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Notes on the black-maned lion
of the Cape, *Panthera leo melanochaita*
(Ch. H. Smith, 1842) and a revised list of
the preserved specimens

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1.

The Black-maned Lion of the Cape, originally described in 1842 by CHARLES HAMILTON SMITH under the name *Leo melanochaitus*, has its place among the most famous African mammals. Though generally recognized by the old naturalists and hunters as a distinct subspecies, or even species, of Lion, the Black-maned Lion of the Cape has for long years been a subject of controversy among more recent authors as far as its systematic status is concerned.

The Cape Lion became extinct too soon for zoologists to be able to study this magnificent form of lion properly. The only available material was represented by old descriptions and drawings. The plate that accompanies SMITH's original description shows a lion with some external characteristics that must certainly be considered somewhat peculiar. Only as late as in 1931 the first skin of a topotypic specimen of the Black-maned Lion of the Cape was described by ПОСЛОК, and the first really scientific evidence on this lion form thus came to light. The specimen in question is preserved in the British Museum (Natural History), London. The second scientific evidence on the Cape Lion was brought to light by LUNDHOLM (1952) who described a female skull that had been dug up in sub-fossil deposits near Murraysburg (Cape) and is now deposited in the Museum, Snake Park and Oceanarium in Port Elizabeth. Between 1952 and 1962 more specimens of the Cape Lion were discovered and I thus had a possibility to publish in 1964 a list of the preserved specimens of this lion form known to me at that time. The list contained 5 mounted male skins, 2 mounted female skins, and 1 female skull.

Since the publication of the list mentioned above some new evidence on the Cape Lion became known to me and I intend to discuss in the paper presented here some new aspects of the problem and to give a revised list of the preserved specimens of the Black-maned Lion of the Cape. The study of the material available at the time being has convinced me again that this form represented a very distinct subspecies of the Lion, *Panthera leo* (Linnaeus, 1758).

2.

During my visits to various museums in Europe I succeeded in discovering several specimens that represent new material of the extinct Cape subspecies of the Lion and can, from the point of view of a taxonomist, be useful for better understanding of the whole problem.

2.1. Quite surprisingly two skulls of the Cape Lion have been discovered in the collection of lion skulls in the British Museum (Natural History), London. The skulls in question are as follows:

(1) Intact skull of a full grown male. Though adult the specimen was not a very old one as the state of the basal sutures on the skull shows. The skull bears the original label that runs 'Cape Town, shot 1848. Col. H. W. Murray.' British Museum (Nat. Hist.) No. B.M. 36.5.26.6 (Plate V).

(2) Partly damaged skull, with the occipital region cut off. British Museum (Nat. Hist.) No. B.M. 18.5.23.2. (Plate IV). The skull is that of an old male and the original label gives the following information: 'South Africa. Capt. H. W. Murray. Shot about 1873 by Capt. Murray's father./Capt. Murray told me that his father shot lions in S. Africa with Oswell & Gordon Cumming. R.I.P.'. It stands to reason that the initials R.I.P. are those of the late Mr. R. I. Pocock, at his time a famous zoologist of the British Museum. There is, however, one very important detail that deserves attention. Mr. Pocock wrote on the label that the lion was shot about 1873. This date was certainly given in error since we know that in 1873 Captain (later Colonel) Murray's father decidedly did not shoot lions 'with Oswell & Gordon Cumming' as at that time these persons were no longer residing in the most southerly parts of Africa. Moreover, as far as known to me, in 1873 Mr. Murray himself was no longer in Africa either. This problem can, however, be solved without any great difficulty as CUMMING in his book gives a very precise information about his meetings with Mr. Oswell and Mr. Murray. He mentions having met Mr. Murray (i.e. Capt. Murray's father) twice during his five-year-adventures in South Africa. On both occasions he met Mr. Murray at Colesberg, and each time in the company of Mr. Oswell. The first time was in April, 1844 and the second time in February/March, 1849, shortly before CUMMING left South Africa for good in April, 1849 (cf. CUMMING, 1850, ed. 1911, pp. 172 and 496). Thus, there is considerable evidence that the date in question was misread by Mr. R. I. Pocock and that it should correctly be given as 'about 1843'.¹

CUMMING's information also indicates that both lions, the skulls of which are now deposited in the British Museum (Natural History), could have been shot in the Orange River basin within reach of Colesberg which was, at that time, the real centre of hunters and explorers, and that the actual date of their collecting could be 1843 and 1848 respectively.

2.2. In Naturhistoriska Riksmuseet in Stockholm another lion skull from southernmost Africa was found. It is an intact skull of an adult and rather old male; Stockholm Naturhistoriska Riksmuseet No. 1310. In the old museum catalogue written by the late Dr. SUNDEVALL the following information on this specimen is to be found: 'Felis leo. 1310. ♂ adult, Caffr. int. J. Wahlb. 1845.' This note thus means that the skull

¹ No doubt it is very easy to confuse the numbers 4 and 7, especially if these are written by hand.

was collected by the famous Swedish naturalist and explorer J. WAHLBERG in the interior of Caffraria² in 1845. Though having originated from southernmost Africa the skull cannot explicitly be referred to the Black-maned Lion of the Cape. The systematic position of this specimen is more complicated. Details of this problem will, however, be discussed in extenso in sections 3.1. and 3.3. of this paper.³

2.3. A very interesting mounted specimen of a male lion is preserved in the Zoölogisch Museum of the Amsterdam University. The specimen is registered in the museum collections under the number ZMA 9185 (Plate I). No precise data on this specimen are known save that it was in the museum collections (or in the former Cabinet of *Natura Artis Magistra*) at least as early as in 1845, this being clear according to a publication by BOTTARD to which Dr. P. J. H. van Bree, Curator of the Amsterdam Museum, has turned my attention. A foot-note in BOTTARD's work (1845, p. 242) gives the following information: 'Niet onbelangrijk kan het zijn . . . nog eens de fraaie monographie van de leeuw, door de heer H. Schlegel, te vergelijken. Uitgegeven bij M. Westerman & Zoon, te Amsterdam. Ook kan men nog in het kabinet van N. A. M. te Amsterdam, twee fraaie opgezette Leeuwen aanschouwen'. (Translation: It may be not unimportant . . . to compare once more the fine monograph on the Lion by Mr. H. Schlegel; published by M. Westerman & Zoon of Amsterdam. Also one may yet behold the two fine mounted lions in the Cabinet of the *N./atura/ A./rtis/ M./agistra/* in Amsterdam). This quotation certainly concerns the specimen in question, as in the Amsterdam Museum collections there is no other mounted male lion that could be taken into consideration. In addition the way in which the specimen is mounted seems to be typical of taxidermists' work at that time. There also is no doubt that in the 1840's and 1850's lions and lion skins were imported into the Netherlands from the Cape.⁴ Dr. P. J. H. van Bree has tried to find more detailed data concerning the specimen in question but he has not so far succeeded in coming across any really relevant

² As 'Caffraria', or 'Kaffraria', might be fruitlessly searched for on many a map I would like to indicate that the region in question lies on the eastern coast of Southern Africa, south of the region of the modern Transkei.

³ The skull in question was mentioned for the first time by LÖNNBERG (1912, p. 74) when he compared it with a lion skull from East Africa.

⁴ I can, for example, mention at this point the two mounted specimens of the Cape Lion of the Wiesbaden Städtisches Museum that were purchased from a certain Mr. Frank of Amsterdam (cf. MAZAK, 1964a, pp. 53-54). In addition, in the oldest part of the Lion file-card of the Amsterdam Zoo a lion from 'Kaapland' is mentioned on the list for the year 1854 (cf. Amsterdam Zoo file-card No. 247, *Felis leo*, dated 1839-1865). It may be interesting to note that the Royal Zoological Society 'Natura Artis Magistra', of which the Amsterdam Zoo as well as the Amsterdam Zoological Museum have formed parts, was founded in 1838 (Dr. P. J. H. VAN BREE, in litt. Dec. 9, 1969).

information that could clarify the origin of this mounted skin. The external characteristics of this specimen are none the less in such a first degree accordance with those of the specimens of known origin that I do not hesitate to refer it provisionally to the Cape subspecies of the Lion. There is also no contradiction as far as the date 1845 is concerned as at that time lions still lived in those parts of the Cape Province and of the Orange Free State that are considered to have constituted the former distributional area of the subspecies *melanochaita*.

3.

3.1. Geographical distribution of *Panthera leo melanochaita* (Ch. H. Smith, 1842) (fig. 1). It has sometimes been stated that the extinct Black-maned Lion of the Cape inhabited at one time the entire Cape Province and Natal (cf. HARPER, 1945, p. 297; MAZAK, 1968, p. 23; and others). The detailed study of the question has none the less led me to a somewhat different conclusion. The first clue was represented by numerous statements on diverse 'species' of the Lion, that allegedly formerly lived in the southernmost Africa, which are frequently found in the old literature. There is no doubt that a great many of these statements can be explained by the fact that the respective authors had referred to lions of different age as already suggested by some old hunters and naturalists, such as HARRIS (1840, p. 168) or CUMMING (1850, ed. 1911, p. 153). Yet, the possibility cannot be excluded that diverse types of the Lion really occurred in the southernmost parts of Africa.

If one looks at a map of South Africa where the vegetation and weather conditions are shown it becomes clear that the characteristics of biotopes in the eastern areas of the southernmost Africa are quite different from those in the interior of this part of the African continent; this being due to distinct orographical, hydrographical, geological, and climatological conditions in the respective areas. The problem is rather complex and detailed information in this respect can be found in ROBERTS (1951, pp. xxiv-xxx). In general, we can, however, say that the eastern parts of southern Africa as well as a narrow coastal belt in the extreme south are characterized by forest and shrub jungle, and by considerably high rainfalls, whilst the interior has a character of rather dry inland plateau plains, with hills and mountains, covered mainly with grass, scrub, and bush. The approximate borders of these two different types of country are formed by a system of mountain chains running from the extreme south in a more or less northern, or north-eastern direction and being principally parallel to the eastern coastal line. ROBERTS (1951, p. xxvi) calls this mountain system 'the great eastern escarpment' and adds (l.c.): 'Besides the great escarpment, which is situated well back from the coast in the south, there are two major and more minor parallel ranges nearer the coast which have a distinct bearing upon the flora and fauna.' West

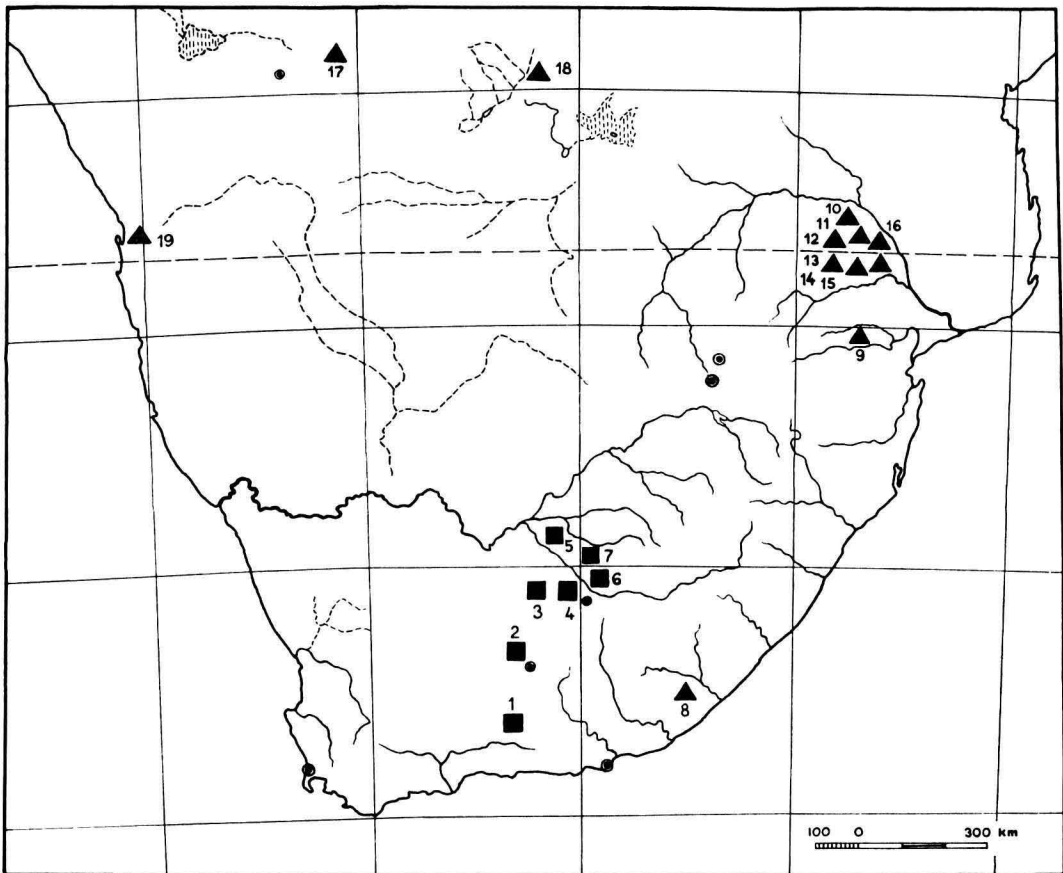


Fig. 1. A map showing principal localities of *Panthera leo melanochaita* (Ch. H. Smith, 1842) (squares), and *Panthera leo krugeri* (Roberts, 1929) (triangles). 1. Bier Valley, near Willowmore (cf. PATERSON, 1789, p. 33). 2. Murraysburg (LUNDHOLM, 1952). 3. Plains west of Colesberg (cf. CUMMING, 1850, ed. 1911, pp. 79 and 84). 4. Bontebok flats near Colesberg, mounted specimen, British Museum (Nat. Hist.), No. B.M. 68.268. 5. Riet River basin (cf. CUMMING, 1850, ed. 1911, pp. 139 and 141). 6. and 7. Orange River basin, supposed localities of the British Museum (Nat. Hist.) skulls Nos. B.M. 18.5.23.2. and B.M. 36.5.26.6. 8. Caffraria Interior, Naturhistoriska Riksmuseet, Stockholm, skull No. 1310. 9. Sabie River, British Museum (Nat. Hist.), skull No. B.M. 30.12.3.1. 10. to 16. Manzemntondo River, N.E. Transvaal, British Museum (Nat. Hist.), skulls Nos. B.M. 25.6.17.5., B.M. 25.6.17.6., B.M. 25.6.17.7., B.M. 25.6.17.8., B.M. 25.6.17.9., B.M. 25.6.17.10., and B.M. 25.6.17.12. 17. Karkuwisa, Grootfontein, British Museum (Nat. Hist.), skull No. B.M. 35.9.1.129, 18. Mababe Flats, Mogogelo River, British Museum (Nat. Hist.), skull No. B.M. 31.2.1.4. 19. Walvis Bay, Damaraland, Naturhistoriska Riksmuseet, Stockholm, skull No. 1971.

of the 'Great Eastern Escarpment Mountains' of 900 to 3400 m lie plains of the interior plateau at altitudes of 500 to 2000 m. On the eastern side of the 'Great Eastern Escarpment'⁵ then lie forested areas of

⁵ On some maps edited in Europe this huge mountain system is from time to time called Drakensberge, though this name can, in fact, be applied to just a relatively small part of the 'Great Escarpment', situated in south-eastern Basutoland (Lesotho) and in adjacent parts of the Cape Province.

mountains and of the coastal belt. The difference in general aspects of these two types of country cannot be better illustrated than by CUMMING's account of his travels from Grahamstown to Colesberg. At the beginning of his journey he traversed a 'country which . . . was densely covered with one vast jungle' and gives his testimony about 'the forests and jungles of Albany and Kaffraria' where 'many varieties of noble forest-trees are found of considerable size and great beauty'. Later on, when having left Cradock, he came into a country that 'presented in every direction endless chains of barren stony mountains' where 'not a tree was to be seen except a few thorny mimosas . . . the country being covered with grass and heaths, dwarfish shrubs, and small thorny bushes'. After crossing these chains of mountains he finally reached the great plains and in his account he uses such expressions as 'immense flats', 'wide open flats', and 'a plain of unlimited length' (cf. CUMMING, 1850, ed. 1911, pp. 41, 42, 53, 60 and 64).

Considering all the above mentioned data and the fact that it is not uncommon to find different mammal forms in the eastern areas and in the interior of the most southerly parts of Africa, I came to the conclusion that the distribution range of the Black-maned Lion of the Cape embraced not the entire territory of southernmost Africa (i.e., the whole Cape Province, the Orange Free State, and Southern Natal) but just the temperate inland plateaux of the Cape and of the southern parts of the Orange Free State. The former range of the extinct lion subspecies *Panthera leo melanochaita* (Ch. H. Smith, 1842) can thus be restricted to the vast plains of the South African interior that lie west of the 'Great Eastern Escarpment'. This system of plains covers the wide karroo plains of the interior of the Cape, intersected by numerous typical hill and table-mountain formations, further the complex of flats of basins of the Vaal River, including the Riet River system, and the plains on the northern bank of the middle course of the Orange River that are situated south of the Kuruman Hills and bordered by the Lange Berge on the west and by the lower course of the Vaal on the east. North and east of the area defined in this way there probably lived a different subspecies that was, or most probably was, that which we now know as *Panthera leo krugeri* (Roberts, 1929).⁶ This interpretation of the range of the Black-maned Lion of the Cape is also supported by a statement of ROBERTS (1951, p. xxvi) who says that the 'Great Eastern Escarpment' mountains ' . . . do not furnish barriers to distribution as one might expect, though the climatic conditions prevailing on opposite sides of them usually promote differences in the flora and fauna.'

