

Divided infraorbital foramen in the lion (*Panthera leo*): its implications for colonisation history, population bottlenecks, and conservation of the Asian lion (*P. l. persica*)

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Abstract

A divided infraorbital foramen is an important morphological feature in lion taxonomy and has previously been considered to occur only in the Asian lion, *Panthera leo persica*. Based on an examination of 498 lion skulls from museum collections in Europe and southern Africa, we report for the first time on the prevalence of the divided infraorbital foramen in African lions, as well as its occurrence in the tiger, *P. tigris* and the extinct Pleistocene European cave lion, *P. leo spelaea*. The higher frequency of this characteristic in Asian lions may have occurred after the lion colonised Asia, and can be considered an important morphological feature characterising this population. It is not clear whether recent anthropogenic population bottlenecks have influenced changes in its prevalence over the last 200 years.

Contents

Introduction	77
Materials and methods	78
Results	78
Discussion	79
Does the divided infraorbital foreamen diagnose the Asian lion?	79
Divided infraorbital foreamen and past bottlenecks	79
Acknowledgements	80
References	80
Appendix 1	82

Introduction

Although Smee (1835) had clearly referred to a divided infraorbital foramen in his description of the ‘mane-less lion of Guzerat’, it was Pocock (1930) who drew zoologists’ attention to the presence of the divided infraorbital foramen (DIF) in modern lion, *Panthera leo*

Linnaeus, 1758 skulls from India. The infraorbital foramen is an opening in the skull, through which the infraorbital artery, the infraorbital vein and the infraorbital nerve emerge (Fig 1a). The infraorbital foramina are found below the orbits at the anterior end of the zygomatic arches of the skull and in Indian lions they are frequently divided by a bridge of bone into smaller upper and larger lower portions (Pocock, 1930) (Fig 1b). Although zoologists, including Pocock, were fully aware that DIF did not always occur in the Indian lion, it has become one of the most important morphological characteristics distinguishing the skulls of Indian and African lions (Pocock, 1930; Todd, 1965; Joslin, 1984; O’Brien *et al.*, 1987; Rashid and Reuben, 1992; Nowell and Jackson, 1996; Srivastav and Srivastav, 1997; Divyabhanusinh, 2005; Singh, 2007). Pocock (1930) stated that DIF never occurred in the African lion and, to date, this statement has been referred to, and accepted uncritically, by subsequent authors when describing distinctions between Indian and African lion skulls. However, perhaps ironically for the importance of DIF to characterise the Indian lion, Todd (1965) suggested, based on 34 Indian lion skulls, that DIF may have been shifting its frequency of occurrence in the Indian lion in the last 200 years, declining between the 19th century and the mid-20th century.

We here report on the frequency of occurrence of DIF in the African lion for the first time, and discuss whether this characteristic is useful for distinguishing Asian and African lion skulls, both for individuals and at the population level. Also, we re-examine the hypothesis presented by Todd (1965) concerning the temporal shift of the frequency of occurrence of DIF in the Indian lion based on a larger sample size.



Fig 1a. Undivided infraorbital foramina of a Sub-Saharan African lion (Amathole Museum, King William's Town, South Africa, ID number: 18319, origin: Etosha Pan, Namibia) (photo: Nobuyuki Yamaguchi).

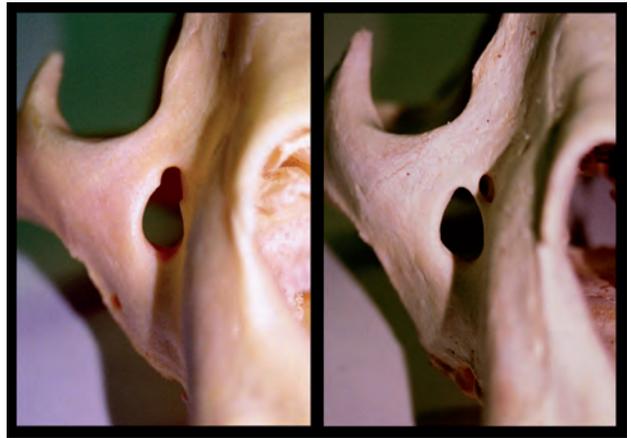


Fig 1b. A partially-divided infraorbital foramen (left: National Museums Scotland, ID number: NMS.Z.2008.004), and a divided infraorbital foramen (right: National Museums Scotland, ID number: NMS.Z.2001.185.1) of Asian lion skulls (photo: Andrew Kitchener).

