, owing to a recent transverse fracture through the diaphysis at the upper end of the robust deltoid ridge. The specimen (fig. 3, G-I) forms part of the Mulder collection and has been recovered in the area West of the Brown Ridge. Its colour is shiny black, while the spongiosa (visible at the break) is light brown to grey. Part of the spongiosa is absent and may have dissolved. In sheltered places near the trochlea a number of bryozoan colonies can be observed. The circular supra-trochlear perforation is slightly smaller than that of the Ellewoudsdijk specimen. The two bones each display a nutrient foramen (as in human anatomy) on the middle of the inside (the anteromedial surface) of the diaphysis, just below the point of origin of the deltoid ridge. This ridge appears to be developed somewhat more robustly in the Brown Ridge specimen than in the other one. Its diaphysis may also have been slightly larger and longer (see table II).

The third, fourth and fifth specimens have been collected in January 1982 by Mr. Van Es at the already mentioned locality 52°N 02°40'E. They are inscribed in Mr. Mol's collection as nos. 934 (6th cervical vertebra), 935 (8th thoracic vertebra) and 936 (atlas). Comparison with the separate elements of the vertebral column in the skeleton of the earlier mentioned recent Spotted Hyaena (ZMA no. Mamm. 715) not only convinced me of their identity, that of vertebrae of Cave Hyaenas, but also of their exact position in the column. Although they were collected at approximately