The distribution area of the Black-maned Lion of the Cape interpreted in this way practically coincided with the range of several other big

⁶ I would like to state at this place that I am aware of the fact that this conclusion is supported mainly by more or less circumstantial evidence and not by actual material.

mammals, such as the True Quagga, *Equus (Hippotigris) quagga* Gmelin, 1788, the Black Wildebeest, *Connochaetes gnou* (Zimmermann, 1777), the Cape Hartebeest, *Alcelaphus buselaphus caama* (G. Cuvier, 1804), or the Blesbok, *Damaliscus dorcas phillipsi* Harper, 1939. Dr. COLIN P. GROVES adds (in litt., Dec. 2, 1969) that the distribution of the Cape Lion as interpreted here '... corresponds exactly with the distributions of species and subspecies within such genera as *Diceros*... *Phacochoerus*... *Syncerus*... *Sylvicapra*, *Hippotragus*, *Damaliscus*, *Antidorcas* etc. (to mention but a few!) all of which have species, or sometimes just subspecies, restricted to the area in question: i.e., western and central Cape Province, the Orange Free State, and perhaps neighbouring portions of South West Africa... It all seems to indicate a unique indigenous fauna, which of course was largely destroyed by Boer meat-hunters as they spread north'.

Lions known as having once inhabited the countries in southern Africa that lie on, and/or east of, the 'Great Eastern Escarpment', i.e. the easternmost parts of the Cape Province, Albany, Caffraria, and Natal, most probably represented a different lion form, obviously akin to, or identical with, the subspecies *Panthera leo krugeri* (Roberts, 1929).⁷ Hence, two different forms of lion could really have occurred in southernmost Africa, having lived in somewhat different environments and having been more or less separated geographically. This could suggest an explanation for at least some of the old hunters' statements concerning different lion 'species' of South Africa.

As far as the records go the Black-maned Lion of the Cape did survive none too long into the second half of the 19th century, and was the first of the African lion geographical races that became extinct. HARPER (1945, p. 297) supposes that the last specimens of this subspecies were killed in the Cape and in Natal in 1858 and 1865 respectively; this information having been based on the data quoted by SHORTRIDGE (1934, p. 80) and SCLATER (1900, p. 31). The last records of the Lion for the Cape south of the Orange River generally mentioned (cf. SHORTRIDGE, l.c., PALMER, 1950, p. 13, SPEIGHT, 1964, p. 23, and others) are Port Alfred in 1846, Lombards Post near Bathurst in about 1850, and Ingonyama Tributary of the Tsomo River, Transkei, in 1858. All these localities are, however, situated to the east of the 'Great Eastern Escarpment' and if the above given interpretation of the distribution range of the Cape Lion is accepted these data cannot be referred to the subspecies *melanochaita*, but most probably to another form (cf. *krugeri*) that was distributed along the eastern parts of southernmost Africa.

⁷ I suppose, according to various materials (skulls, skins, photos) that I have studied, that the so-called Kalahari Lion, *Panthera leo vernayi* (Roberts, 1948), described from the Matapa Pan, Central Kalahari, Bechuanaland, does not sub-specifically differ from the Kruger Lion and I consider the name *vernayi* Roberts, 1948 a synonym of *krugeri* Roberts, 1929.

The Stockholm Naturhistoriska Riksmuseet skull collected by J. WAHLBERG in 1845 in Caffraria, that I have mentioned in section 2.2., constitutes an analogous case and it is one of the reasons why I do not refer it to the Cape Lion. The other, equally important reason concerns its difference from the two skulls of the British Museum (Natural History) as will be shown in another part of this paper.

As to the area to which the range of the subspecies *melanochaita* has here been restricted it is rather difficult to find exact data concerning the extermination of this race of lion. In the time of ANDREW SMITH (quoted according to GUGGISBERG, 1961, pp. 38–39), i.e., in the years 1834–36, lions could still be found between Colesberg and Visser. However plentiful lions once had been on the great plains of the Karroo at the end of the 18th and at the beginning of the 19th centuries (cf. SPEIGHT, 1964, p. 22) they became scarce very soon; already when CUMMING was hunting in South Africa in the years 1843 to 1849 he was not able to collect many data about the occurrence of lions on the plains south of the Orange River. According to CUMMING (1850, ed. 1911, p. 84) lions were formerly extremely abundant on the vast karroo plains west of Colesberg,⁸ and at the time of his expeditions a few were still to be met with there. In 1844 he also saw ‘two fine lions, a male and female’ that were shot by the Boers on the plains south of the Riet River (CUMMING, l.c., p. 141).⁸ In the Riet River basin he met lions several times (cf. pp. 151 and 163 of his publication). When reading attentively CUMMING’s account of his expeditions, one has to conclude that lions were already rather rare in the Orange and Riet River regions at that time and that CUMMING was very probable one of the last competent hunters and explorers who left for us their testimony of direct personal experience with the extinct Black-maned Lion of the Cape. According to all the known evidence I presume that this lion subspecies did not long survive the end of the 1850’s and that the last specimens could have been met with on the plains of the southern parts of the Orange Free State in the Riet River basin. In the northern parts of the Orange Free State the lions survived somewhat longer, certainly into the second half of the 1860’s. It is, however, very improbable that the lions formerly inhabiting northern regions of the Orange Free State could be referred to the subspecies discussed here.

3.2. External Characteristics of *Panthera leo melanochaita* (Ch. H. Smith, 1842). For about three quarters of a century after the Black-maned Lion of the Cape became extinct there was no material evidence that could support the old statements that this lion form really represented a distinct geographical race. No wonder then that doubts arose as far as the

⁸ For the determination of these localities see pp. 79 and 139 respectively of CUMMING’s quoted work.

systematic status of the lion form in question was concerned. These doubts have even sometimes outlasted the discovery of the first mounted skin of a male lion that was undoubtedly a representative of the extinct Cape race. This was the specimen that is now deposited in the collections of the British Museum (Natural History) and was described for the first time by POCOCK (1931). At the present time it is, however, generally agreed that the subspecies *melanochaita* should be considered valid.

At the time being there is a greater amount of material that forms a rather solid basis for a more detailed study of the Cape Lion. External characteristics of this subspecies of lion have already been several times discussed (cf. STEVENSON-HAMILTON, 1947, p. 126, ROBERTS, 1951, pp. 190–191, MAZAK & HUSSON, 1960, MAZAK, 1964) and I intend to summarize here the known data as well as to bring forward some new aspects of this subject.

When describing his *Leo melanochaitus*, SMITH (1842, p. 177) pointed out several features that he considered characteristic of this form of lion; the most important of which were a very extensive mane of black colour, the presence of a fringe of long hair under the belly, the bulldog-like shape of the head, large pointed ears fringed with black, and the structure in general proportions lower than in other lions. A more or less identical description was also given by FITZINGER (1868, p. 438) who apparently did not know SMITH's work. All the characteristics mentioned above could principally be confirmed or explained by the study of the available material except the one concerning the shape and colour of the ears as will be shown further.

There are 7 mounted skins of the Cape Lion preserved in various museums that represent the evidence relevant for a study of the external characteristics of this subspecies. The Natural History Museums of Leiden, London, Stuttgart and Wiesbaden possess each one adult, wild-shot male specimen, the Paris Museum National d'Histoire Naturelle has a young-adult, not full grown male specimen from the Paris Menagerie, and the Museums of Stuttgart and Wiesbaden, in addition to their respective male specimens, possess each one adult, wild-shot female specimen. This amount of material can, however, provisionally be enlarged by an adult, wild born and apparently wild-shot, male specimen from the Amsterdam Zoological Museum that I referred to in section 2.3. of this paper. I can only repeat that I am fully convinced that the Amsterdam specimen can be regarded as a genuine Cape Lion. Its accordance with the other adult male specimens, especially with those of the Leiden and London museums, is perfect and as thorough as it can at all be; the only difference between the Leiden specimen on the one hand and the London and Amsterdam specimens on the other being the extent of the belly mane.

All the adult male specimens, including the Amsterdam one, show splendid manes. The mane extends from the crown of the head well in front of the ears and covers the whole of the back of the head, neck,

throat, chest and shoulders, reaching far behind the latter. The arm itself (i.e. the humerus region) is generally free of mane, though the long hairs can more or less fall onto it from the shoulder region which is completely covered by the mane.⁹ A rather wide banner of long mane hairs extends from the back and shoulders down along the hind outline of the arm, joining a very heavy and long elbow tuft and the chest fringe between the fore limbs.

One of the external characteristics of the Cape Lion that was emphasized in all the old descriptions (HARRIS, 1939 and 1940, SMITH, 1842, FITZINGER, 1868), was that this subspecies developed a very distinct belly mane which clearly separates it from other wild living South African, and more northerly forms of lion except the extinct Barbary Lion, *Panthera leo leo* (Linnaeus, 1758). All the six preserved male specimens of the Cape Lion (i.e. including the Amsterdam Museum adult specimen as well as the young-adult one from the Paris Museum) display well developed belly manes. In three specimens, viz. in those of the museums of London, Stuttgart, and Amsterdam, a thick growth of long hairs traverses the abdomen in two parallel bands, being very heavy, long, and thick behind but disappearing just in front of the chest. In the other three specimens, i.e. in the specimens of the Leiden, Wiesbaden and Paris museums, the belly mane covers the whole of the underparts, becoming nevertheless much thinner and shorter in front of the chest.

This form of the belly mane as well as the variability of its extent is found not only in the Cape Lion but more or less in the extinct Barbary Lion as well (cf. MAZAK, 1970).

The elbow tufts and the tail tuft are in all the specimens that were examined very long and thick.

As to the colour of the mane it is, in general, tawny around the face, and sometimes on the crown and back of head, and deeply blackish, or pure black, on the neck, throat and shoulders. The elbow tufts, belly mane and the tail tuft display the same black colour. In the Leiden, London and Amsterdam specimens, and more or less in the Wiesbaden one also, the most remarkable feature is a very sharp colour contrast between the tawny fringe around the face and the blackness of the mane on the throat, neck, shoulders, and chest that thus gives an impression of a tawny-coloured 'collar'. The Stuttgart Museum specimen is rather faded, yet it is obvious that the tawny colour has to a certain degree graded into the darker shades, so that the mane was black under the throat and chest, and on the hind parts of the shoulders only. This might be explained by supposing that the lion in question was shot near to the eastern or western limit of the range where an influence of other lion populations could have been manifested since such an intergradation

⁹ The London and Wiesbaden museum specimens have, however, somewhat longer hairs on the arm.

of colours in the mane can commonly be observed in lions inhabiting Transvaal and Bechuanaland as well as in lions from the more northerly parts of Africa. Unfortunately the exact locality of the Stuttgart specimen is not known; it has only been stated to have originated from the Cape. The mane of Paris specimen is much lighter in colour, this being due partly to the action of light, partly to the fact that it was a rather young animal in which the mane was not yet fully developed as far as its colour is concerned (cf. MAZAK, 1964a, p. 57, 1964b, p. 125).

The mane hair of the subspecies *melanochaita* can sometimes reach a really extraordinary length. The respective measurements of the mane hair in the Leiden, Amsterdam, and Wiesbaden specimens are as follows: crown of the head and neck, 130 to 220 mm, 130 to 250 mm, 160 mm; shoulders, 220 mm, 250 mm, 220 mm; throat, 300 mm, 290 to 310 mm, 250 mm; chest, 290 to 310 mm, 310 to 340 mm, 250 mm; elbow tufts, 140 to 150 mm, 150 to 160 mm, 70 mm; the posterior part of the belly, 275 mm, 120 to 135 mm, 80 mm. When looking at either the Leiden, London or Amsterdam specimen one perfectly understands why CUMMING (1850, ed. 1911, p. 153) says that the male lion '... is adorned with a long, rank, shaggy mane which in some instances almost sweeps the ground...'.

All the above described characteristics of the mane of the Black-maned Lion of the Cape that were ascertained on the basis of preserved specimens are also perfectly visible on the representations of this form of lion made by W. CORNWALLIS HARRIS (1840, pl. XXIX and a black-and-white engraving of a skin of a male lion shot by HARRIS, p. 170).

As far as can be ascertained the ground colour of the Black-maned Lion of the Cape in both sexes seems to be somewhat darker than that of the most other populations of lions. It can be described as deep tawny, with a certain greyish shade. This is in full accordance with a statement of HARRIS (1840, p. 168) who describes the ground coloration of the South African Lion as varying from ash colour to tawny dun. The material I studied shows that the hairs of upper body parts, flanks, and exposed surfaces of limbs have blackish or dark-brown tips which, especially in males, results in a very dark-grey or blackish grey aspect of certain areas, mainly on the back. The tail becomes in its most distal part increasingly dark toward the tip, grading thus into the black colour of the tail tuft. None of the preserved male specimens of the Cape Lion displays, however, a completely black-coloured terminal fourth of the tail as stated by ROBERTS (1951, p. 191) for the adult males of the Kruger Lion, *Panthera leo krugeri* (ROBERTS, 1929) and as I have seen myself on some skins from the Kruger National Park and on the skins of lions from other areas of South Africa.

The body hair is relatively long, decidedly longer in average than is usual in more northerly forms of lion, except the Barbary Lion (cf. MAZAK, 1970). In the Leiden Museum male specimen the average hair

length varies from 27 to 30 mm on the back and from 26 to 28 mm on the flanks, the individual hairs being however as long as 35 mm. In the Amsterdam Museum male the hair is slightly shorter, yet it averages from 22 to 28 mm in length. Contrary to this the average length of body hairs of lions from Transvaal and Bechuanaland that I examined in various museums was about 10 to 13 mm and in the majority of the East African lions the hair was even shorter. Similarly, ALLEN (1924, p. 224) states that in lions from north-eastern Belgian Congo the hair is short, being only about 8 to 10 mm in length in the type specimen of *Leo leo azandicus* described by him.¹⁰

As to females, both the Stuttgart and Wiesbaden skins show fairly long hair, with small elbow tufts and very long, almost mane-like hair on the throat, breast, and under the belly.

All the specimens show crests of somewhat longer tawny hair that run along the hind surfaces of the legs, extending from the elbow tufts or from the heels respectively down to the paws. This feature is most conspicuous in the Leiden, London, Stuttgart, and Amsterdam males as well as in the Stuttgart female.

It seems that one of the characteristics that appeared in most Cape Lion specimens was a dark marking on the anterior surfaces of both the fore and hind paws, i.e. on the anterior surfaces of the autopodial parts of legs. This marking, being more conspicuous in males, is demonstrated by several spots of irregular shape and dark brown to almost black colour, and has absolutely nothing to do with the juvenile spotting of young or young-adult lions. The small interdigital tufts of black hairs, commonly found in all other forms of lion, are, of course, present as well. In none of the skins of the other subspecies that I have studied, including the Barbary Lion, *Panthera leo leo* (Linnaeus, 1758), there was to be ascertained a marking similar to that described above.

The marking in question is most distinct in the Leiden (fig. 2) and Amsterdam (fig. 3) specimens, in which it is almost pure black. In the Wiesbaden Museum male it seems, on the contrary, to be completely lacking, which might, however, have perhaps been caused by a rather greater degree of loss of colour. In other specimens the darker spots on the autopodial parts of the legs are less conspicuously displayed.

It is indeed very difficult to state whether this characteristic can or cannot be considered one of the typical features of the Black-maned Lion

¹⁰ I consider the form *Panthera leo azandicus* (Allen, 1924) as being consubspecific with the East African Lion. The East African Lion is generally listed as *Panthera leo massaica* (Neumann, 1900) but the material I studied has convinced me that several lion forms described from various regions of East Africa and from eastern regions of Central Africa belong, in fact, to a single subspecies that should be, according to the rules of priority, called *Panthera leo somaliensis* (Noack, 1891) (cf. also MAZAK, 1968, p. 21).

of the Cape. None the less, for the time being, I am inclined to regard it as such.

As to the shape and the colour of the ears in the subspecies *melanochaita* the following statement is found in SMITH (1842, p. 177): ‘. . . large pointed ears edged with black . . .’. This description of ears, however, cannot be confirmed by the available data. The ears of all the preserved specimens are very large, it is true, but cannot certainly be characterized as being pointed, nor are they edged with black. There is a certain possibility, though not a very probable one, that the shape of the ear may have been altered by the respective taxidermists but there is decidedly no possibility that the colour-pattern of the ears was changed. The dorsal surface of the ears of all the known specimens of the Cape Lion show the same type of marking as the one usually found in all other subspecies, viz. a rather broad, dark-coloured transverse band of irregular shape. I conjecture that the above quoted description by SMITH of the ears is erroneous as it seems very unlikely that the lions of the Cape would have had the ears of a different shape and/or colour pattern than the other representatives of the species.