Materials and methods

We examined 498 lion skulls kept in museum collections in Europe and southern Africa, originating from as many locations as possible across the species' natural distribution, including recently extinct populations such as North African Barbary lion, *Panthera leo leo* Linnaeus, 1758. In addition, previously published information concerning the occurrence of DIF for 23 Indian lion skulls (Smee, 1835; Todd, 1965) was included in the analysis. To investigate the occurrence of DIF in the nearest internally-coherent taxon to the lion, we examined skulls of the extinct Pleistocene European cave lion, *P. l. spelaea* (Goldfuss, 1810), which is considered to have shared a common ancestor with the modern lion as recently as at c. 500–600 thousand years ago (Burger *et al.*, 2004; Yamaguchi *et al.*, 2004; Barnett *et al.*, 2009). All eight examined cave lion skulls originate from Europe. We also examined 304 tiger, *P. tigris* Linnaeus, 1758, skulls kept in Europe and the former Soviet Union – from as many locations as possible across its natural distribution, representing all customarily recognised subspecies (Luo *et al.*, 2004), including three extinct ones. The occurrence of DIF was assessed as 'present' or 'absent' regardless at which side it occurred. The broken specimen recorded by Todd (1965), 'Mumbai 1261' in Appendix 1, was excluded from the analysis because it was not known whether DIF occurred in the skull. The two incomplete divisions recorded at National Museums Scotland (Edinburgh (Z.2001.174.2) and Edinburgh (Z.2008.004) see Appendix 1) were classified as DIF present (Fig 1b). All

statistical analyses were carried out using SPSS (SPSS Inc., Chicago, USA), and statistically significant differences were detected using the likelihood ratio chi-square test, which is also referred to as the G-test.

Results

Amongst 435 African lion skulls and ten specimens whose origins are likely to be in Africa, five (c. 1%) had DIF (Table 1). Curiously, all African lions with DIF originated from between Tanzania and Zimbabwe, and especially from a relatively small area around Lakes Edward and Albert (central Tanzania – eastern Democratic Republic of Congo) (Appendix 1). In contrast, approximately 46% (26 out of 56) of Indian lion skulls had this characteristic (Table 1).

Two lions from Iran had DIF (Appendix 1). Amongst lions, Iranian and Indian populations are phylogenetically very similar (Barnett *et al.*, 2006a), and customarily have been classified as the same subspecies, *P. l. persica* (Meyer, 1826), in which DIF therefore occurred in approximately 48% (28 out of 58) of skulls. In the African lion the skulls only had DIF either on the left side (three individuals) or on the right side (two individuals), but in the Asian lion there were seven individuals that had it on both sides (in addition to six left-sided and 13 right-sided specimens). The extinct Barbary lion is suggested to be phylogenetically closer to the Asian lion than to sub-Saharan lions (Barnett *et al.*, 2006a) and yet, amongst the 12 skulls we examined, none had a DIF (Table 1, Appendix 1).

In terms of the frequency of occurrence of DIF, there were statistically significant differences between Asian and African lions (G-test, two tailed, $N = 503$, $df = 1$, likelihood ratio $\chi^2 = 108.4$, $P < 0.001$), as well as between Asian and Barbary lions (G-test, two tailed, $N = 70$, $df = 1$, likelihood ratio $\chi^2 = 13.9$, $P < 0.001$), whilst a statistically significant difference was not detected between Barbary and sub-Saharan African lions (G-test, two tailed, $N = 445$, $df = 1$, likelihood ratio $\chi^2 = 0.3$, $P = 0.60$). In comparison to the lion where DIF occurred in more than 5% of all examined skulls, it occurred only in c. 0.3% (one out of 304) of tiger skulls (lion vs tiger: G-test, two tailed, $N = 807$, $df = 1$, likelihood ratio $\chi^2 = 25.0$, $P < 0.001$), and in 13% (one out of eight) of examined skulls of the extinct Pleistocene European cave lion (lion vs. cave lion: G-test, two tailed, $N = 511$, $df = 1$, likelihood ratio $\chi^2 = 0.4$, $P = 0.55$).