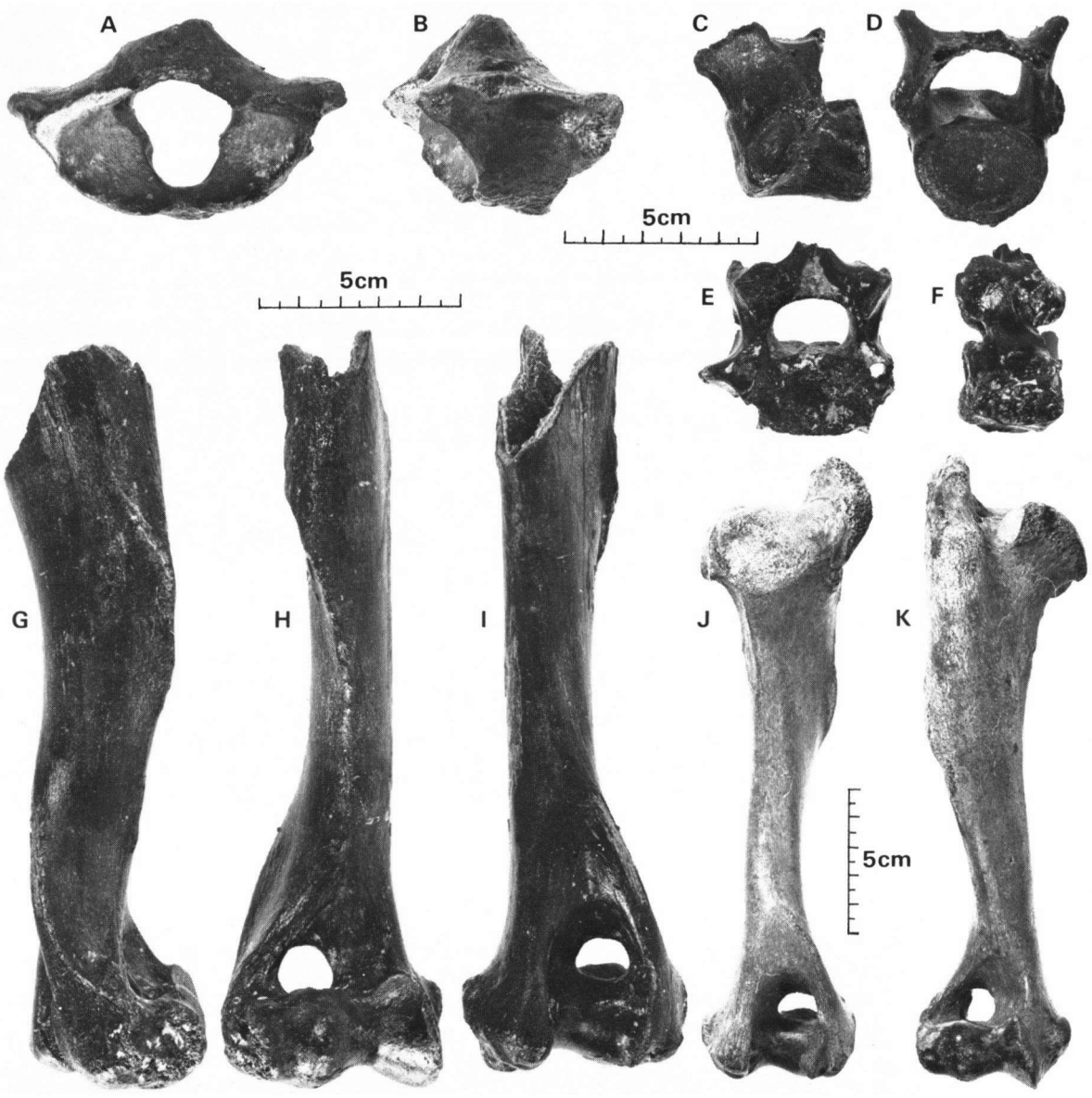

Fig. 3. Fossil remains of Hyaenidae.
A-B, Atlas, Mol coll. no. 936, Brown Ridge area 52°N 02°40'E, January 1982: A, anterior view; B, left lateral view.
C-D, Eighth thoracic vertebra, Mol coll. no. 935, Brown Ridge area 52°N 02°40'E, January 1982: C, left lateral view; D, posterior view.
E-F, Sixth cervical vertebra, Mol coll. no. 934, Brown Ridge area 52°N 02°40'E, January 1982: E, posterior view; F, left lateral view.
G-I, (Incomplete) humerus dext., Mulder coll., Brown Ridge area: G, external lateral view; H, anterior view; I, posterior view.
J-K, Humerus dext., ZMA coll., Ellewoudsdijk 1954: J, posterior view; K, anterior view.

the same locality, it does not appear very likely that they belonged to a single individual in view of the morphological differences (colour, fusion of epiphyseal portions to the vertebral body, etc.).

No. 934, the sixth cervical vertebra, is shiny black in appearance (its compacta as well as its cancellous bone tissue) with encrustations of bryozoan colonies in many (usually sheltered) places. It not only lacks the anterior and posterior epiphyses of the vertebral body, indicating that the individual cannot have been fully adult at the time of its death, but it is also much damaged elsewhere. The general size of the specimen corresponds well with that in the above-mentioned skeleton of a recent adult *Crocuta crocuta*. The vertebral arch is entire; the spinous process has broken off, and so have the two transverse processes. At the right side slightly more of the base of the transverse process remains. The left anterior and the two posterior articular processes are still present and so are the two foramina transversaria; that on the right side has been completely blocked by bryozoans. The ventral and dorsal surfaces of the vertebral body are almost flat. The vertebral foramen has an oval form with its largest diameter in a transverse sense (table II).

No. 935, the eighth thoracic vertebra, has belonged to an adult individual. Complete fusion of anterior and posterior epiphyses to the drumlike, waisted, almost platycoelous vertebral body has occurred. Slight damage to the caudal part of the basal keel over the middle of this vertebral body has resulted in the absence of a sliver of compacta, enabling the observation that the cancellous bone inside the body has the same blackish brown colour also displayed on the outside of the specimen. A few whitish to rust-coloured bryozoan colonies occur, mainly inside the vertebral canal. The vertebral arch is only just present. The spine has broken off at its base, and only the basal portions of the anterior articular facets are still present. On both sides the demifacets for the heads of the ribs are easily discernible along the anterior upper parts of the vertebral body. The

TABLE II

Measurements (in mm) of the described fossil hyaenid specimens compared with data taken from Ballesio (1979).