Perhaps none of the other characteristics of the Black-maned Lion of the Cape given by SMITH (1842) has so much been discussed as the one regarding the form of the head. SMITH’s words ‘The species is of the largest size, with a bull dog head; the facial line much depressed between the eyes . . .’ have caused many a surmise of what the head of the Cape Lion could have looked like (cf. STEVENSON-HAMILTON, 1947, p. 126; PALMER, 1950, p. 13; MAZAK & HUSSON, 1960, p. 103, and others). It has been shown elsewhere (MAZAK & HUSSON, l.c., pp. 109–110) that we apparently have at our disposal a perfect representation of a male Cape Lion made by the famous artist of the XVIIth Century Rembrandt Harmensz van Rijn. His drawing ‘Reposing Lion’ (deposited in the Paris Louvre, No. H. 751) represents a lion with a big, massive, and relatively short-muzzled head that shows quite clear bulldog-like features.¹¹ Skulls of the genuine Cape Lions that I had the opportunity to study display certain characteristics in their structure which seem to indicate that the head of this subspecies was massive and robust, with heavy mandible, slightly straighter upper profile line, and somewhat higher placed nostrils than is the case with other lions (cf. next section of this paper). These characteristics could have thus been responsible for a more foreshortened appearance of the head and for a somewhat retroussé-like nose of the Cape Lion. The basis of the nose could also have been more wrinkled than that of other lions as the plate published by SMITH (1842, pl. X) as well as Rembrandt’s drawing (cf. MAZAK & HUSSON

¹¹ There are several other drawings of the same lion in various collections, the Paris one being however most famous and showing all the characteristics of the Black-maned Lion of the Cape in the best way.

1960, pl. X) suggest. All these features might result in the general impression of a heavy bulldog head.

It is certainly not without interest to quote at this place a brief description of the South African Lion given by D. F. WEINLAND, the first editor of the well-known journal 'Der Zoologische Garten' who had, in 1860, seen two adult captive specimens of the Black-maned Lion of

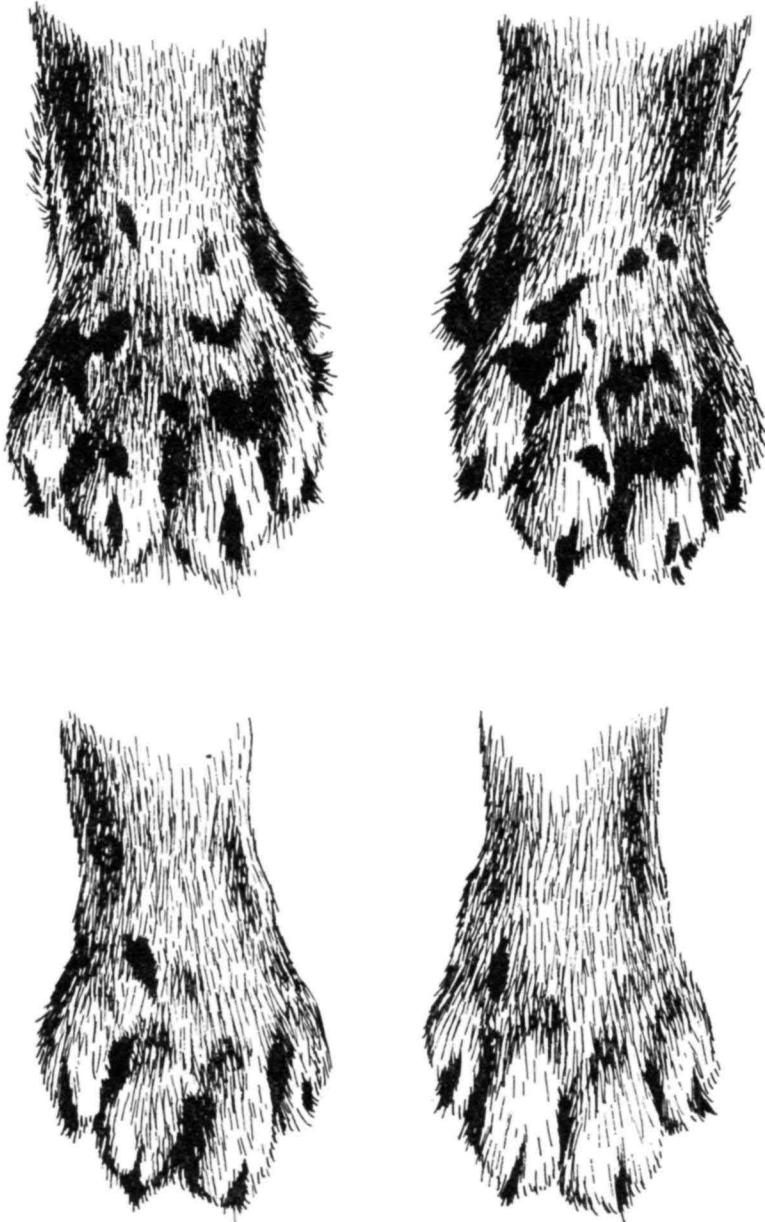


Fig. 2. Dark markings on the anterior surface of the autopodial parts of the legs in the male of the Black-maned Lion of the Cape, Leiden Museum, no. 'a'. Above: right and left fore leg; below: right and left hind leg.

the Cape in Frankfurt a. M.: '...südafrikanische Löwen; mit fast schwarzer Mähne, breiterem, aber kürzerem, fast bullenbeisserartigem Kopfe und Schnauze, auch etwas vorstehendem Unterkiefer und fast ganz schwarzen Ohren. Von dieser Race haben wir zwei Prachtexemplare, beide Männchen, in der Menagerie von Renz hier gesehen, die, so viel wir hörten, nachher nach England gekommen sind'. (cf. WEINLAND, 1861, p. 174).

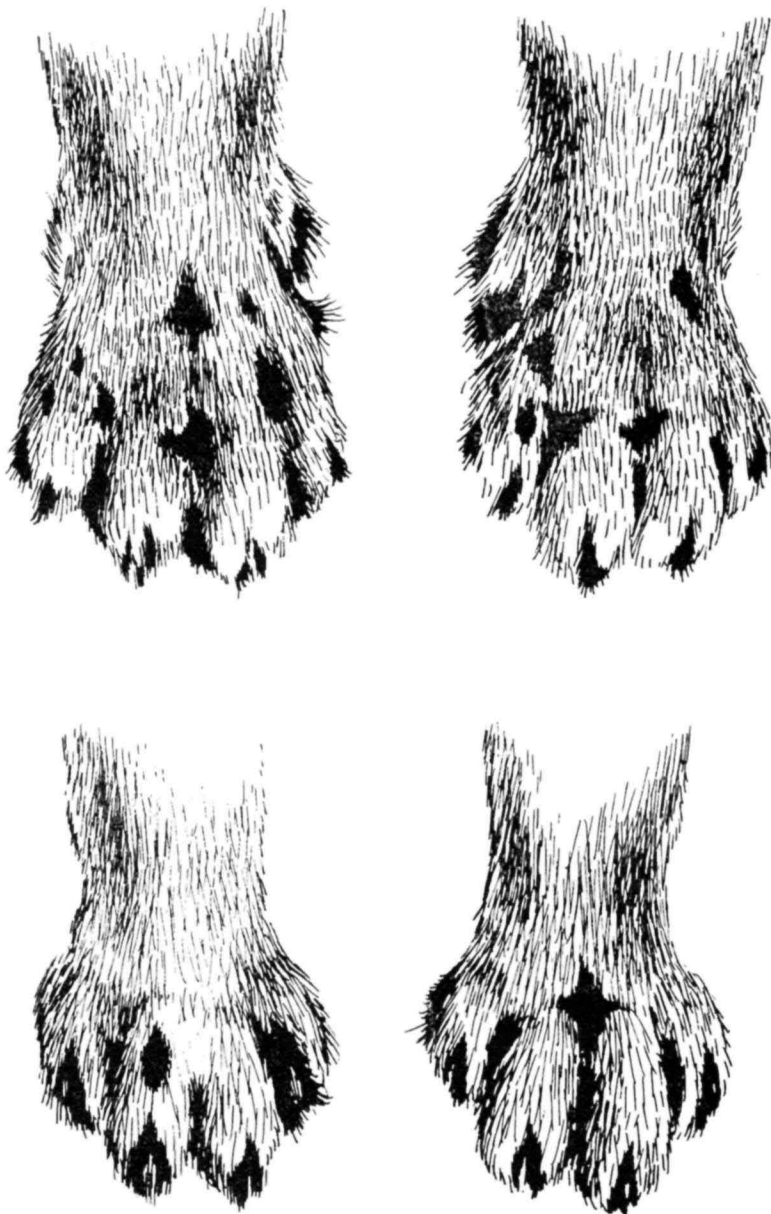


Fig. 3. Dark markings on the anterior surface of the autopodial parts of the legs in the male of the Black-maned Lion of the Cape, ZMA 9185. Above: right and left fore leg; below: right and left hind leg.

As far as SMITH's (1842, p. 177) statement 'in general proportions lower than in other Lions' is concerned, I suppose that a long and large mane, and especially the ridge of long hairs under the belly could have made the Black-maned Lion of the Cape seem relatively lower than other lions. In addition, this was certainly accentuated by a somewhat more powerful, more robust and heavier body structure which has always been emphasized in all the accounts concerning this splendid extinct subspecies of the Lion.

As already mentioned in the section 1. of this paper the plate that accompanies SMITH's description (1842, pl. X) shows a lion of a somewhat peculiar appearance and I would like to mention here that a much better and certainly much more realistic representation of the Black-maned Lion of the Cape can be found on a very fine plate made and published by HARRIS (1840, pl. XXIX).

3.3. The Skull Structure of *Panthera leo melanochaita* (Ch. H. SMITH, 1842). LUNDHOLM (1952) published a description of a Cape Lioness skull that was dug out of a river bank near Murraysburg in the Karroo area. The skull is now deposited in the Museum, Snake Park and Oceanarium in Port Elizabeth. LUNDHOLM (l.c.) pointed out two features in which the Murraysburg skull distinctly differed from other female African lion skulls. The features in question are (1) relatively shorter occipital region and (2) somewhat broader muzzle. Later on, MAZAK & HUSSON (1960) found that the mandible of the Murraysburg skull was relatively somewhat longer than in other lions. At that time no other Cape Lion skull had become known and the Murraysburg skull of a female specimen thus represented the only evidence on the basis of which the craniological characteristics of the subspecies *melanochaita* could be assessed.

I have very carefully studied the paper of LUNDHOLM (l.c.) again, and, especially, the photos of the Murraysburg skull published there. The result of this quite undubitably shows that the Murraysburg skull is not that of an adult. There is absolutely no doubt that the skull belonged to a rather young specimen, the age of which I estimate at about 2 to 2½ years. The most important fact that led me to this conclusion is the state of the skull sutures. LUNDHOLM (1952, p. 21) himself says: 'The basal sutures are rather open, which may have been caused in part by the soil conditions where the skull was found, as repeated changes in the moisture content of the soil can have widened the sutures'. I cannot agree with this suggestion. My experience with different fossils from Pleistocene deposits shows that those skull sutures which had been completely ossified and closed during the lifetime of the respective animal, have never become separated again; not even in the most extreme conditions of the deposit. I studied, for example, a skull of a Cave Lion, *Panthera spelaea* (Goldfuss, 1821) found on Lyakhov Island (Zool. Mus. Leningrad, No. 15 572) that had for many millennia been exposed to

frost and to changes in temperature as well as in the moisture content of the soil, yet the basal sutures and the sutures of the skull-roof were perfectly closed. Hence, in my opinion, the explanation given by LUNDHOLM (l.c.) can be applied in those cases only when the sutures had not become completely closed before the death of the animal concerned. There is no doubt that the Murraysburg skull was exposed to much less severe conditions, and for a considerably shorter period than the above mentioned skull of the Cave Lion. The photos published in LUNDHOLM's paper (l.c., pl. III) show that not only the basal sutures are open but that the same state can be found in some other sutures as well. Parieto-temporal, fronto-parietal, palato-maxillary, and interfrontal sutures are clearly visible, being not at all ossified, which would never be the case with any really fullgrown specimen of lion. A comparison with big cat skulls of known age has shown that the Murraysburg skull is of a specimen that might have been, as already mentioned, about 2 to 2½ years old, at the most, when it died. In addition, the general shape of the skull (relatively flatter rostral part, highly vaulted neurocranium, and a very convex lower edge of the mandible) also show that the growth of the skull was not definitely finished which once again contradicts LUNDHOLM's (l.c.) statement that '... the animal must have been full grown and of middle age'.

Accordingly, all the circumstances described above make the description of a skull of a fullgrown Cape Lion most necessary. The two male skulls from the collections of the British Museum (Natural History), that I mentioned in section 2.1., are undoubtedly those of fullgrown, adult specimens, being thus very suitable for a taxonomical examination. There also is no doubt that they originated from a region that lies within the range of the extinct Cape subspecies of the Lion.

As mentioned above one of the skull features of the Cape Lion given by LUNDHOLM was relatively shorter occipital region. LUNDHOLM (l.c.) demonstrated this by the finding that the occipital length, as a percentage of the greatest length of skull, in the Murraysburg skull was considerably higher than that of the more northerly lion populations. This relation between the two respective skull lengths can be expressed as $100 \times \text{condylobasal length} / \text{greatest length}$ (further on only '100 Cb/Gtest l.', fig. 4). LUNDHOLM (l.c.) found in the Murraysburg female skull that this ratio was equal to 94.8, whilst in 10 female skulls from northern Transvaal and Ngamiland the average was 89.2, with a variation from 87.4 to 90.8, and σ was 0.95.

The British Museum male skull No. B.M. 18.5.23.2 (Plate IV) has its occiput cut off which makes it impossible to examine the skull as far as the ratio 100 Cb/Gtest l. is concerned. The other British Museum male skull, i.e. the skull No. B.M. 36.5.26.6., is intact and I found that the condylobasal length was 90.9% of the greatest length of skull. This figure is practically equal to the maximum value given by LUNDHOLM (l.c.) for the female skulls of northern Transvaal and Ngamiland (Bechuanaland).

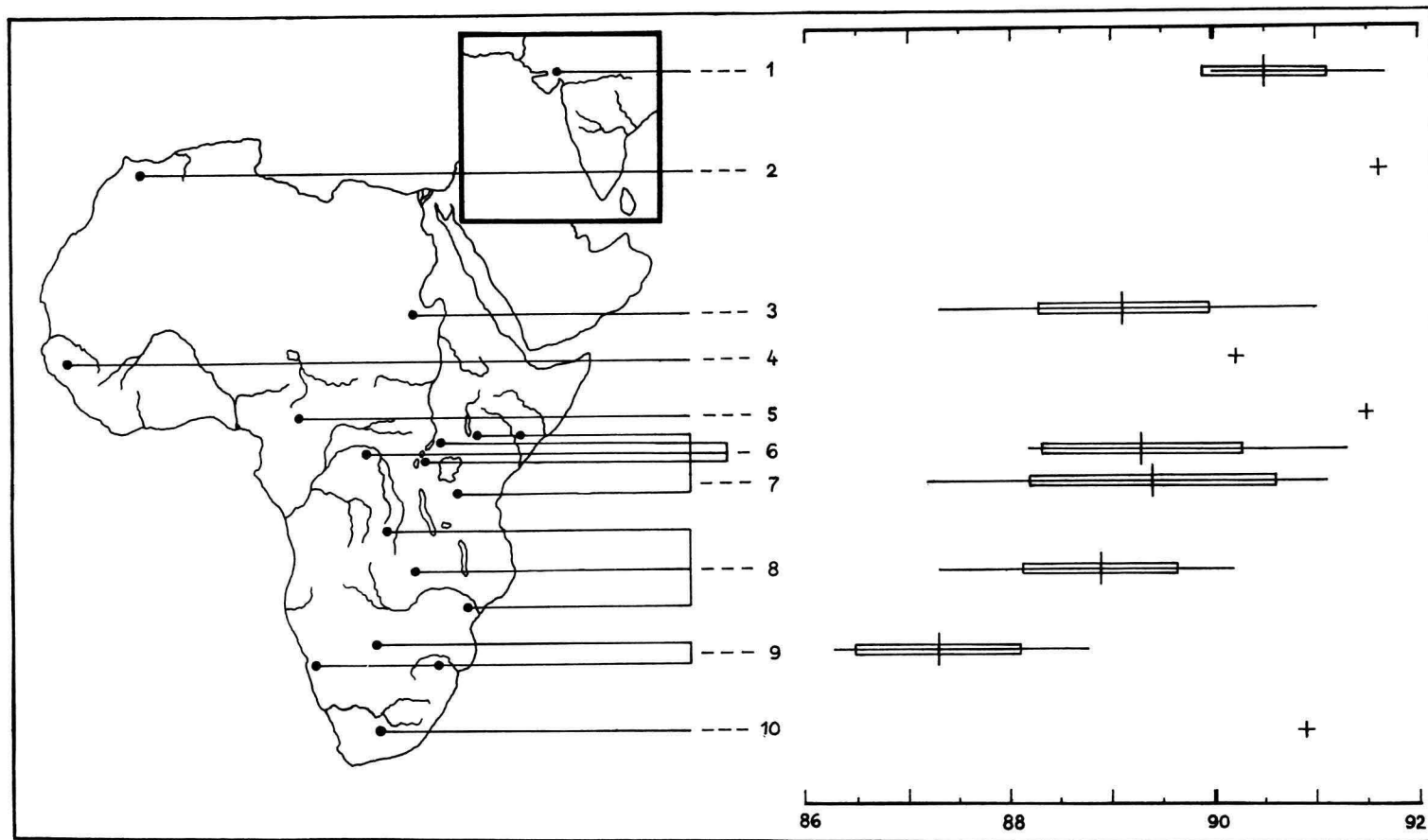


Fig. 4. A graph to show the differences in the ratio '100 Cb/Gtest 1.' in males of various lion populations. 1. India and Persia (n=5). 2. Barbary (n=1). 3. Sudan (n=21). 4. Gambia (n=1). 5. French Cameroon (n=1). 6. North Congo, Ruanda Urundi, and Uganda (n=20). 7. Kenya, Tanganyika, and Somaliland (n=22). 8. South and North Rhodesia, South Congo, Mozambique (n=16). 9. North-Eastern Transvaal, Bechuanaland, and Damaraland (n=11). 10. Cape, ?-Orange River basin (n=1). Where it was possible mean value, \pm standard deviation, and limits of individual variation are indicated. For details see Table 2. Geographical names are indicated according to original labels.