Divided infraorbital foramen occurred in 45% (5/11) of Indian lion skulls collected in the 19th century, which rose to 67% (10/15) in the early 20th century (pre-1950, including those without recorded collecting dates, yet likely to have been collected during this period as indicated by from their museum register numbers), but this fell to 38% (13/29) post-1950 (Table 2).

However, no statistically significant difference was detected by the G-test at the significant level of 0.05 either between those three periods or between any dyads, although a marginally significant difference was detected between pre- and post-1950 samples (G-test, two tailed, $N = 44$, $df = 1$, likelihood ratio $\chi^2 = 3.32$, $P = 0.069$).

Discussion

Does the divided infraorbital foramen diagnose the Asian lion?

Two lions from Iran have DIF (Appendix 1), contradicting the hypothesis that DIF distinguishes the skulls

of Indian lions from Gujarat, from not only those of all other lions, including other Asian lions, but also from those of all other felids (O'Brien *et al.*, 1987). Although our results show that DIF is not exclusive to the Gir Forest lions, it can be confidently reported that DIF rarely appears in sub-Saharan African lions, which, on the basis of a molecular phylogeny, are likely to be ancestral to the North African -Asian population (Barnett *et al.*, 2006a). Also, our results suggest that the extinct North African Barbary lion does not seem to have DIF, at least at a high frequency. Furthermore, it is suggested based on maternally inherited mitochondrial DNA, that the modern lion does not appear to have hybridised with the extinct northern Holarctic lions of the Pleistocene, including the European cave lion (Burger *et al.*, 2004; Barnett *et al.*, 2009), where 13% have DIF. Therefore, a higher DIF frequency in the Asian population may be a characteristic that developed after the lion colonised Asia, potentially reflecting the recent colonisation history of the lion. These arguments suggest that the higher frequency of DIF in Asian lions is still an important morphological feature that distinguishes their skulls from those of African lions, even though we now know that some African individuals have it.

Divided infraorbital foramen and past bottlenecks

Todd (1965) speculated that the degree of expression and/or penetrance of DIF are under the influence of only a few polygenes, which have shown shifts in frequency in the Indian lion population, possibly due to genetic drift. As the phylogenetic ancestor of the Asian lion (i.e. the sub-Saharan African lion: Barnett *et al.*, 2006a) does not show a high prevalence of DIF, has the Asian lion experienced any severe population/genetic bottleneck in the past, where genetic drift (and/or founder effect) could have been a major factor influencing the frequency of occurrence of the population's genetic and morphological characteristics? Driscoll *et*

Table 1. Observations on the presence / absence of the divided infraorbital foramina (DIF) in lion, European cave lion, and tiger.

Species/Population	With DIF	Without DIF
Lion	33	487
Asian	28	30
African	5	440
Barbary	0	12
European cave lion	1	7
Tiger	1	303

Table 2. Observations on the presence / absence of the divided infraorbital foramina (DIF) in Indian lion skulls over time.

Period	With DIF	Without DIF
19 th Century	5	6
Pre-1950	10	5
Post-1950	13	16

al. (2002) suggested, based on an analysis of 88 nuclear microsatellite loci, that the extreme genetic homogenisation in the current Gir Forest lion population results from a population genetic bottleneck around 1,100 - 4,300 years ago, which was probably caused by natural events.