Humeri	Complete humerus dext. coll. ZMA	Distal fragment humerus dext. coll. Mulder	Recent *C. crocuta* ($n = 7$) after Ballesio	Pleistocene Cave Hyaenas from Jaurens after Ballesio
Total length	225	>195	208-248	237-241 ($n = 3$)
Proximal transverse width	59.5	—	—	—
Proximal ant.-post. width	52.5	—	—	—
Distal transverse width	55.5	59.5	47-62.4	55-59 ($n = 5$)
Distal ant.-post. width	43.5	46	—	—
Mid-shaft transverse width	20	20.5	17.5-20	19-21.5 ($n = 4$)
Mid-shaft ant.-post. width	29	34.5	—	—
Mid-shaft circumference	92	93	—	—

Vertebrae	Coll. Mol no. 934 (6th cerv.)	no. 935 (8th thor.)	no. 936 (atlas)*
Anterior transverse width of neural canal	19.6	24.8	31.7
Posterior transverse width of neural canal	20.3	26.1	26.1
Anterior height of neural canal	13.4	15.0	28
Posterior height of neural canal	13.9	15.9	31.5
Dorsoventral height of vert. body	20.9	27.0	—
Max. transverse width of vert. body	31.0	34.6	—
Craniocaudal length of vert. body	>25	35.1	—
Transverse width over neural arch	38	38	—
Distance between alar foramina	—	—	58

* = The entire dorsoventral height of the atlas no. 936 is larger than 54.

vertebral foramen has a rounded rectangular form (see table II).

No. 936, the atlas, is somewhat lighter coloured than the two other vertebrae. It is shiny dark brown to black in some places and light brown to rust-coloured elsewhere. The spongious matter inside is generally much lighter in colour, almost white, as is apparent at two damaged areas: behind the dorsal tubercle, and in front at the base of the left articular facet for the left occipital condyle. The tip of the ventral tubercle, on the lower arch, has also suffered some damage; there the spongiosa is very light brown. The rather conspicuous left and right foramina transversaria are present in their entirety. These alar foramina have an internal connection towards the vertebral foramen. The thin alae on the left and right external sides of this vertebra have broken off, displaying light brown spongiosa. The posterior face of the atlas is concave when seen from above or from behind; it contains a number of shallow crests and ridges. The neural canal has the form of a number eight. The internal crests for the transverse ligament, retaining the odontoid process of the axis in place, are easily observable. Some measurements are given in table II.

DISCUSSION AND CONCLUSIONS

Felidae

The preceding description and figures of felid specimens clearly demonstrate their affinity with the Pleistocene Cave Lion, *Panthera leo spelaea* (Goldfuss, 1810). In a single case, that of the cranial fragment in the ZMU collection, a theoretical possibility exists that the specimen might be ascribed to a stratigraphically older form or species. The intense black colour of its external *and* internal bone tissues point to a possibility mentioned by Kortenbout van der Sluys (1972), namely that it could be a Villafranchian (Tiglian or Pretiglian) fossil. As no precise data are known about the locality where it was collected, beyond the rather vague notice "West of the Brown Ridge", it may have been recovered from the more westerly situated Deep Water Channel, in the direction of Smith's Knoll (see fig. 1; Mr. Van Es is known to have fished here), where there are depths of approximately 28 fathoms. Here Villafranchian deposits appear to crop out on the North Sea bottom. No other quantified indications of a possible specific identity were found by me than the computed distance between the entrances to the two auditory meatus; this falls within the range of recent lions and tigers, as we have seen. Whether the cranial fragment may belong to *Panthera schaubi* Viret, 1954, that little-known Villafranchian big cat, or to the slightly larger *Panthera gombaszoegensis* (Kretzoi, 1938), a jaguar considered characteristic of the European late Villafranchian and Cromerian by Hemmer (1971), remains an open question. Kurtén (1968) has pointed to the possibility that *P. schaubi* could be identical with Owen's *Felis pardoides* from the English Crags, an area not too distant from the Deep Water Channel in the North Sea. In the mean time it seems the most prudent procedure to identify the specimen provisionally as *Panthera* cf. *leo spelaea*, because such a form is known to occur as a fossil in the deposits on the bottom of the North Sea. The same arguments valid in the case of an identification as *P. schaubi* or *P. gombaszoegensis* hold for *Panthera leo fossilis* (Von Reichenau, 1906), the mainly Cromerian form considered by Schütt & Hemmer (1978) to be the forerunner of *P. leo spelaea.* The subspecies *fossilis* has, up to now, not been found in the North Sea area or in immediately adjacent regions and may be more characteristic of Central Europe.