When the male skull No. B.M. 36.5.26.6. (Plate V) from the Cape Province was compared with a set of 11 adult male skulls from other parts of Southern Africa, it **did**, none the less, differ from them in the same way as the Murraysburg female skull differs from the female skulls of northern Transvaal and Ngamiland. The mean value of the ratio 100 Cb/Gtest l. of the 11 male skulls from north-eastern Transvaal, Bechuanaland, and Damaraland is 87.3, with an actual variation of 86.3 to 88.8, and σ is 0.81. Hence it seems that there exists sexual dimorphism in the ratio 100 Cb/Gtest l.¹² An unusually high value of this ratio found in the Murraysburg female skull is obviously due to the fact that the animal was rather young as I have shown above. There is no adult female skull at our disposal and it is thus impossible to determine what the mean value of the ratio 100 Cb/Gtest l. could be like for adult females. I estimate, however, the respective figure might vary around 92 or 92.5.

Data concerning the relation between the condylobasal length and the greatest length of skull in different forms of lion are summarized in Table 2. The respective figures show clearly that the Cape Lion is rather distinctly separated from other South African lions, i.e., from the subspecies *Panthera leo krugeri* (ROBERTS, 1929); the British Museum male skull No. B.M. 36.5.26.6. being 4.4 units of the standard deviation from the mean value of the eleven male skulls from Transvaal, Bechuanaland, and Damaraland. It is, however, no less clear that the Cape Lion cannot in this way be distinguished from all the lion forms as in more northerly lion populations an increase in the average values of the ratio 100 Cb/Gtest l. can be observed, reaching its maximum in the Barbary and Indian Lions (cf. Table 2, fig. 14).

As to the Stockholm Museum male skull No. 1310, collected by J. WAHLBERG in the 'interior of Caffraria' (see section 2.2. of this paper), its condylobasal length is 86.3% of the greatest skull length which is equal to the minimum value for the 11 skulls of *krugeri*. This finding thus supports the suggestion that *Panthera leo krugeri* penetrated in the past into the southernmost Africa through coastal areas situated east of the Great Eastern Escarpment (cf. section 3.1. of this paper).

The same can be said about a male skull of the Leiden Rijksmuseum van Natuurlijke Historie mentioned by MAZAK & HUSSON (1960, pp. 108-109). This skull (No. 'i'-663 Br), said to have come from the 'Kaap' (cf. JENTINK, 1887, p. 81), is not of a fullgrown adult male as was originally supposed (cf. MAZAK & HUSSON, l.c.) but that of a young adult male as its half-closed basal suturae demonstrate. The ratio

¹² Somewhat higher values of the ratio in question in female skulls could be considered one of the so-called juvenile characteristics; I think I need hardly emphasize that the Lion is one of those species of Carnivora in which the skulls of adult females display certain juvenile features when compared with those of adult males.

TABLE 1. Skull measurements of wild shot males of *Panthera leo melanochaita* (Ch. H. Smith, 1842) and *Panthera leo krugeri* (Roberts, 1929).

No.	British Museum (Natural History), London								Naturhistoriska Riksmuseet, Stockholm	
	B.M. 36.5.26.6	B.M. 18.5.23.2	B.M. 25.6.17.5	B.M. 25.6.17.6	B.M. 25.6.17.7	B.M. 25.6.17.8	B.M. 25.6.17.9	B.M. 25.6.17.10	1310	1971
Subspecies	<i>melanochaita</i> (Ch. H. Smith, 1842)		<i>krugeri</i> (Roberts, 1929)							
Sex	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂
Locality	Cape, ?Orange River Basin	Cape, ?Orange River Basin	N.E. Transvaal, Manzemntondo River						Caffraria Interior	Damaraland Walvis Bay
Greatest length	358.1	—	366.0	386.0	382.3	385.0	378.0	379.5	394.0	396.0
Condylbasal length	325.5	—	322.8	335.0	330.0	335.6	327.8	329.4	340.0	350.5
Basal length I	308.5	—	305.4	318.0	312.0	318.0	308.3	311.0	322.5	332.0
Basal length II	300.0	—	296.8	309.0	303.0	308.4	297.4	301.3	312.0	324.0
Rostral breadth	96.0	104.5	95.3	100.5	98.3	104.0	101.5	101.3	103.0	103.0
Rostral depth	84.0	85.0	82.0	81.0	78.0	81.0	78.0	80.0	78.0	79.0
Greatest length of nasals	102.5	106.3	108.7	110.0	105.0	111.5	106.0	106.5	109.0	110.0
Prosthion-meatus acusticus externus	—	281.0	—	272.0	271.0	270.5	264.7	263.5	274.0	277.0
Interorbital breadth	68.3	75.5	72.8	71.5	76.8	78.8	74.5	77.0	71.0	74.6
Postorbital breadth	65.0	68.3	69.6	65.0	65.3	65.3	69.7	68.4	68.0	67.0
Bizygomatic breadth	235.5	255.8	247.5	245.2	254.6	249.0	250.5	247.0	251.0	270.0
Mastoid breadth	128.6	—	138.8	136.0	140.4	143.5	139.8	140.5	137.5	147.5
Pm ⁴	37.9 × 19.2	39.3 × 18.0	36.2 × 17.5	38.2 × 18.5	36.0 × 16.8	39.0 × 18.4	39.4 × 18.8	39.3 × 18.6	40.0 × 18.0	38.5 × 18.5
C-Pm ⁴	109.0	118.8	105.8	116.5	107.0	116.0	113.5	112.0	118.0	116.0
Length of mandible	246.0	257.0	242.0	252.0	247.0	256.0	255.0	253.0	256.0	269.0
Mandible depth I	60.0	57.0	54.5	53.0	56.0	53.0	53.0	56.0	52.0	55.0
Mandible depth II	43.0	47.0	43.0	45.0	44.5	44.0	47.0	47.0	44.5	47.0
Greatest height of mandible	117.5	134.0	123.0	127.0	127.5	124.8	126.4	127.0	132.0	138.5
M ₁	28.8 × 15.3	30.8 × 16.0	28.4 × 14.3	29.0 × 15.4	27.5 × 14.0	28.1 × 15.6	29.4 × 14.4	28.8 × 15.0	28.0 × 14.5	28.0 × 15.0
C-M ₁	130.0	136.0	125.0	132.0	127.0	131.0	128.5	132.0	134.0	134.0

TABLE 2

Mutual relation of the greatest skull length and the condylobasal length in adult specimens of different lion populations

	Locality, or territory	Sex	Greatest skull length	Condylobasal length	$\frac{100 \times \text{Cb}}{\text{Gtest l.}}$	σ
Lundholm (1952)	Murraysburg, Cape	♀	307	291	94.8	
	N. Transvaal and Ngamiland	♀♀ n=10	302.7	269.6	89.2 (87.4-90.8)	0.95
	East Africa	♀♀ n=10	296	267	90.3	1.13
	East Africa	♀♀ n=13	295	264	89.5	0.84
B.M.(N.H.) 36.5.26.6	Cape (Orange River -?)	♂	358.1	325.5	90.9	
B.M.(N.H.) N.R.-S.	N.E. Transvaal, Bechuanaland and Damaraland	♂♂ n=11	377.6 350-396	329.5 310.8-350.5	87.3 (86.3-88.8)	0.81
N.R.-S. 1310	Caffraria Interior	♂	394	340	86.3	
R.N.H.-L. 'i'-663 Br	'Kaap'	♂	325	288	88.6	
B.M.(N.H.) M.N.H.N. R.N.H.-L. M.R.A.C.	South and North Rhodesia, Mozambique, South Congo	♂♂ n=16	359.3 340.8-379	319.6 300.6-338	88.9 (87.3-90.2)	0.75
B.M.(N.H.) M.R.A.C. I.R.S.N.	North Congo, Ruanda-Urundi, Uganda	♂♂ n=20	357.4 335.5-382.6	318.3 297.7-337.8	89.3 (88.2-91.3)	0.97
B.M.(N.H.) M.N.H.N.	Tanganyika, Kenya, Somaliland	♂♂ n=22	354.5 331.5-386.5	316.7 298-339.5	89.4 (87.2-91.1)	1.19
B.M.(N.H.) I.R.S.N. Z.M.A.	British Sudan	♂♂ n=21	344.1 321-375	305.9 284-331.8	89.1 (87.3-91.0)	0.84
B.M.(N.H.) 21.7.23.1	Gambia	♂	347.8	310.3	90.2	
M.N.H.N. 1880-462	French Cameroon	♂	329	301	91.5	
I.R.S.N. 2405/902	Morocco	♂	338	309.6	91.6	
B.M.(N.H.) M.N.H.N.	India, Persia	♂♂ n=5	334.7 330-340.4	302.8 296.5-312	90.5 (90.0-91.7)	0.63

B.M.(N.H.)=British Museum (Natural History), London; M.N.H.N.=Museum National d'Histoire Naturelle, Paris; N.R.-S.=Naturhistoriska Riksmuseet, Stockholm; I.R.S.N.=Institut Royal des Sciences Naturelles, Bruxelles; M.R.A.C.=Musée Royal de l'Afrique Centrale, Tervuren; Z.M.A.=Zoologisch Museum, Amsterdam; R.N.H.-L.=Rijksmuseum van Natuurlijke Historie, Leiden.

Note: Geographical names are indicated according to original labels.

100 Cb/Gtest l. of this skull is equal to 88.6 which falls within the variation limits of 11 skulls of *krugeri*.

As to the other skull characteristics, viz., a relatively broader muzzle and a somewhat greater relative length of the mandible, shown for the Cape Lion by LUNDHOLM (1952, p. 22) and by MAZAK & HUSSON (1960, p. 103) respectively, I would like to state that these cannot be confirmed by the present study. Both British Museum male skulls of the Cape Lion (i.e., Nos. B.M. 18.5.23.2 and B.M. 36.5.26.6) display absolutely as well as relatively very broad muzzles, it is true, but the difference from other South African lions is not significant, though the skull No. B.M. 18.5.23.2. has, in fact, the broadest muzzle (i.e., the greatest rostral breadth) of all the lion skulls I have ever seen.

In spite of the fact that no significant difference in the relative mandible length could be found either, the mandibles of both Cape Lion skulls from the British Museum are still more heavily built than those of most other lion skulls. A more robust general structure of the mandible of the Black-maned Lion of the Cape is demonstrated by the ratio between the greatest length of the mandible and the sum of six other mandible measurements (see Table 3). In the 8 biggest skulls from Transvaal, Caffraria, and Damaraland the greatest length of the mandible, as a percentage of the sum of six other mandible measurements, varies from 62.2% to 64.6%, the mean value being 63.2%, whilst in the Cape Lion specimens the respective figures are 60.8% and 61.1%. Although not being very significant these figures still show that the mandible of a Cape Lion is, on an average, more robust and heavier than a mandible

TABLE 3
Mandible indices of wild shot male lions from South Africa

Museum No.	Locality	Md l.	$\Sigma(a+b+c+d+e+f)$	$\frac{100 \times \text{Md l.}}{\Sigma(a+b+c+d+e+f)}$
B.M. 25.6.17.5	Manzemntondo River, N.E. Transvaal	242.0	388.2	62.3
B.M. 25.6.17.6		252.0	401.4	62.8
B.M. 25.6.17.7		247.0	396.5	62.2
B.M. 25.6.17.8		256.0	396.5	64.6
B.M. 25.6.17.9		255.0	398.7	64.0
B.M. 25.6.17.10		253.0	405.8	62.3
N.R.-S. 1310	Caffraria Interior	256.0	405.0	63.2
N.R.-S. 1971	Damaraland, Walvis Bay	269.0	417.5	64.4
B.M. 18.5.23.2	?-Orange R. Cape	257.0	420.8	61.1
B.M. 36.5.26.6	?-Orange R. Cape	246.0	404.4	60.8

B.M. = British Museum (Natural History), London; N.R.-S. = Naturhistoriska Riksmuseet, Stockholm.
Md l. = Length of mandible; a = Mandible depth I; b = Mandible depth II; c = Greatest height of mandible; d = length of M₁; e = breadth of M₁; f = C-M₁. For actual measurements see Table 1.

of equal size belonging to any other South African lion. In both Cape Lion skulls the most conspicuous of all the mandible measurements, it is the depth (or height) of the mandibular ramus, measured just behind the lower carnassial (M_1), which in these two skulls reaches the greatest absolute values.

Nevertheless, the most striking characteristic in the structure of both male skulls of the Black-maned Lion of the Cape, compared with other forms of lion, is that the rostral part of skull is much deeper (fig. 5). The rostrum depth (measured as a vertical distance from the highest point on the vault of oral ends of the nasals to a point situated just behind the canine alveolus) is in the British Museum Cape Lion skulls (Nos. B.M. 18.5.23.2. and B.M. 36.5.26.6.) equal to 80.0% and to 81.9% of the respective greatest length of the nasals. In 14 big skulls of other lions (nine of them being the biggest skulls of *Panthera leo krugeri* that I have ever studied) the average value is 72.9%, with the variation limits 70.3% and 75.4%, σ being 1.43. The British Museum Cape Lion skulls

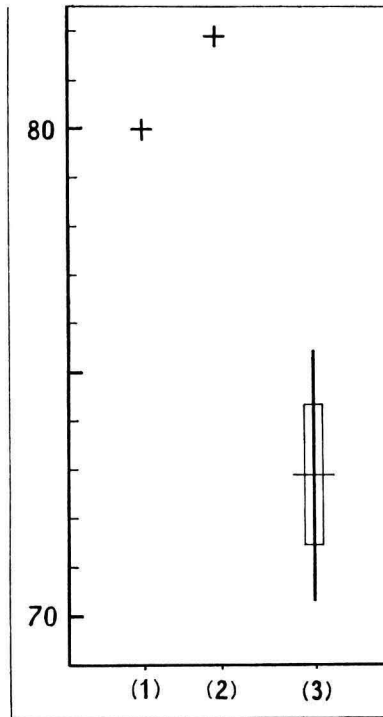


Fig. 5. A graph to show differences in the depth of the rostrum between males of the Black-maned Lion of the Cape and males of other lion populations. On the ordinate values of the depth of the rostrum as a percentage of the greatest length of the nasal bones are shown. 1. Cape Lion skull No. B.M. 18.5.23.2. 2. Cape Lion skull No. B.M. 36.5.26.6. 3. 14 male skulls of various lion forms (cf. Table 4). The mean value, \pm standard deviation, and the extent of the individual variation are indicated.

TABLE 4

Measurements and indices of the rostral part of skull in various lion forms (adult males)

Museum No.	Locality	Gtest l.	Cb l.	Rostral depth	Gtest nas.	$100 \times$ Rostral depth
						Gtest l. nasals
Univ. Prague F 1.010	Zoo Prague	359	308.6	69	96	71.9
Univ. Prague F 1.011	Zoo Prague	381	339	77	105	73.3
I.R.S.N. 2405/902	Morocco 1862	338	309.6	71	101	70.3
M.N.H.N. 1897-286	Atlas Algérie	-	-	80.5	113	71.7
M.R.A.C. RG 17.120	Ruanda-Urundi	377.5	336.5	80	111.5	71.7
B.M.(N.H.) 93.5.21.1	Bechuanaland	382	331	81	113	71.7
N.R.-S. 1971	Damaraland Walvis Bay	396	350.5	79	110	71.8
B.M.(N.H.) 25.6.17.5	Manzemntondo River	366	322.8	82	108.7	75.4
B.M.(N.H.) 25.6.17.6	(N.E. Transvaal)	386	335	81	110	73.6
B.M.(N.H.) 25.6.17.7		382.3	330	78	105	74.3
B.M.(N.H.) 25.6.17.8		385	335.6	81	111.5	72.6
B.M.(N.H.) 25.6.17.9		378	327.8	78	106	73.6
B.M.(N.H.) 25.6.17.10		379.5	329.4	80	106.5	75.1
N.R.-S. 1310	Caffraria Interior	394	340	78	109	73.9
B.M.(N.H.) 18.5.23.2	Cape (Orange River-?)	-	-	85	106.3	80.0
B.M.(N.H.) 36.5.26.6	Cape (Orange River-?)	358.1	325.5	84	102.5	81.9

Gtest l. = Greatest skull length; Cb l. = Condylbasal length; Gtest nas. = Greatest length of nasal bones.