A more recent, and probably human-caused, population bottleneck appears to have been most severe at the end of the 19th century when it was estimated that 'no more than ten or a dozen' individuals survived (Fenton, 1909; Kinnear, 1920; Wynter-Blyth and Dharmakumarsinhji KS, 1949; Dharmakumarsinhji and Wynter-Blyth, 1950; Talbot, 1960), although the severity of this bottleneck may have been exaggerated (Srivastav and Srivastav, 1997; Divyabhanusinh, 2005). Todd (1965) analysed the temporal change in frequency of DIF in Indian lions – DIF occurred in 85% (4/5) of Indian lion skulls collected in the 19th century, and 60% (6/10) of early 20th century skulls (pre-1950: 1910-1931), whilst only 27% (5/18.5: Todd (1965) gave the broken specimen (Mumbai 1261: Appendix 1) 0.5) had DIF in post-1950 specimens. Our results based on a larger sample indicate that DIF occurs in 45% (5/11) of Indian lion skulls collected in the 19th century, which rises to 67% (10/15) in the early 20th century (pre-1950, including those without recorded collecting dates yet likely to have been collected during this period as indicated by from their museum register numbers), but this falls to 38% (11/29) post-1950. There is no detectable significant differences in prevalence of DIF between these periods, and therefore the results do not support the previous hypothesis that there have been considerable shifts in DIF frequency over the past 200 years (Todd 1965). Granted, the combined sample size is still small, and there is a possibility that the sample is not a fair representation of the population. Also, we emphasise that there is a marginally statistically significant difference between pre-1950 and post-1950 samples, which may be strong enough for scientists to further investigate this issue. In other words, it may be possible that the recent anthropogenic population bottleneck and subsequent population increase (Nowell and Jackson, 1996) have influenced the prevalence of this population-specific characteristic of Asian lions. The foregoing arguments suggest that, although the shift may not be as dramatic as Todd (1965) speculated, conservationists may need to monitor carefully the morphological characteristics of the Asian lion both in the wild and in captivity. Captive breeding programmes for the Asian lion in Europe and India provide a unique opportunity to study the

inheritance of DIF and other morphological characteristics in the Asian lion, in order to better understand changes in the prevalence of these characters in historical wild populations.

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References

- Barnett R, Shapiro B, Barnes I, Ho SYW, Burger J, Yamaguchi N, Higham TFG, Wheeler HT, Rosendahl W, Sher AV, Sotnikova M, Kuznetsova T, Baryshnikov GF, Martin LD, Harington CR, Burns JA, Cooper A. 2009. Phylogeography of lions (*Panthera leo*) reveals three distinct taxa and a late Pleistocene reduction in genetic diversity. *Molecular Ecology* 18: 1668-1677