Measurements of the other five lion specimens described here have been compared, in table I, with data taken from a recent publication by Ballesio (1980) and from an earlier paper by Terzea (1965). It becomes apparent from this that there exists a fair amount of agreement with the measurements ascribed by Ballesio to his "small form" (he has advanced a number of good quantificational and statistical reasons to distinguish a group of large Cave Lions from another with smaller dimensions). The two groups cannot be explained by

assuming sexual size differences as the responsible factor. Probably they have either coexisted in slightly different biotopes, or else they have been separated from each other through small differences in time (in a stratigraphical sense).

Ballesio (1980) points out that the measurements of Terzea's specimens from La Adam cave in Rumania all fall in the range of his large form. Measurements from Taunton, Equi and l'Herm are all copied by me from Terzea (table I). In the case of the radius sinister (coll. Mol, no. 933) a very curious discrepancy exists with the data given by Ballesio. Although these data are considered to belong to the "petite forme", they very much exceed the measurements of the Mol specimen. I have already stated that I do not consider it possible, for morphological reasons, that this radius is ascribable to a leopard, but that it is definitely that of a lion. Might it be possible that, in some measurements, Ballesio could have erroneously interchanged the transverse with the antero-posterior widths? This does not explain, however, the larger total length of the radii of his small form.

Except for the one metatarsal bone (a third metatarsal) in the Mol collection (no. 924), which has dimensions that agree with Terzea's specimen from La Adam cave (and thus, with Ballesio's "grande forme"), all other specimens fall into the range of the small form distinguished by Ballesio. This is even true for the three mandibular specimens described by me in 1981, when they are incorporated (see fig. 4) in Ballesio's fig. 6, depicting the correlation between the lengths of the first lower molar and the fourth premolar. Evidently the small form seems to be the most commonly occurring one in and immediately around the (dry) North Sea basin during the Late Pleistocene. The material is too scanty for any drawing of conclusions; nonetheless one is temptingly reminded of Bergmann's rule, according to which the small form is indicative of not too cold climatological circumstances. This line of thought is rather in accordance with the fact that the Brown Ridge Beds, the already mentioned freshwater clays forming a supposed lake deposit, are considered to date back to the very beginning of the Weichselian glaciation. Thus the fossil bones could either have a final Eemian, or a very early Weichselian age, when extreme cold was still some time off. This in turn might imply that Ballesio's large form of lion could date from slightly later times, being the better adapted to extreme cold of the two; and the relative proximity to the Weichselian (= Würmian) icecap, for animals inhabiting the then dry plain of the North Sea bottom, might not favour the presence of a large amount of herbivorous prey for carnivores, explaining why the large form of Cave Lion would rarely occur there at the height of the (Weichselian) cold. In view, however, of the rather vigorous tendencies towards various subspecific developments displayed by fossil and recent lion populations, as is rightly pointed out by Schütt & Hemmer (1978: 251-252), one has to be extremely cautious. The trend of ideas set forth above should be seen as nothing more than a series of speculative ruminations.

In any case the five specimens should be identified, irrespective of the circumstance whether they have to be ranged among the small forms or the large forms, as *Panthera leo spelaea* (Goldfuss, 1810), in accordance with the remarks made by Schütt & Hemmer (1978: 252).

Hyaenidae

The five hyaenid fossils do not give rise to so much diverse arguments. The two humeri are compared in table II with regard to their measurements, while data given by Ballesio (1979: 52) on recent Spotted Hyaenas and on Würmian finds from the Jaurens cave in Corrèze (France) are likewise incorporated in that table. It is clear that the Ellewoudsdijk humerus has a size more in accordance with recent *Crocuta crocuta* than with the slightly larger Pleistocene subspecies, the Cave Hyaena *Crocuta crocuta spelaea* (Goldfuss, 1810). This may, or may not, indicate that the Ellewoudsdijk specimen may have an Eemian age because its smaller size would be in accordance with a