Univ. Prague = Institute of Systematic Zoology, Charles University, Prague; I.R.S.N. = Institut Royal des Sciences Naturelles, Bruxelles; M.N.H.N. = Muséum National d'Histoire Naturelle, Cabinet d'Anatomie, Paris; M.R.A.C. = Musée Royal de l'Afrique Centrale, Tervuren; B.M.(N.H.) = British Museum (Natural History), London; N.R.-S. = Naturhistoriska Riksmuseet, Stockholm.

are thus, respectively, 4.96 and 6.29 units of the standard deviation from this average. The detailed figures for different skulls are shown in Table 4. This table also shows that the two Cape skulls do display not only the greatest relative values of the rostral depth but that this measurement also reaches the greatest absolute values, of all specimens examined, in these two skulls.

Due to the great depth of rostrum in the Black-maned Lion of the Cape the nostrils might have been placed slightly higher than in other forms of lion, and, accordingly, the nose, or the nasal bones respectively, could thus seem to be somewhat shorter.

The Stockholm Museum male skull from the interior of Caffraria has a rather flat rostrum, its depth being just 73.9% of the greatest length

of the nasal bones. This shows once again that the skull in question falls into the variation limits of *Panthera leo krugeri*.¹³

As to their general structure both British Museum male skulls of the subspecies *melanochaita* are very robustly shaped and more powerfully built than the majority of skulls of other forms of lion. The skull No. B.M. 18.5.23.2., being that of a very large adult male, is, in fact, the most massive and the biggest lion skull that I have ever seen. The occiput of this skull had been cut off, making it thus impossible to determine either the condylobasal length or the greatest skull length. In order to show the size of this skull I measured its length from the oral margin of the meatus acusticus externus to the prosthion and compared the result with the same measurement of the 7 biggest skulls from North-Eastern Transvaal and Bechuanaland, that are deposited in the British Museum (Natural History), as well as with that of 2 very big skulls from the Stockholm Naturhistoriska Riksmuseet (Table 1). The dimension in question was 281 mm for the Cape Lion skull No. B.M. 18.5.23.2., whilst the mean value for the 9 other skulls was equal to 270.03 mm, with an actual variation from 263.5 to 277.0 mm. The condylobasal and greatest length of these 9 skulls show a variation from 327.8 to 350.5 mm and from 379.3 to 396 mm respectively. The condylobasal length of the Cape Lion skull No. B.M. 18.5.23.2. could thus be estimated as having very probably been near to 355 mm.

The skull No. B.M. 36.5.26.6., though being that of a not very old animal, displays a very strong and high sagittal crest. The skull No. B.M. 18.5.23.2. has, as already mentioned, its occipital part cut off, yet it is evident that it had an unusually massive, mighty, and high sagittal crest.

The zygomatic arches of both Cape Lion skulls are rather thin in their cross-section but very deep posterior to the processus frontalis ossis zygomatici, being thus strongly vaulted. Their structure is decidedly more robust than that of an average East African Lion skull. The upper outlines of both British Museum skulls of the Cape Lion, when compared with skulls of other forms of lions are somewhat straighter, which is in part due to a comparatively deeper muzzle. As a result of the relatively great depth of rostrum as well as of its rather great breadth and a more heavily built mandible the muzzle of the Cape Lion seems to be larger and/or more massive than in other lions. The occipital region, as already

¹³ According to a schematic drawing published by LUNDHOLM (1952, p. 22) the Murraysburg female Cape Lion skull displays a somewhat flatter rostrum when compared to a female skull of *krugeri* of the same condylobasal length, though the nasal bones seem to be shorter in the former. It is difficult to state whether or not this is due to the sexual dimorphism in males and females of the Cape Lion. I would, however, like to point out that in all young lions the muzzle is generally relatively flatter than in the adults. Knowing that the Murraysburg animal was rather young, I suppose its not very deep rostrum is just one of the juvenile features

stated above, is relatively shorter and, accordingly, points more upwards than in other South African lions, viz., in the subspecies *Panthera leo krugeri* (ROBERTS, 1929).

Concluding the section on the skull structure of *Panthera leo melanochaita* (Ch. H. SMITH, 1842) I would like to recall once again SMITH's (1842, p. 177) statement concerning the shape of the head of the Cape subspecies of the Lion. The skull features listed above could have really resulted in a somewhat different external appearance of the head of the Black-maned Lion of the Cape, making it to a certain extent bulldog-like in shape, with deep large muzzle, and with a somewhat shorter and slightly more retroussé nose wrinkled at its base, especially in large adult male specimens.

Whether the skull characteristics of the Cape Lion listed here are or are not significantly specific for this subspecies of lion could, of course, be proved by nothing else than a greater amount of material.

3.4. Dental Pattern of *Panthera leo melanochaita* (Ch. H. Smith, 1842). Describing the Murraysburg female skull, LUNDHOLM (1952, p. 24) found that it had relatively more powerful teeth than lionesses of other African populations. However, he adds: '...the animal may have been comparatively small, as compared with other members of the same population, for it is well known that small individuals have relatively bigger teeth than larger specimens'.

As for the two British Museum male skulls of the Cape Lion, both of them have relatively strong and big teeth though their measurements do not fall outside the variation of other skulls from southern Africa (cf. Table 1).

The most astonishing thing about the British Museum Cape Lion skulls is that both of them have fully developed second lower premolars (Pm₂)! In the skull No. B.M. 36.5.26.6. both the left and right Pm₂ are in their sites, whilst in the skull No. B.M. 18.5.23.2. only the left one is preserved. The structure of the bone at the place where the right Pm₂ should have been situated however indicates that it had been present, but that was lost in the course of the animal's life. The measurements of the crown of these teeth in the respective skulls are as follows: No. B.M. 36.5.26.6., right Pm₂ 6.7 × 4.9 mm, left Pm₂ 7.5 × 5.4 mm; No. B.M. 18.5.23.2. (right Pm₂ lost during life), left Pm₂ 7.4 × 5.9 mm. The size of these teeth is, in fact, almost the same as that of an average second upper premolar of a regular lion skull.

The importance of this finding is pointed out by the fact that in none of 217 wild-shot lion skulls from various sectors of the range and in none of about 60 zoo lion skulls that I examined any trace of the second lower premolars has been found.

Neither the Stockholm Museum male skull No. 1310 nor the Leiden Museum male skull No. 'i'-663/Br. show any indication that a Pm₂ was present in the right or left mandibles, which is in full accordance with

the presumption that they belong to the subspecies *Panthera leo krugeri*. The Murraysburg female skull does not, however, seem to have developed any Pm_2 either. Mr. G. J. B. Ross of the Museum, Snake Park and Oceanarium in Port Elizabeth examined the skull and has kindly informed me he could not find any trace of Pm_2 alveoli in the right or left lower jaws (in litt., May 9, 1968). An X-ray photograph might none the less lead to a different result, though there is a certain probability that sexual dimorphism may have existed in this respect.

In my opinion the second lower premolars found in both male skulls of the Cape Lion from the British Museum collections cannot be certainly interpreted as mere occasional and atavistic rudiments for it is most improbable that two skulls preserved just by a freak of chance would show the same kind of anomaly. It seems obvious that the extinct Black-maned Lion of the Cape represented a subspecies that had, at least in males, a tendency to develop second lower premolars, a characteristic completely unknown in any other form of lion.

3.5. The Size of the Black-maned Lion of the Cape, *Panthera leo melanochaita* (Ch. H. Smith, 1842). Unfortunately, we know next to nothing about the actual size of the extinct Cape Lion. The dimensions of mounted specimens cannot, of course, give any exact idea about the true size of the respective animals. It is only possible to state that all the preserved mounted specimens of the subspecies *melanochaita* seem to show that the animals were rather big when alive.

Only very few measurements made on Cape Lions in the flesh are known. WILLIAM PATERSON (1789, p. 33; quoted by ROBERTS, 1951, p. 190) gives the following dimensions of a lioness killed at Bier Valley (near Willowmore, Cape Province): total length, 8 feet 9½ inches (2682 mm); tail, 3 feet (914 mm); shoulder height, 3 feet 8 inches (1118 mm). ROBERTS (1951, p. 190–191) then gives data as follows: ‘. . . Mrs. HELEN MCKAY has kindly furnished me with extracts from early publications not formerly available to me, namely, from *The Tower Menagerie*, comprising the Natural History of the Animals contained in that Establishment’, dedicated to George IV, London, Nov., 1828, pp. 17–22, in which comparisons are made and a pale and a black form are described, and from which it seems clear that the first refers to a young lion about 10 months old, and the second to a young adult about 2 years and 6 months old; the latter ‘sometimes measuring the enormous distance of eight feet from the tip of the nose to the origin of the tail, which is generally about half the length of the body’ (which would mean at least 11 ft. in total length). The second is PRINGLE’s *A Residence in South Africa*, chapter VIII, April, 1822, in which the length of a lion killed on ‘Glen Lynden’ is given as ‘fully eleven feet.’

HARRIS (1840, p. 163) when giving an account of the Lion of the interior of the southernmost Africa says that the lion is ‘about three feet eight

inches high at the shoulder'. If this referred to the actual height of a living animal and not to a height measured on the dead lion with his fore leg stretched out, it would, of course, mean that the Cape Lion was really considerably larger than any of other subspecies living to-day. Unfortunately, HARRIS does not say whether his information on the shoulder height concerns a living animal or a dead one.

Though being not completely satisfactory, the above given data seem to indicate that the Black-maned Lion of the Cape reached a somewhat larger size than other forms of lion. The Barbary Lion, *Panthera leo leo* (Linnaeus, 1758), has frequently been stated to have reached an exceptionally big size; as was shown elsewhere (MAZAK, 1970) it does, however, not seem that this subspecies was larger than an average East African Lion, *Panthera leo somaliensis* (NOACK, 1891). On the contrary, the above quoted measurements of the Cape Lion are larger than those of lions of other forms taken by reliable hunters and zoologists. In my opinion Colonel STEVENSON-HAMILTON is one of the most competent persons to be quoted here (1947, pp. 127-128): 'I dare say I have measured over 150 lions . . . , most of them in the Transvaal, but some in other parts of Africa; and though I may have been unlucky, I have only once found an animal, from tip of nose to tip of tail, excluding the tail tuft and including the curious horny projection at the base, which even approached 10 feet in length . . .'. Similarly, S. Downey, an experienced professional hunter, states on the East African Lion (in CULLEN, 1959, p. 71): 'I have shot or have supervised the shooting of more than two hundred lions. Many were superb specimens by any standard, yet the largest—properly and scrupulously measured—was 9 feet 7 inches in length'. ROBERTS (1951, p. 192) says of *Panthera leo krugeri* (Roberts, 1929), the subspecies that seems to be one of the biggest forms living at the present day: 'Measurements . . . of lions and lionesses kindly supplied by Mr. W. CAMPBELL, 'Toulon', Sabi district, are as follows: 10 largest males (out of 18 recorded): Total length 9 ft. 1 in. – 9 ft. 7 in., on the curves 9 ft. 5 in. – 9 ft. 10 in. . . . 13 lionesses (out of 14 measured): Total length 8 ft. to 8 ft. 4½ in., three on the curves 8 ft. 2 in. to 8 ft. 6 in.'.

The biggest lion that I was able to find a report about in the reliable sources is a black-maned male shot by Dr. A. BERGER on Dec. 8, 1908 on the Nzoia River, some 45 miles north-east of Lake Victoria. The lion in question was a giant, measuring, most probably on the curves, 326 cm (i.e. about 10 ft. 8½ ins.) from the tip of the nose to the tip of the tail (cf. BERGER, 1909, p. 272 and the plate facing that page), which would mean about 10 ft. 4 ins. to 10 ft. 5 ins. measured 'between pegs'. The measurements of the Cape Lion quoted by ROBERTS (l.c.) are none the less still bigger, though the respective sources might perhaps seem to be somewhat less trustworthy than Dr. BERGER's statement. Their reliability could, however, be supported by two facts: (1) Measurements of a Cape lioness killed by W. PATERSON (see above) are rather larger

than those of any lioness of any other population reported in the literature; hence, why should the males of the Cape Lion not also be bigger? (2) a so experienced hunter and naturalist as HARRIS (1840, p. 163, quoted also in his 1839-work), who made his explorations, or at least a part of them, in the area then inhabited by the Black-maned Lion of the Cape, gives the total length of an average large male as being 10 ft. 6 ins. (3200 mm) and states in another place that the South African Lion is usually 10 to 11 feet (ca. 3050 to 3350 mm) in length (cf. HARRIS, 1840, p. 168).

As to the weight there is no verified information known to me that could concern the Cape subspecies of the Lion. LYDEKKER (1893-1894, p. 359, quoted also by TJADER, 1910, p. 32) nevertheless says that a male was shot 'in the Orange Free State in 1865, which on good evidence is reported to have weighed over 583 lbs.'. No exact locality is, however, given and so it is rather difficult to state whether this information can or cannot be referred to the Black-maned Lion. In any case this is the greatest weight of a lion recorded in the reliable sources known to me.

However scarce are the actual data on the size of the extinct subspecies *melanochaita* of the Cape, I still believe that it represented a more powerful and more robustly built form that was unusually large, if not the largest subspecies of all. The British Museum skull No. B.M. 18.5.23.2. that I described in section 3.3. of this paper suggests this rather explicitly.

4.

All the available data on the extinct Black-maned Lion shown in previous sections of this paper seem to indicate that this form of lion was one of the best characterized subspecies of the species *Panthera leo* (Linnaeus, 1758). This subspecies, inhabiting quite characteristic biotopes in the interior of southernmost Africa, the type of which has not been noticeably changed for long ages, and being thus more or less separated from other populations of lion by a complex of various physico-geographical factors, might have represented one of the most primitive evolutionary lines of the species. This assumption is supported mainly by the fact that at least part of the Cape Lion population developed the second lower premolar. This characteristic is entirely unknown in any other subspecies or population of lion and it must be certainly considered a primitive feature.

The basic taxonomic particulars of the Black-maned Lion of the Cape can be summarized as follows:

***Panthera leo melanochaita* (Ch. H. Smith)**

1842. *Leo melanochaitus* Ch. H. Smith. Jardine's Naturalist's Library, Introduction to Mamm., Vol. 15, p. 177. Cape.
 1842. *Felis (Leo) melanochoetus* Ch. H. Smith. Jardine's Naturalist's Library, Introduction to Mamm., Vol. 15, pl. X. Cape of Good Hope.

1829. *Felis leo capensis* J. B. Fischer. Synopsis Mamm., adenda, p. 565. Nomen praeoccupatum; the name is preoccupied by *Felis capensis* Forster, 1781, for the South African Serval, *Leptailurus serval serval* (Schreber, 1776).
1843. *Felis leo Capensis* Blainville. Ostéographie. Mammifères. Genus *Felis*, p. 186, pl. 6. Cap de Bonne Espérance.
1868. *Leo capensis* Fitzinger. Sitzber. Akad. Wiss. Wien. Mathem.-naturw. Classe, Bd. 58, I. Teil, p. 438. Capland.

Type specimen: Not known; Smith's picture of the 'Black Maned Lion' (1842, pl. X) could, however, be considered that of the type.

Type locality: 'Cape' (SMITH, 1842, p. 177), 'Cape of Good Hope' (SMITH, 1842, pl. X). Restricted here to the Karroo plains south of the Orange River in the interior of the former Cape Province.

Description: A very large, if not the largest, subspecies of the Lion; ground coloration somewhat darker than in other forms, except the Barbary Lion, being deep tawny with a certain greyish shade; males with large manes that reach far behind the shoulders, belly mane developed; the yellowish colour of the mane around the face contrasts sharply with the blackish, or pure black, colouring of the mane on the neck, shoulders, throat, and chest, giving thus the impression of a yellowish 'collar' around the face; the skull is very massively built, being deeper in the rostral part than is the case with other subspecies, and somewhat shorter in the occipital region than in other South African lions; mandible heavy and strong; dentition powerful, with an obvious tendency to develop the second lower premolar, which does not occur in any other form. The differences in the structure of the skull listed above might be responsible for a slightly different shape of the head, with certain bulldog-like features.

Distribution: Plains of the temperate inland plateaux of the Cape and of the southern parts of the Orange Free State, west of the 'Great Eastern Escarpment'.

Entirely extinct since the beginning of the 1860's.

Note: Since the type specimen of this subspecies has not been preserved and since the figure by SMITH (1842, pl. X), that is here considered to be that of the type, shows some misleading details I take the liberty to suggest that the British Museum (Natural History) mounted skin of a male Black-maned Lion of the Cape, No. B.M. 68.268, and the British Museum (Natural History) skull No. B.M. 36.5.26.6. of another male specimen of this subspecies should be regarded as 'standard specimens' that every zoologist dealing with problems of the intraspecific taxonomy of South African lions or working on a revision of the species *Panthera leo* (Linnaeus, 1758) should see.

5.

Some time ago I published (MAZAK, 1964a) a preliminary list of the specimens of *Panthera leo melanochaita* preserved in various museums; a revised list of the preserved specimens of the Black-maned Lion of the Cape is given below.

(1) Mounted skin of an adult male (Plate I, below).

British Museum (Natural History), London, England.

Museum No.: B.M. 68.268.