- Barnett R, Yamaguchi N, Barnes I, Cooper A. 2006a. The origin, current diversity, and future conservation of the modern lion (*Panthera leo*). *Proceedings of the Royal Society B: Biological Sciences* 273: 2119-2125.
- Barnett R, Yamaguchi N, Barnes I, Cooper A. 2006b. Lost population and preserving genetic diversity in the lion *Panthera leo*: implications for its *ex situ* conservation. *Conservation Genetics* 7: 507-514.
- Barnett R, Yamaguchi N, Shapiro B, Nijman V. 2007. Using ancient DNA techniques to identify the origin of unprovenanced museum specimens, as illustrated by the identification of a 19th century lion from Amsterdam. *Contributions to Zoology* 76: 87-94.
- Barnett R, Yamaguchi N, Shapiro B, Sabin R. 2008. Ancient DNA analysis indicates the first English lions originated from North Africa. *Contributions to Zoology* 77: 7-16.
- Burger J, Rosendahl W, Loreille O, Hemmer H, Eriksson T, Götherström A, Hiller J, Collins MJ, Wess T, Alt KW. 2004. Molecular phylogeny of the extinct cave lion *Panthera leo spelaea*. *Molecular Phylogenetics and Evolution* 30: 841-849.
- Dharmakumarsinhji KS, Wynter-Blyth MA. 1950. The Gir forest and its lions Part III. *Journal of the Bombay Natural History Society* 49: 685-694.
- Divyabhanusinh C. 2005. *The Story of Asia's Lions*. Mumbai, Marg Publications.
- Driscoll CA, Menotti-Raymond M, Nelson G, Goldstein D, O'Brien SJ. 2002. Genomic microsatellites as evolutionary chronometers: a test in wild cats. *Genome Research* 12: 414-423.
- Fenton LL. 1909. The Kathiawar lion. *Journal of the Bombay Natural History Society* 19: 4-15.
- Joslin P. 1984. The environmental limitations and future of the Asian lion. *Journal of the Bombay Natural History Society* 81: 648-664.
- Kinnear NB. 1920. The past and present distribution of the lion in south eastern Asia. *Journal of the Bombay Natural History Society* 28: 33-39.
- Luo SJ, Kim JH, Johnson WE, van der Walt J, Martenson J, Yukhi N, Miquelle DG, Uphyrinka O, Goodrich JM, Quigley HB, Tilson R, Brady G, Martelli P, Subramaniam V, McDougal C, Hean S, Huang SQ, Pan W, Karanth UK, Sunquist M, Smith JL, O'Brien SJ. 2004. Phylogeography and genetic ancestry of tigers (*Panthera tigris*). *PLoS Biology* 2: 2275-2293.
- Nowell K, Jackson P. 1996. *Wild Cats. Status Survey and Conservation Action Plan*. Gland: IUCN.
- O'Brien SJ, Joslin P, Smith III GL, Wolfe R, Schaffer N, Heath E, Ott-Joslin J, Rawal PP, Bhattacharjee KK, Martenson JS. 1987. Evidence for African origins of founders of the Asian Lion Species Survival Plan. *Zoo Biology* 6: 99-116.
- O'Regan HJ, Turner A, Sabin RC. 2005. Medieval big cat remains from the Royal Menagerie at the Tower of London. *International Journal of Osteoarchaeology* 15: 1-10
- Pocock RI. 1930. The lions of Asia. *Journal of the Bombay Natural History Society* 34: 638-665.
- Rashid MA, Reuben D. 1992. *The Asian Lion*. Baroda: Vishal Offset.
- Singh HS. 2007. *The Gir Lion*. Ahmedabad: Pugmark Qmulus.
- Smee, W. 1835. Some account of the maneless lions of Guzerat. *Transactions of the Zoological Society of London* 1: 165-174.
- Srivastav A, Srivastav S. 1997. *Asian Lion: on the Brink*. Dehradun: Bishen Singh Mahendra Pal Singh.
- Talbot LM. 1960. Asian lion: Indian lion *Panthera leo persica* Meyer. *Oryx* 5: 216-239.
- Todd NB. 1965. Metrical and non-metrical variation in the skulls of Gir lions. *Journal of the Bombay Natural History Society* 62: 507-520.
- Wynter-Blyth MA, Dharmakumarsinhji KS. 1950. The Gir forest and its lions Part II. *Journal of the Bombay Natural History Society* 49: 456-470.
- Yamaguchi N, Cooper A, Werdelin L, Macdonald DW. 2004. Evolution of the mane and group-living in the lion (*Panthera leo*): a review. *Journal of Zoology London* 263: 329-342.

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Appendix 1

List of examined lion and tiger specimens that have divided infraorbital foramina, extinct North African Barbary lion specimens, and Lidian lion specimens. Specimens are kept in Natural History Museum, London, UK (London), National Museums Scotland, Edinburgh, UK (Edinburgh), Natural History Museum, University of Oxford, Oxford, UK (Oxford), Royal College of Surgeons, London, UK (RCS), National Museum of Natural History, Paris, France (Paris), Zoological Museum, Strasbourg, France (Strasbourg), Zoological Museum, University of Amsterdam, Amsterdam, The Netherlands (Amsterdam), National

Museum of Natural History, Leiden, The Netherlands (Leiden), Swedish Museum of Natural History, Stockholm, Sweden (Stockholm), and Museum of Natural History, Berlin, Germany (Berlin), Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany (Frankfurt), American Museum of Natural History, New York, USA (New York), Field Museum, Chicago, USA (Chicago), and Bombay Natural History Society, Mumbai, India (Mumbai). The position, either left (L) or right (R), of trifurcated (3), bifurcated (2), or undivided normal (1) foramen is also indicated.