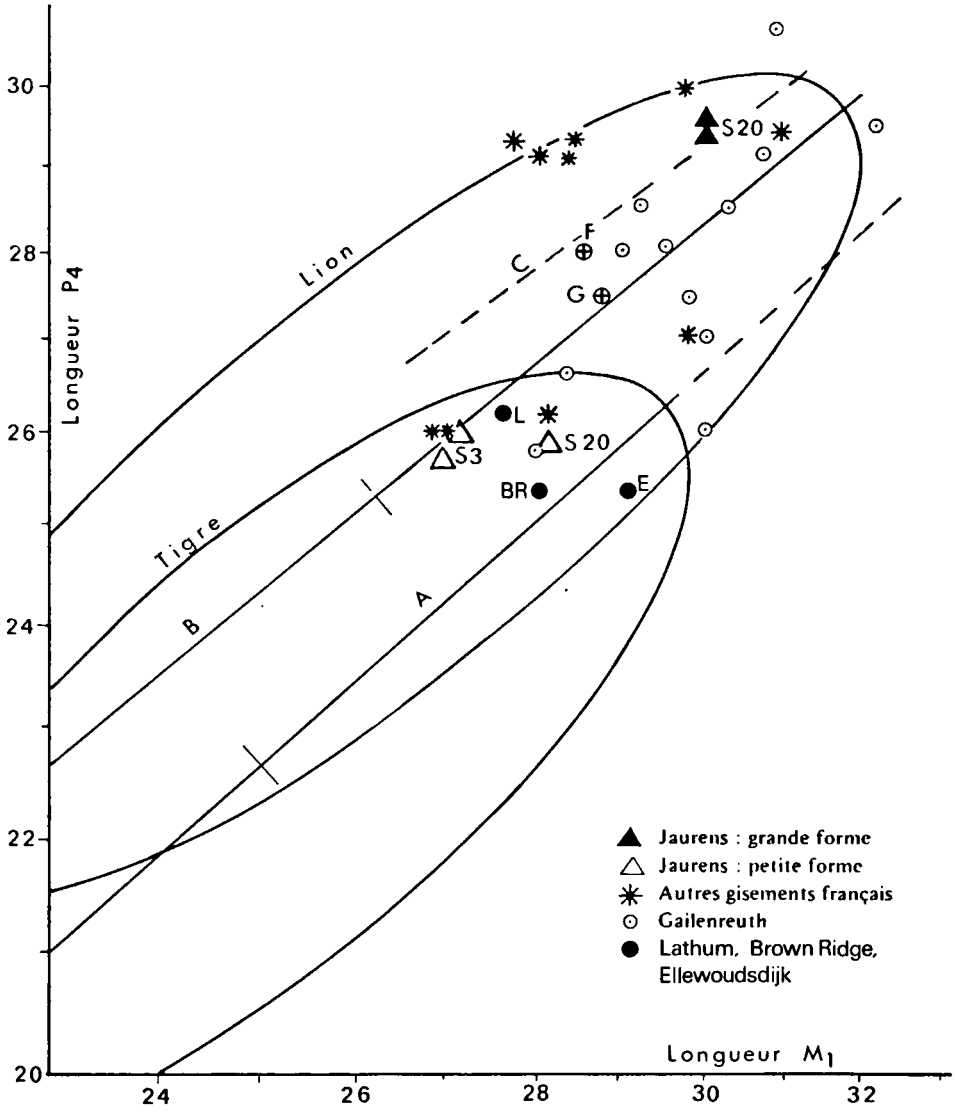

Fig. 4. Reproduced after fig. 6 in Ballesio's 1980 paper (the relation of lengths of P_4 and M_1) with, superimposed, the values for the three specimens from Lathum, the Brown Ridge area, and Ellewoudsdijk (Bosscha Erdbrink, 1981), to show that these belong to the small form distinguished by Ballesio.

milder climate. The (incomplete) Brown Ridge specimen in the Mulder collection appears to be as large and robust as the individuals investigated by Ballesio. Its determination as a Cave Hyaena is not open to doubt.

As has been stated in the description, the three vertebrae conform with those of a recent Spotted Hyaena as regards their morphology and size. As I have not been able to find sufficient data for purposes of comparison in literature, I think that the most prudent course of action is to give some measurements (equally in table II) of the fossil specimens, and to identify them provisionally as *Crocuta crocuta* cf. *spelaea* (Goldfuss, 1810).

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