Origin: The specimen was said '... to have been killed near the Orange River about 1830, probably on the Bontebok Flats near Colesberg in the Cape Colony, though possibly on the plains to the north of the river' (POCOCK, 1931, p. 208).

'Selous believed that this lion had been killed on the Bontebok flats, near Colesberg, about 1830'. (PALMER, 1950, p. 13).

The lion was shot by Captain (later General) Copland-Crawford of the Royal Artillery. The skin was '... not set up till approximately 1896... it must have been carefully folded up and kept from the light by the family until given to the Junior United Services Club, of which he was a member, by the last surviving son of Captain Peter Crawford, before he went to West Africa, where he was killed in 1896.' (STEVENSON-HAMILTON, 1954, p. 188). 'From about 1895 (or so) till 1954 this unique specimen was housed in the Junior United Services Club in London' (C. T. ASTLEY MABERLY, in litt., Nov. 6, 1955). Finally the specimen was sent to the British Museum (Natural History), London, in January, 1954 (J. E. HILL, in litt., Febr. 13, 1968).

Measurements of the mounted skin: It is impossible to give any measurements as the specimen is at present housed in the original showcase in which it came from the Junior United Services Club and this case is built without means of access. Everyone who looks at this lion must however agree that he was a very large one.

First description of the specimen: POCOCK (1931).

Figures: POCOCK (1931, p. 208), STEVENSON-HAMILTON (1954, p. 188), MAZAK & HUSSON (1960, pl. IX), MAZAK (1964a, fig. 1).

Remarks: The specimen is in excellent state of preservation; not bleached by light; wild-shot; suggested here to serve as one of the two 'standard specimens' of the Black-maned Lion of the Cape (cf. section 4. of this paper).

(2) Mounted skin of an adult male (Plate II, above).

Rijksmuseum van Natuurlijke Historie, Leiden, Holland.

Museum No.: specimen 'a' of JENTINK's Catalogue (1892, p. 95).

Origin: 'Cap. Du Cabinet d'Anatomie, 1860'. (JENTINK, 1892, p. 95). Other data unknown; the date 1860 mentioned by JENTINK obviously indicates the year when the specimen was transferred to the Leiden Museum

from the Cabinet d'Anatomie and not the date when the lion was killed.

Measurements of the mounted skin: head and body (over curves), 2050 mm; tail (without terminal hair tuft), 1040 mm; total length, 3090 mm; length of right hind foot, 405 mm; length of left hind foot, 420 mm; shoulder height (straight), 990 mm.¹⁴

First description of the specimen: MAZAK & HUSSON (1960).

Figures: MAZAK & HUSSON (1960, pl. IX), BLONK (1963, pl. facing p. 164), MAZAK (1964a, fig. 2).

Remarks: The specimen is in an excellent state of preservation; not bleached by light; obviously wild-shot.

(3) Mounted skin of an adult male (Plate III, above)

Staatliches Museum für Naturkunde, Stuttgart, Germany.

Museum No.: 518.

Origin: Originally labelled as 'Löwe, Kapland, Von Barth, 1854'.

Measurements of the mounted skin: head and body (over curves), 1930 mm; tail, 970 mm; total length, 2900 mm; length of right hind foot, 400 mm; length of left hind foot, 420 mm; shoulder height (straight), 1010 mm.

First description of the specimen: GUGGISBERG (1961, p. 46).

Figures: MAZAK (1964a, fig. 3).

Remarks: well preserved but somewhat bleached by light; wild-shot.

(4) Mounted skin of an adult male (Plate II, below).

Städtisches Museum, Wiesbaden, Germany.

Museum No.: Säugetierkatalog Nr. 358.

Origin: 'Kapland'. - 'In den Jahrbüchern des Nassauischen Vereins für Naturkunde, Heft 19/20 von 1864-1866, wird im Jahresbericht für 1864 gesagt, dass die Administration der Curetablissemments 250 Holländische Gulden zur Anschaffung eines männlichen Löwen bewilligt habe und dass dieses grosse prachtvolle Exemplar vom Cap zur besonderen Zierde des Museums gereichen wird. Von dem weiblichen Tier ist an dieser Stelle nichts gesagt, doch enthält der Jahresbericht für 1866 eine Zusammenstellung der in den letzten sieben Jahren gekauften Gegenstände und darin ist erwähnt 'capischer Löwe und Löwin'./Die Bezugstelle für das Männchen geht aus den Jahrbüchern nicht hervor; doch findet sich im Jahresbericht 1865 der Hinweis, dass ein Löwenweibchen von dem Naturalienhändler Frank in Amsterdam gekauft wurde. Es ist anzunehmen, dass auch der männliche Löwe aus derselbe Quelle stammt'. (Dr. FILL, Wiesbaden, in litt., March 6, 1963).

Measurements of the mounted skin: head and body (over curves),

¹⁴ I measured the specimen myself in May, 1968; the measurements given here thus somewhat differ from those mentioned in my previous paper (MAZAK, 1964a, p. 53) that had been made by the Leiden Museum staff.

1950 mm; tail, 855 mm; total length, 2805 mm; length of right hind foot, 435 mm; length of left hind foot, 440 mm; shoulder height (straight), 1000 mm.

First description of the specimen: Mentioned, without any exact description, for the first time by GUGGISBERG (1961, p. 46).

Figures: MAZAK (1964a, fig. 4).

Remarks: In good state of preservation, though somewhat bleached by light; wild-shot.

(5) Mounted skin of a young adult male.

Museum National d'Histoire Naturelle, Galerie de Zoologie, Paris, France.
Museum No.: Not known.

Origin: Originally labelled as 'Lion du Cap de Bonne Espérance. Mort à la Ménagerie, en 1834'.

Measurements of the mounted skin: shoulder height (straight), 860 mm.

First description of the specimen: MAZAK & HUSSON (1960).

Figures: MAZAK & HUSSON (1960, pl. X), MAZAK (1964a, fig. 5).

Remarks: Not fullgrown (cf. MAZAK, 1964a, p. 57), the mane being, however, well developed; well preserved but very considerably bleached by light; obviously wild-caught, died in captivity.

(6) Mounted skin of an adult female (Plate III, below).

Staatliches Museum für Naturkunde, Stuttgart, Germany.

Museum No.: 519.

Origin: Originally labelled as 'Löwe, Kapland, Von Barth, 1854'.

Measurements of the mounted skin: Head and body (over curves), 1700 mm; tail, 880 mm; total length, 2580 mm; length of right hind foot, 380 mm; length of left hind foot, 420 mm; shoulder height (straight), 890 mm.

First description of the specimen: GUGGISBERG (1961, p. 46).

Figures: MAZAK (1964a, fig. 6).

Remarks: Well preserved but considerably bleached by light; wild-shot.

(7) Mounted skin of an adult female.

Städtisches Museum, Wiesbaden, Germany.

Museum No.: Säugetierkatalog Nr. 359.

Origin: 'Kapland'. For details see sub (4).

Measurements of the mounted skin: Head and body (over curves), 1980 mm; tail, 905 mm; total length, 2885 mm; length of right hind foot, 417 mm; length of left hind foot, 450 mm; shoulder height, 990 mm.

First description of the specimen: Mentioned, without any exact description, for the first time by GUGGISBERG (1961, p. 46).

Figures: MAZAK (1964a, fig. 7).

Remarks: In rather good state of preservation, though somewhat bleached by light; wild-shot.

(8) Skull of a young adult female (Plate VI)

Museum, Snake Park and Oceanarium, Port Elizabeth, South Africa.
Museum No.: Not known.

Origin: 'The . . . skull . . . was dug out of a river bank near Murraysburg, in the Karroo area . . .' (LUNDHOLM, 1952, p. 21).

Measurements: see LUNDHOLM (1952, tabs. 1-4) and MAZAK & HUSSON (1960, tabs. 1-2).

First description: LUNDHOLM (1952).

Figures: LUNDHOLM (1952, pl. III), MAZAK (1964a, fig. 8).

Remarks: Rather well preserved, nearly intact; in the preliminary list of the preserved specimens of the Cape Lion (MAZAK, 1964a, p. 55) this skull was mentioned as being that of an adult female, a more detailed study has, however, shown that the specimen in question was rather young at the time of its death (cf. section 3.3. of this paper).

(9) Skull of an adult male (Plate V).

British Museum (Natural History), London, England.

Museum No.: B.M. 36.5.26.6.

Origin: Originally labelled as 'Cape Town, shot 1848. Col. H. W. Murray'. By 1848 lions had been extinct in the Cape Town area for many years (cf. SPEIGHT, 1964, p. 22); as was shown in section 2.1. of this paper Mr. Murray started his hunting expeditions from Colesberg and it can thus be supposed that the lion in question was killed somewhere on the plains in the Orange River basin.

Measurements: see Table 1.

First description: Described for the first time in this paper.

Figures: Figured for the first time in this paper.

Remarks: In a very good state of preservation, intact; wild-shot specimen that is suggested here to serve as one of the two 'standard specimens' of the Black-maned Lion of the Cape (cf. section 4. of this paper).

(10) Skull of an adult male (Plate IV)

British Museum (Natural History), London, England.

Museum No.: B.M. 18.5.23.2.

Origin: Originally labelled as 'South Africa. Capt. H. W. Murray. Shot about 1873 by Capt. Murray's father'. As shown in section 2.1. of this paper the date 1873 should correctly be read 1843; according to all the evidences summarized in the section 2.1. the lion in question was shot somewhere on the plains in the Orange River basin.

Measurements: See Table 1 (cf. also section 3.3.).

First description: Described for the first time in this paper.

Figures: Figured for the first time in this paper.

Remarks: In a very good state of preservation, the whole occipital part of the skull cut off; wild-shot specimen.

? (11) Mounted skin of an adult male (Plate I, above).

Zoölogisch Museum, Universiteit van Amsterdam, Holland.

Museum No.: ZMA 9185.

Origin: Not known; supposed to have been killed in the Cape Province before 1845, which is the date when the specimen is documented to have been in the Museum collections (cf. section 2.3. of this paper).

Measurements of the mounted skin: Head and body (over curves), 1580 mm; tail, 840 mm; total length, 2420 mm; length of right hind foot, 380 mm; length of left hind foot, 370 mm.¹⁵

First description: Described for the first time in this paper.

Figures: Figured for the first time in this paper.

Remarks: In good state of preservation, though being somewhat bleached by light; supposed to have been wild-shot.

According to the above list 8 mounted skins, viz. 5 adult males, 1 young adult male, and 2 adult females, and 3 skulls, viz. 2 adult males and 1 young adult female, of the extinct Black-maned Lion of the Cape, *Panthera leo melanochaita* (Ch. H. Smith, 1842) are preserved in various scientific institutions of Europe and Africa, constituting thus the only known material of the splendid Cape subspecies of the Lion. It is hoped that some other preserved specimens will be discovered in the course of the next years.

6.

HEMMER (1966) described a male lion specimen (mounted skin and skull) from the collections of the Naturhistorisches Museum in Vienna which he believed to represent the Cape subspecies (mounted skin registered as No. 711, the skull as No. 1422 of the Vienna Museum collections). I am none the less of the opinion that this specimen cannot be referred to the subspecies *melanochaita*. The lion in question was purchased by the Zoo Schönbrunn on May 10, 1887 from a certain Herr Bode and was euthanized on October 18, 1892 (Dr. FIEDLER of the Schönbrunn Zoo, in litt. Dec. 16, 1964). These data are the only relevant information concerning the specimen of the Vienna Natural History Museum. Thus there is absolutely no information that could clarify the origin of the specimen in question. HEMMER (1966, p. 57) suggests the following: 'Es wäre dann eher anzunehmen, dass er [i.e. the lion in question] aus einer Menagerie stammt, die ihre Zucht auf Kaplöwen aufgebaut hatte und diese noch einige Jahrzehnte nach ihrem Ausserben

¹⁵ The measurements of the mounted skin are exceptionally small, bearing even less relation to those of the animal in life than it is the case with other mounted skins of the Black-maned Lion of the Cape mentioned in this paper. From the way the specimen is mounted it is quite obvious that the skin had been very considerably shrunk and shrivelled before it was set up, which took place at least some 125 years ago.

in freier Wildbahn züchtete. 'In my opinion this suggestion is, however, very doubtful. As was shown above the Cape Lion very probably became extinct as early as the beginning of the 1860's, or at the very end of the 1850's. Hemmer's suggestion implies that there would have been a zoo that bred Cape Lions for about 30 to 35 years. I can hardly suppose that there really was any Zoo in Europe which could have kept for so long a time a pure line of the true Cape Lion. We know that even in these days there is many a zoo, the authorities of which do not care very much about the subspecific purity of their animals, interbreeding different subspecies of tigers, of lions, of leopards etc. In addition, in the course of the last century it was certainly not so common a thing to breed lions successfully without any important difficulty as is very often the case to-day.

HEMMER (l.c.) based his determination of the specimen in question on a certain amount of similarity of the external characteristics with those of the Cape Lions of known origin, and on some morphological features of the skull and teeth. As to the external characteristics one has to admit that the features mentioned by HEMMER (l.c., pp. 57-58) are not completely in accordance with those of preserved specimens of the genuine Cape Lions. HEMMER's identification is, in fact, based on a somewhat similar form of the mane only, i.e., on the presence of a belly mane that is longer in the posterior parts of the abdomen. Such a form of the mane can, however, be found in the Barbary Lion as well. The colour of the mane of the Vienna Museum specimen is yellowish or yellow-tawny around the face and greyish to grey-brown, mixed with dark grey or grey-brown hair on the shoulders, and especially on the throat and chest, being thus decidedly not as dark, i.e., brownish black or pure black as it is in Cape Lion specimens of known origin. In addition, the yellowish hair around the face graduates into the darker coloured mane hair on the shoulders, throat and chest, whilst in the genuine specimens of the Cape Lion the colours of the mane are sharply separated. This characteristic is typical of the Cape Lion as was already emphasized in section 3.2. of this paper. The form and colour of the mane of the Vienna Museum specimen, in fact, resemble much more those of a Barbary Lion (cf. MAZAK, 1970). It also seems that the ground coloration of the specimen in question is somewhat paler than is usual in the subspecies *melanochaita*.

As far as the characteristics of the skull are concerned, HEMMER (l.c., p. 58) found that the index ' $100 \times \text{condylobasal length} / \text{greatest length of skull}$ ' was equal to 93.1 which was one of the most important reasons why he thought that the Vienna Museum specimen represented a Cape Lion. In section 3.3. of this paper I have, however, demonstrated that this index cannot be always used as a definite criterium separating the subspecies *melanochaita* from other geographical races, for relatively high values of the index in question are also found in lions from the northern parts of Africa as well as in Asiatic lions.

HEMMER (l.c., p. 59) also mentions another characteristic, viz. the relation between the length and breadth of the crown of the lower carnassial (M_1). He states that the index ' $100 \times \text{breadth of } M_1 / \text{length of } M_1$ ' was 55.4 in the Murraysburg female skull described by LUNDHOLM (1952) and 56.9 and 57.2 for the right and left carnassials respectively of the Vienna Museum specimen. Contrary to this, in 48 lion skulls from East and South Africa the maximum value of the respective index was 54.5. Among the lion skulls studied by me there have, however, been several specimens in which the mentioned index exceeded, or has varied around, the figure 55 which HEMMER (l.c.) gives as the lower limit for the subspecies *melanochaita*. A male lion skull from North-Eastern Transvaal (British Museum (Natural History), No. B.M. 25.6.17.8.), for example, showed the value of the mentioned index as being equal to 55.5 (which is more than in the Murraysburg female skull) and in a male skull from the Rotterdam Zoo (Rijksmuseum van Natuurlijke Historie, Leiden, No. 308) it was equal even to 58.3. On the contrary, the two genuine Cape Lion male skulls of the British Museum (Natural History) have the M_1 index equal to 52.6 (No. B.M. 18.5.23.2.) and to 53.1 (No. B.M. 36.5.26.6.) respectively, i.e. the index values vary within the limits of variation given by HEMMER for other populations. It is thus possible to conclude that the craniological and dental features mentioned by HEMMER cannot be used as a demonstration that the Vienna Museum specimen represents the extinct Black-maned Lion of the Cape. Hence, I am sorry to state that, in my opinion, the Vienna Museum male lion specimen (skin and skull Nos. 711 and 1422 respectively) described by HEMMER (1966) should be removed from the list of the preserved specimens of *Panthera leo melanochaita* (Ch. H. Smith, 1842).

In this context I would like to mention once again the Amsterdam Natural History Museum mounted skin of a male lion that I referred to in previous sections of this paper. One could object that I have included this specimen in the list given in section 5. of this paper whilst I have omitted the Vienna Museum specimen. The origin of the Amsterdam specimen is not exactly known either, it is true, but contrary to the Vienna Museum specimen the circumstantial evidence is much stronger: (1) The date 1845 when the specimen was already known to be present in the Amsterdam Museum collections precedes the time of the Cape Lion extinction. (2) At the respective times the Dutch activity in the most southerly parts of Africa was rather considerable and lions are known to have been frequently brought into the Netherlands. (3) In addition, the external characteristics of the Amsterdam specimen are really in a first degree accordance with those of the genuine Cape Lion specimens the origin of which is undubitable, this being, however, not at all the case with the Vienna Museum specimen. Despite all these arguments I am still including the Amsterdam specimen with a question-mark in the list of the preserved specimens of the Black-maned Lion of the Cape.