Museum (ID)	Life stage/Sex	L/R	Origin
Lion (originated from outside India)			
Paris (1962.2847)	adult/female	2/1	Iran
Paris (1962.2854)	adult/male	1/2	Iran
Leiden (1751)	adult/female	1/2	Zimbabwe (Rotterdam Zoo, 1929)
Stockholm (A59: 5066)	adult/female	2/1	south of Lake Edward, east Democratic Republic of Congo (1921)
Berlin (55299)	subadult/female	2/1	Albert-Edward Lakes, southwest Uganda/Rwanda
Berlin (55317)	adult/male	2/1	northwest Uhehe, central Tanzania
Berlin (55327)	adult/female	1/2	Rwanda (1907)
Tiger			
Leiden (23085)	adult/male	2/1	Sumatra (Rotterdam Zoo, 1957)
Pleistocene European cave lion (fragmented upper right jaw)			
Berlin (MBMa14297a)		2/?	Hermannshöhle, Rübeland, Harz, central Germany (Late Pleistocene)
North African Barbary lion			
London (1952.10.20.15)	adult/male	1/1	North Africa (assigned based on mitochondrial DNA by Barnett <i>et al.</i> 2008) (1280-1385) ^f
London (1952.10.20.16)	subadult/male	1/1	North Africa (assigned based on mitochondrial DNA by Barnett <i>et al.</i> 2008) (1420-1480) ^f
Paris (A1873)	adult/female	1/1	Algeria (zoo, 1833)
Paris (A7912)	adult/male	1/1	North Africa (zoo, 1839)
Paris (1862.54)	adult/female	1/1	Algeria
Paris (1882.502)	adult/male	1/1	North Africa (assigned based on mitochondrial DNA by Barnett <i>et al.</i> 2006b) (c. 1830)
Paris (1897.286)	adult/male	1/1	North Africa
Paris (1196367)	adult/female	1/1	Algeria
Strasbourg (939h)	adult/female	1/1	North Africa (before 1890)
Stockholm (A58.5287)	adult/female	1/1	North Africa (King of Sweden, 1831)
Berlin (15960)	adult/female	1/1	North Africa
Frankfurt (15766)	adult/female	1/1	North Africa (Frankfurt Zoo, 1899)
Indian lion			
London (1857.2.24.1)	adult/female	1/1	Gujarat, northwest India (presented to London Zoo in 1854)
London (1919.7.15.18)	adult/female	2/2	“India” by Pocock (extracted from one of the Selous’ lion skins) ^g
London (1930.6.6.1)	adult/male	1/1	Amreli, Kathiawar, Gujarat, northwest India (c. 1910)
London (1930.6.6.2)	juvenile/male	1/2	Amreli, Kathiawar, Gujarat, northwest India (c. 1910)
London (1930.6.6.3)	juvenile/female	2/1	Amreli, Kathiawar, Gujarat, northwest India (c. 1910)
London (1931.1.5.1)	adult/male	1/2	Kathiawar, Gujarat, northwest India (c. 1930 by Maharajah of Nawanagar?) ^h
London (1931.1.5.2)	adult/male	1/2	Gir, Gujarat, northwest India (c. 1930 by Maharajah of Nawanagar?) ^h
London (1931.4.13.1)	adult/male	1/2	Gir, Gujarat, northwest India (before 1931)
London (1931.4.13.2)	adult/female	2/2	Gir, Gujarat, northwest India (before 1931)
London (1943.64)	juvenile/female	1/1	Gir, Gujarat, northwest India (1941)
London (1945.136)	adult/female	2/1	Gujarat, northwest India (London Zoo, 1945)