7.

Skull measurements were taken in the following way:

- (1) Greatest length, prosthion-opisthocranion.
- (2) Condylbasal length, prosthion-condylion.
- (3) Basal length I, prosthion-basion.
- (4) Basal length II, orale-basion.
- (5) Rostral breadth, the greatest breadth of the rostrum above the canines.
- (6) Rostral depth, measured as a vertical distance from the highest point on the vault of the oral ends of nasals (i.e. not from the tips of the nasals which reach somewhat more orally) to a point situated just behind the canine alveolus.
- (7) Greatest length of nasals, measured from the most aboral point of the sutura internasalis to a point that is the point of intersection of a line, connecting the most oral tips of the nasal bones, with the medial skull plane.
- (8) distance prosthion-meatus acusticus externus, from prosthion to the oral margin of the meatus acusticus externus.
- (9) Interorbital breadth, the smallest distance between the orbits.
- (10) Postorbital breadth, the smallest breadth of the postorbital constriction.
- (11) Bizygomatic breadth, the distance zygion-zygion.
- (12) Mastoid breadth, the greatest breadth of the skull above mastoidal processūs (taken on the temporal crest).
- (13) Pm⁴, the greatest length and breadth of crown of the upper carnassial.
- (14) C-Pm⁴, the distance between the most oral edge of the alveolus of the upper canine and the most aboral edge of the alveolus of the upper carnassial.
- (15) Length of mandible, infradentale-condylion mediale.
- (16) Mandible depth I, the greatest depth (or height of the ramus of the mandible just in front of the third lower premolar (Pm₃).
- (17) Mandible depth II, the greatest depth (or height) of the ramus of the mandible just behind the lower carnassial.
- (18) Greatest height of mandible, the greatest distance from the top of the processus coronoideus (sive muscularis) to the lower margin of the processus angularis.
- (19) M₁, the greatest length and breadth of the crown of the lower carnassial.
- (20) C-M₁, the distance between the most oral edge of the alveolus of the lower canine and the most aboral edge of the alveolus of the lower carnassial.

ADDENDUM

After the manuscript of this paper had been sent to the Editors a report on a newly discovered skull, without mandible, of the South African Lion was published in 1971 [JURGENS MEESTER: An additional skull of the extinct Cape Lion, *Panthera leo melanochaita* (H. Smith, 1842) (Mammalia: Carnivora). Ann. Transvaal Museum, 27 (3) : 27-29, 2 pls., 1 tab.]. The skull was 'dug up in the sandhills; behind the beach at Betty's Bay, southern Cape coast'.

MEESTER (l.c.), who examined the skull in question very carefully, found it was decidedly that of an adult female (greatest length 310 mm, condylbasal length 281 mm). His study shows that the Betty's Bay

female skull shares only its broader muzzle width with the Murraysburg female skull described by LUNDHOLM (1952). No other features common to the both Murraysburg and Betty's Bay skulls that would distinguish these from skulls of other lion forms could be found. Hence MEESTER concludes that 'the discovery of further material might still further complicate the task of diagnosis, and possibly even render it altogether impossible'.

I would, however, like to say that *if* the results of this my paper are accepted, especially as far as the geographical distribution of the Cape Black-maned Lion is concerned (see section 3.1. of this paper), then the locality itself should indicate the newly discovered skull cannot represent a specimen of the subspecies *Panthera leo melanochaita*. It is therefore quite natural that all the characteristics of the skull in question fall into, or are very close to, the variation limits of measurements and indices of skulls of other lion forms, especially of the subspecies *Panthera leo krugeri* which, according to my interpretation, might once have inhabited coastal areas of the southernmost parts of the Cape Province. The systematic position of the Betty's Bay female skull is thus about the same as that of the male skull of the Stockholm Museum that came from the interior of Caffraria (see sections 2.2. and 3.3. of this paper). This is the reason why I seem to incline not to include the Betty's Bay skull into the 'Revised List of the Preserved Specimens of the Black-maned Lion of the Cape' published in this paper (section 5.).

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SUMMARY

The available data on the extinct Black-maned Lion of the Cape, *Panthera leo melanochaita* (Ch. H. Smith, 1842) are summarized in the present paper. Problems concerning the geographical distribution,

systematic status and taxonomic criteria are discussed in detail, and a revised list of the Cape Lion specimens preserved in various museums of Europe and Africa is given. The list includes 8 mounted skins that are generally in a very good state of preservation, and 3 skulls.

RÉSUMÉ

Cet article résume les données disponibles concernant le Lion du Cap, *Panthera leo melanochaita* (Ch. H. Smith, 1842), aujourd'hui éteint. L'auteur traite en détail des problèmes concernant la répartition géographique, la position systématique et les critères taxonomiques. Il donne également une liste, revue et complétée, des spécimens de Lion du Cap conservés dans les différents musées d'Europe et d'Afrique. Cette liste comporte 8 peaux montées, généralement en bon état de conservation, et 3 crânes.

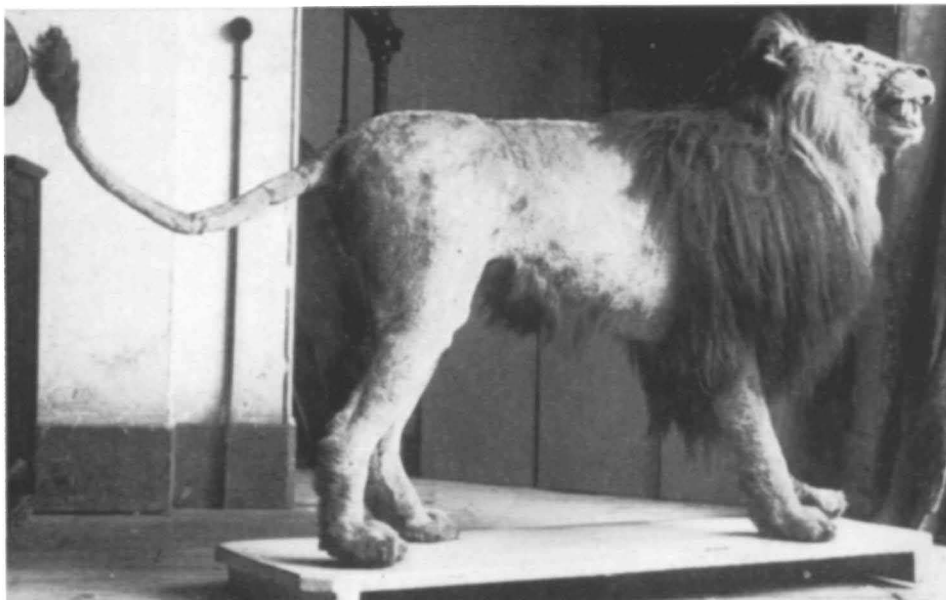
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PLATE I



Above. Mounted specimen of a male (?) Cape Lion from the Zoölogisch Museum, Universiteit van Amsterdam, No. ZMA 9185. The specimen is supposed to have been wild-shot; note extremely long mane hair on the chest. Photo: Mazak.

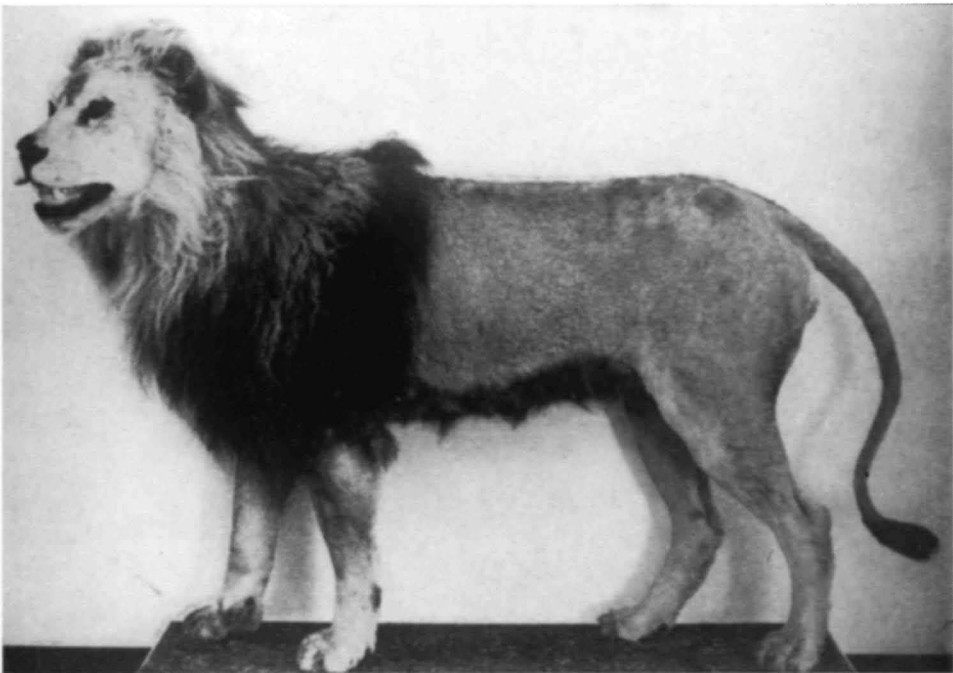


Below. Mounted specimen of a wild-shot male of the Cape Lion from the British Museum (Natural History), London, No. B.M. 68.268. By permission of the B.M.N.H., London.

PLATE II

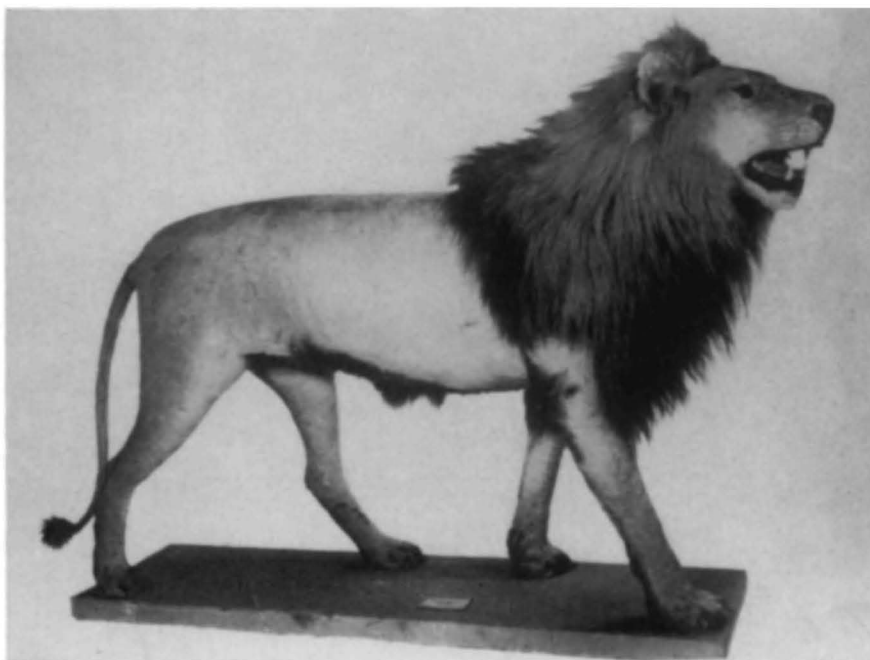


Above. Mounted specimen of a wild-shot male of the Cape Lion from the Rijksmuseum van Natuurlijke Historie, Leiden, No. 'a' of JENTINK'S Catalogue (1892). Note the very long fringe of hair under the belly. Photo: H. F. Roman.

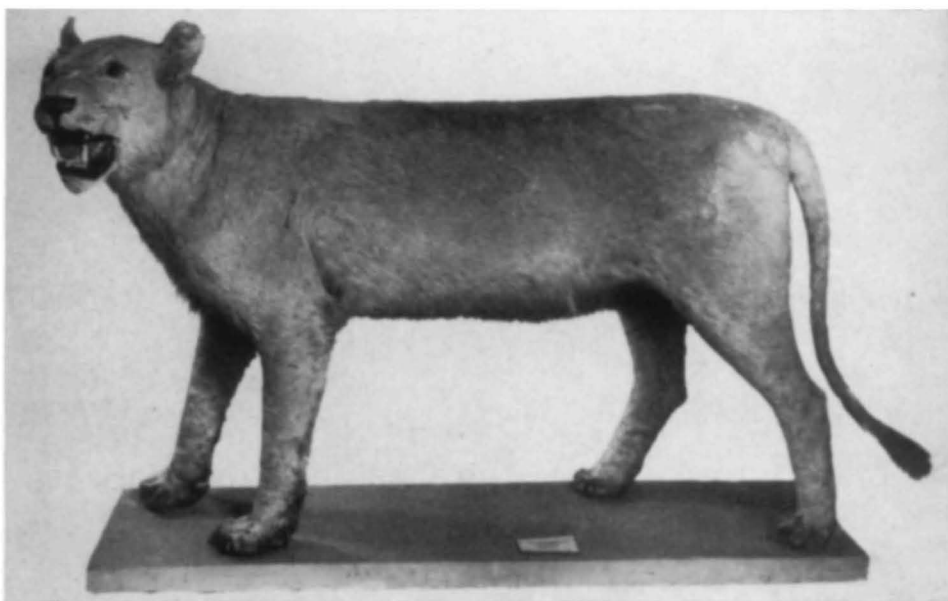


Below. Mounted specimen of a wild-shot male of the Cape Lion from the Städtisches Museum, Wiesbaden, No. 358. By permission of the Städtisches Museum, Wiesbaden.

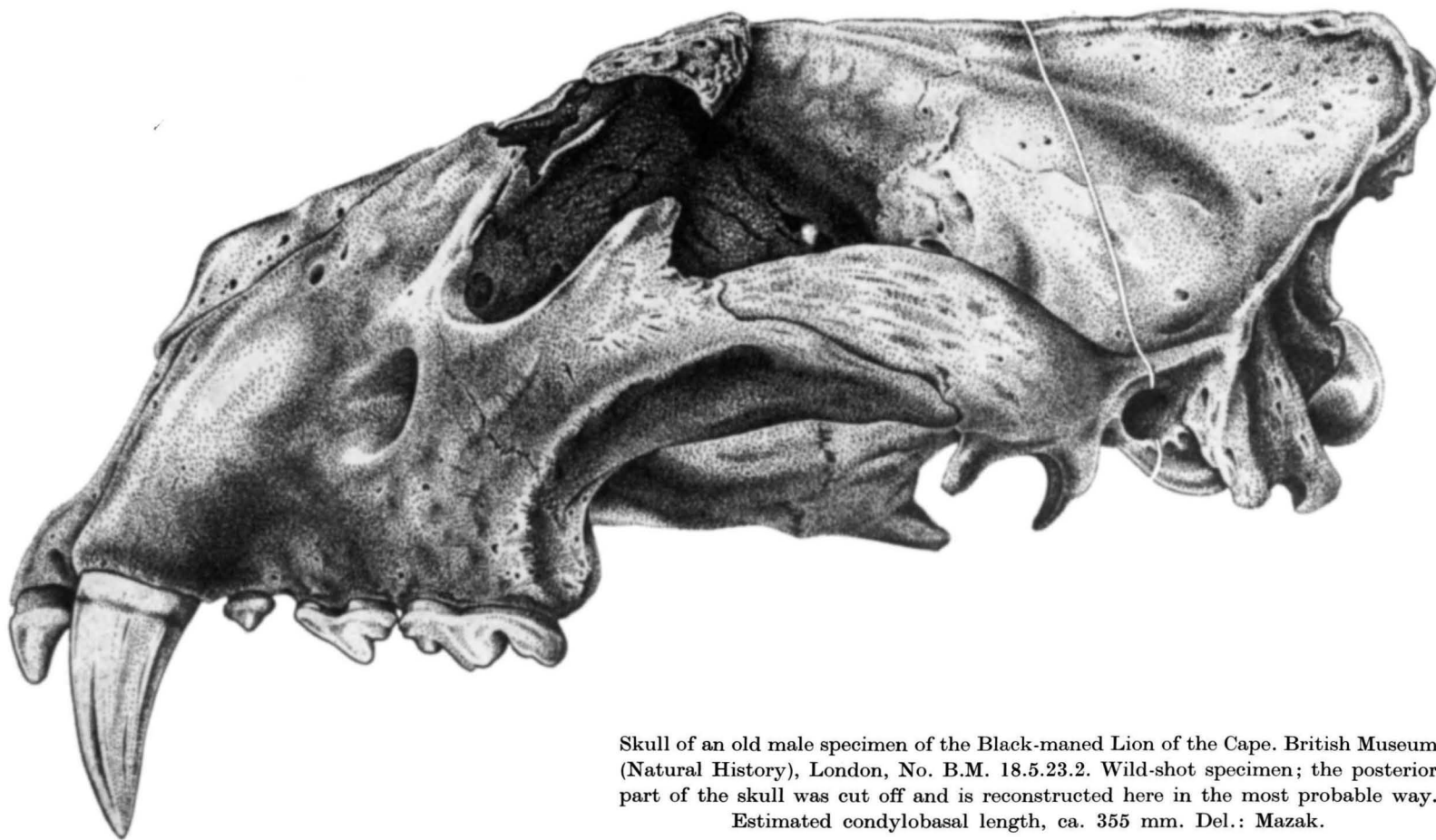
PLATE III



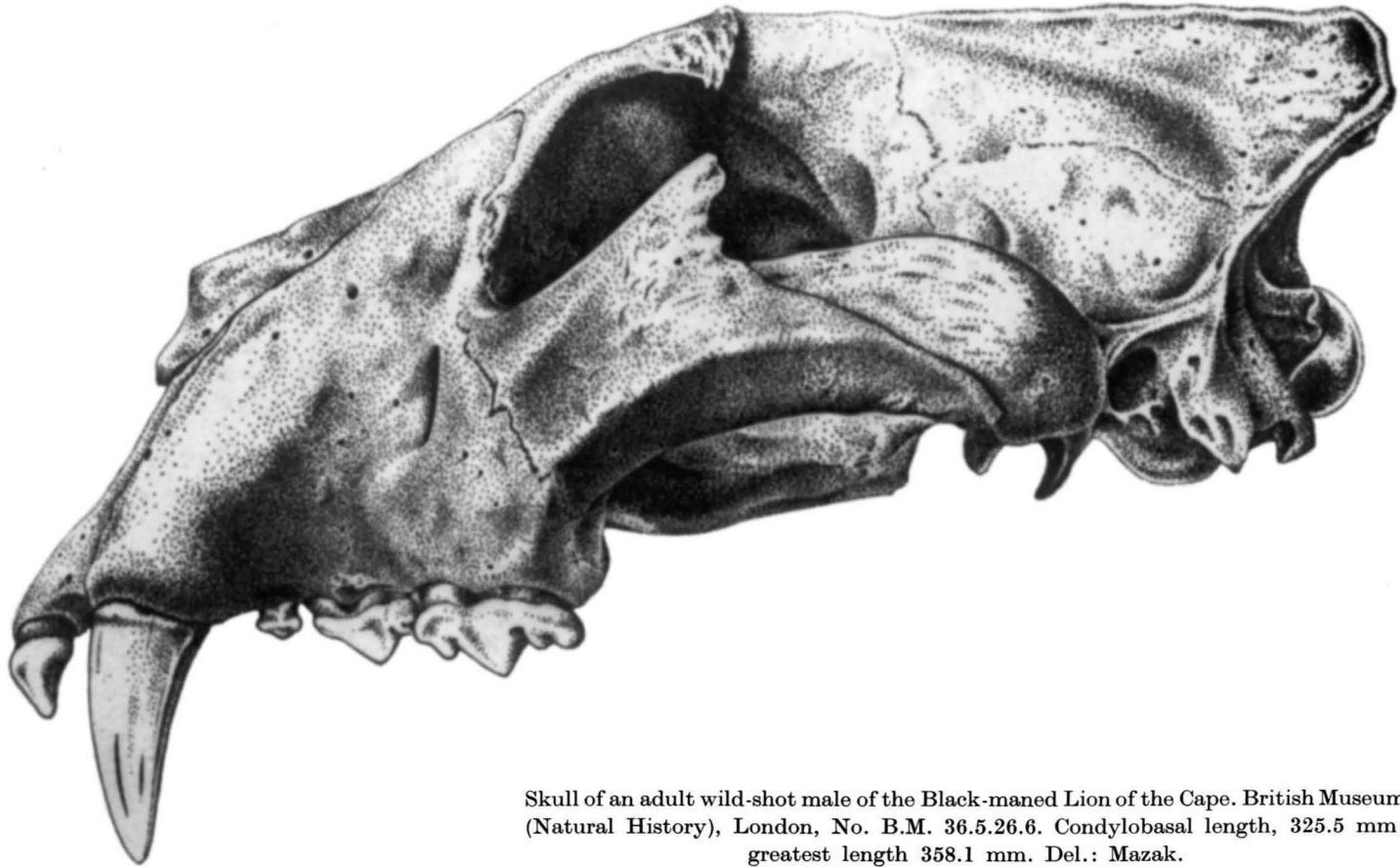
Above. Mounted specimen of a wild-shot male of the Cape Lion from the Staatliches Museum für Naturkunde, Stuttgart, No. 518. By permission of the Staatliches Museum für Naturkunde, Stuttgart.



Below. Mounted specimen of a wild-shot female of the Cape Lion from the Staatliches Museum für Naturkunde, Stuttgart, No. 519. By permission of the Staatliches Museum für Naturkunde, Stuttgart.



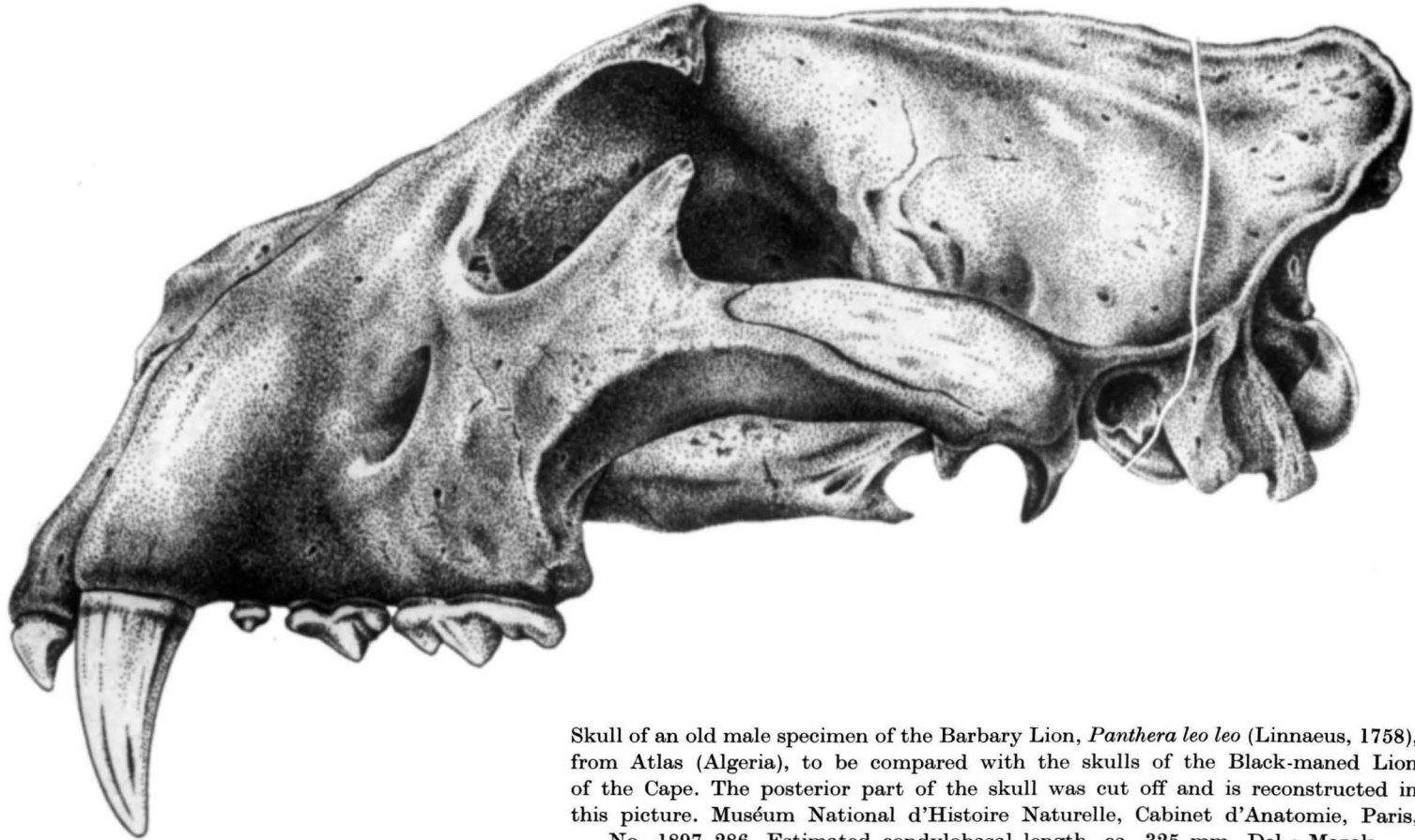
Skull of an old male specimen of the Black-maned Lion of the Cape. British Museum (Natural History), London, No. B.M. 18.5.23.2. Wild-shot specimen; the posterior part of the skull was cut off and is reconstructed here in the most probable way. Estimated condylobasal length, ca. 355 mm. Del.: Mazak.



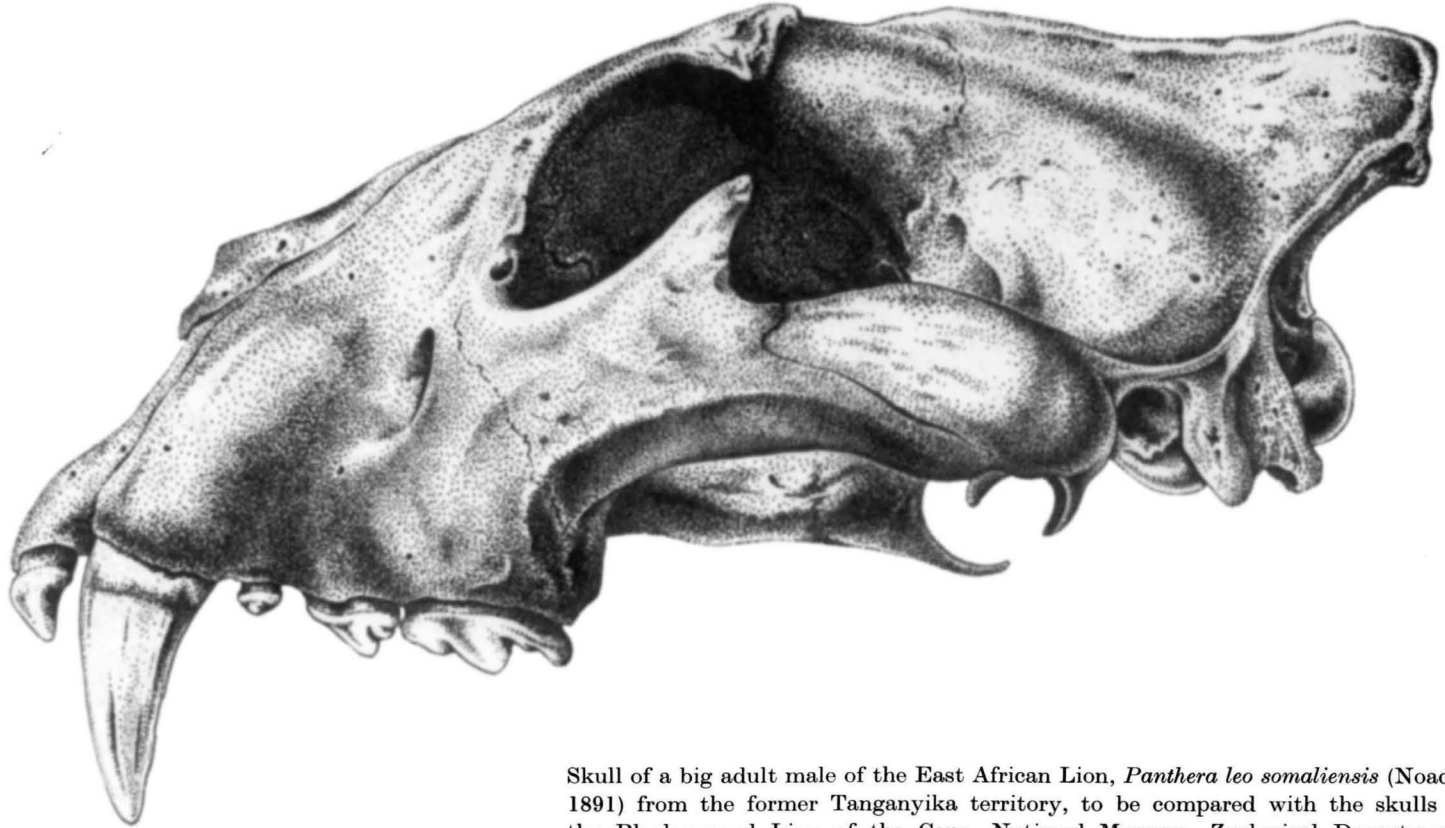
Skull of an adult wild-shot male of the Black-maned Lion of the Cape. British Museum (Natural History), London, No. B.M. 36.5.26.6. Condylbasal length, 325.5 mm; greatest length 358.1 mm. Del.: Mazak.



Skull of a young adult female specimen of the Black-maned Lion of the Cape.
Museum, Snake Park and Oceanarium, Port Elizabeth. Condylbasal length,
291 mm; greatest length, 307 mm. Del.: Mazak.

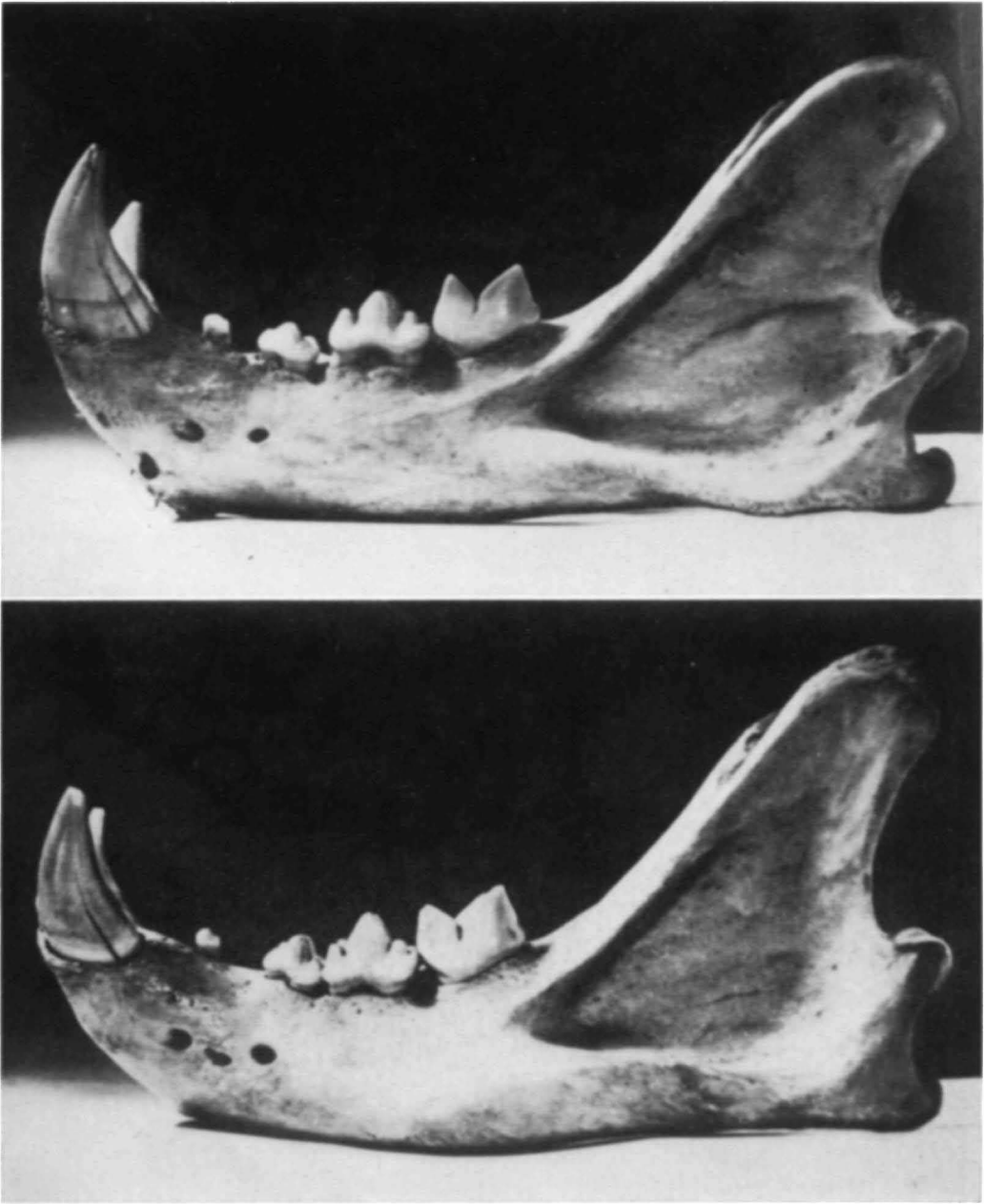


Skull of an old male specimen of the Barbary Lion, *Panthera leo leo* (Linnaeus, 1758), from Atlas (Algeria), to be compared with the skulls of the Black-maned Lion of the Cape. The posterior part of the skull was cut off and is reconstructed in this picture. Muséum National d'Histoire Naturelle, Cabinet d'Anatomie, Paris, No. 1897-286. Estimated condylobasal length, ca. 325 mm. Del.: Mazak.



Skull of a big adult male of the East African Lion, *Panthera leo somaliensis* (Noack, 1891) from the former Tanganyika territory, to be compared with the skulls of the Black-maned Lion of the Cape. National Museum, Zoological Department, Prague, No. 1940/23/11/Mk. Condylbasal length, 314.5 mm; greatest length, 353 mm. Del.: Mazak.

PLATE IX



Mandibles of males of the Black-maned Lion of the Cape displaying fully developed second lower premolars. Above. No. B.M. 18.5.23.2. Below. No. B.M. 36.5.26.6.