^a RCS (4484)	adult/female	2/3	north Gujarat, northwest India (1822) (specimen destroyed 1941)
^a RCS (4485)	adult/female	2/1	northwest India (1830) (specimen destroyed 1941)
^b Smee-1	subadult?/male	[2]	Gujarat, northwest India (c. 1830) (specimen lost?)
^b Smee-2		[2]	Gujarat, northwest India (c. 1830) (specimen lost?)
Edinburgh (Z.1995.5)	adult/male	1/1	Gir, Gujarat, northwest India (1995) (London Zoo)
Edinburgh (Z.2002.185.1)	adult/male	1/2	Gir, Gujarat, northwest India (2000) (Zoo de la Boissiere, Nantes)
Edinburgh (Z.2001.174.1)	adult/male	1/2	Gir-origin, captive-bred (2001) (Ouwehands Dierenpark, Rhenen)
Edinburgh (Z.2001.174.2)	adult/female	2/1 ^d	Gir-origin, captive-bred (2001) (Ouwehands Dierenpark, Rhenen)
Edinburgh (Z.2009.008)	adult female	1/1	Gir-origin, captive-bred (2005) (Chester Zoo)
Edinburgh (Z.2009.009)	subadult female	1/2	Gir-origin, captive-bred (2005) (Paignton Zoo)
Edinburgh (Z.2007.010)	adult male	1/1	Gir, Gujarat, northwest India (2006) (Zoo de la Boissiere, Nantes)
Edinburgh (Z.2007.093)	adult male	1/2	Gir-origin, captive-bred (2006) (Muséum de Besançon, France)
Edinburgh (Z.2007.015)	adult/female	1/1	Gir-origin, captive-bred (2007) (London Zoo)
Edinburgh (Z.2008.004)	adult female	1/2 ^e	Gir-origin, captive-bred (2007) (Twycross Zoo)
Edinburgh (Z.2009.024.3)	adult male	1/1	Gir-origin, captive-bred (2009) (Dudley Zoo)
Edinburgh (Z.1950.101.6)		2/2	India (early 19 th century; < 1818?)
Oxford (14174)	adult/female	1/1	India (1876)
Paris (A1884)	adult/female	1/1	India (1838)
Paris (I-1460)	adult/female	1/1	India (1843?)
Paris (1873.556)	adult/male	1/1	India (1874)
Paris (1962.2872)	adult/female	1/1	India
Amsterdam (710)	adult/male	1/1	India (assigned based on mitochondrial DNA by Barnett <i>et al.</i> 2007) (1809)
^a New York (54995)		1/1	Gir, Gujarat, northwest India (1929)
^a New York (54996)		2/2	Gir, Gujarat, northwest India (1929)
^a Chicago (31121)	subadult/male	2/2	Gir, Gujarat, northwest India (1929)
^a Mumbai (1254)		1/2	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1255)		1/1	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1261)		1/?	Gir, Gujarat, northwest India (1953-1963) (right side broken)
^a Mumbai (1267)		1/1	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1268)		1/1	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1291)		1/1	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1292)		2/1	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1293)		1/1	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1329)		1/2	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1353)		1/1	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1363)		1/1	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1364)		1/1	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1389)		1/1	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1391)		1/2	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1392)		1/1	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1393)		1/1	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (1396)		1/1	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (5744)		1/1	Gir, Gujarat, northwest India (1931)
^a Mumbai (5926)		1/1	Gir, Gujarat, northwest India (c. 1931)
^a Mumbai (no ID-1)		2/2	Gir, Gujarat, northwest India (1953-1963)
^a Mumbai (no ID-2)		1/1	Gir, Gujarat, northwest India (1953-1963)

Sources: ^a Todd (1965), ^b Smee (1835), ^c Pocock (1930)

^d A spur arises from the mesial side of the left infraorbital foramen, but does not completely divide it.

^e A minor constriction indicating an incipient division of the left infraorbital foramen.

^f By radio-carbon dating (O'Regan *et al.*, 2005).

^g This identification may need to be re-evaluated and perhaps tested by extraction of mtDNA. Selous travelled extensively and hunted intensively between South Africa and Sudan, including the small area where most African lion skulls with DIF originate, but he never hunted in India (http://en.wikipedia.org/wiki/Frederick_Selous). It was sometimes the practice of taxidermists to replace damaged or missing skulls in mounted specimens or rugs with mounted heads using alternative specimens, but it would seem unlikely that the skull of a very rare Asian lion would have been selected for this purpose.

^h Probably animals belong to those processed by the Roland Ward for the Maharajah of Nawanager at c. 1930 (Pocock, 1930).

