

A revised taxonomy of the Felidae

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MAMMALIA FERÆ. Felis.

Pardus mas, *Panthera femina*. *Alp. Egypt.* 237. t. 15. f. 2.
Pardalis. *Rej. quadr.* 166.
Tigris mexicana. *Hern. mex.* 498. t. 498.
Pium Dalypus. *Nieremb. nat.* 153. t. 153.
Habitat in India. Pauter

- Onca. 4. *F. cauda elongata*, corpore flavesciente maculis nigris rotundato angulatis medio flavis.
Pardus l. Lynx brasiliensis. *Raj. quadr.* 168.
Jaguara. *Mægr. bras.* 235.
Habitat in America meridionali.

- Pardalis*. 5. *F. cauda elongata*, corpore maculis superioribus virgatis; inferioribus orbiculatis. *Syst. nat.* 4. n. 4.
Cato-Pardus mexicanus. *Hern. mex.* 512. t. 512.
Catus Pardus l. Catus americanorum. *Raj. quadr.* 169.
Habitat in America. Swinhoe
Magnitudo Melis supra fuscus, subtus albicans; Lineæ punctique nigra per totum corpus longitudinaliter sparsa, sed pedes & abdomen tinctura punctis; Lateralibus latioribus albis & fuscis punctantur. Aures breves, margine bifide ubique penicillis. Pedes 5-4. Cauda verticillato-variegata proportionem Cati. Mystaces 4 ordinum; in singula ordine setæ 3. f. 5; alba basi nigra, longitudine capitis.

- Catus*. 6. *F. cauda elongata*, corpore fasciis nigricantibus; dorsilibus longitudinalibus tribus; lateralibus spirilibus.
Felis cauda elongata, auribus aequalibus. *Fann. succ.* 3. *Syst. nat.* 4. n. 6.
Felis vulgo Catus. *Gesf. quadr.* 98. *Aldr. quadr.* 365. *Raj. quadr.* 98.
Felis. *Aldr. dig.* 564. *Jonst. quadr.* 180. t. 72..
Habitat in Europæ australi sylvæ, colla
Moribus cingentem, tranquilla, ore molat, candam erigit; excitata agilissima, scandit, irata fremit odore ambrosiaco, Marum Leo, in prædam intentam candam movet, oculi noctu lucent, inhiando prædam haurit, clamando rixandoque misere amat. Pupilla interdu perpendiculari oblonga, noctu tereti ampliata; ungibus complicatis incedit, parce bibit, urina corrosiva. Sterens sepelit, carnes edit vegetabilique respuit, in instante tempestate manu lavat, dorsum in tenebris electrifas; in altum assa decidit in pedes. Palices non habet. Delectatur Mara, Nepeta, Valeriana.

7. F.

MAMMALIA FERÆ. Viverra.

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- Lynx*. 7. *F. cauda abbreviata*, apice atra, auriculis apice barbatis.
Felis cauda truncata, colore rufescente maculato. *Fann. succ.* 4. *Syst. nat.* 4. n. 7. *It. Woth.* 222.
Lynx cervarius. *Gesf. quadr.* 677. *Tourn. it.* 2. p. 185.
Lynx. *Aldr. dig.* 90. *Jonst. quadr.* 82. t. 31. *Raj. quadr.* 166.
Habitat in Europæ sylvæ & desertis. Swinhoe
Cauda femoribus paulo brevior apice atra. Palpebra inferior albicans, ut & superior versus canthum majorem. Macula linearis fusca pone oculos. Auricularum apices nigri. Palpebre albæ.

Viverra

13. VIVERRA. *Dentes Primores VI: intermediis brevioribus.*
Molares plures quam tres.
Lingua retrorsum aculeata.
Ungues exterti.

- Ichneumon*. 1. *V. cauda e basi incrassata sensim attenuata.*
Meles digitis mediis longioribus; lateralibus aequalibus, ungibus subunitiformibus. *Hasselqv. itin.* 191.
Meles ungibus uniformibus, leucophis. *Syst. nat.* 6.
Mus pharaonis. *Alpin. Egypt.* 14. t. 3.
Ichneumon. *Belon. itin.* 96. *pisc.* 44. *Gesf. quadr.* 368. *Aldr. quadr.* 300. t. 301.
 β. *Mustela glauca.* *Syst. nat.* 5. *Antea. acad.* 2. p. 109. t. 1.
Mustela l. Viverra indis Mangutia. *Kampf. amon.* 574. t. 567.
Quil l. Quirpele. *Garc. arom.* 163.
Serpenticida l. Muncos. *Rumpf. herb.* 7. p. 69. t. 28. f. 2. 3.
Ichneumon indicus. *Edu. av.* 199. t. 199.
Ichneumon l. Vulpecula zeilanica. *Seb. mus.* 1. p. 66. t. 41. f. 1.
Habitat in Ægypto ad ripas Nili, & in India primario; mansuescit. *La Manguste. Buffon.*
Frons plana. Labium superius prominent. *Auricula rotundata.* *Mystaces simplici serie in omnibus latius lateralibus ad marginem.* *Lingua scabra. Pollex a reliquis distinctus.* *Cauda basi crassa, sensim attenuata, longitudine corporis.* *Folliculus ante aperturam ani,*
sub



SPECIES SURVIVAL COMMISSION

CAT SPECIALIST GROUP



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A revised taxonomy of the Felidae

Executive summary

1. The current classification of the Felidae was reviewed by a panel of 22 experts divided into core, expert and review groups, which make up the Cat Classification Task Force CCTF of the IUCN Cat Specialist Group.
2. The principal aim of the CCTF was to produce a consensus on a revised classification of the Felidae for use by the IUCN.
3. Based on current published research, the CCTF has fully revised the classification of the Felidae at the level of genus, species and subspecies.
4. A novel traffic-light system was developed to indicate certainty of each taxon based on morphological, molecular, biogeographical and other evidence. A concordance of good evidence in the three principal categories was required to strongly support the acceptance of a taxon.
5. Where disagreements exist among members of the CCTF, these have been highlighted in the accounts for each species. Only further research will be able to answer the potential conflicts in existing data.
6. A total of 14 genera, 41 species and 80 subspecies are recognised by most members of the CCTF, which is a considerable change from the classification proposed by Wozencraft (2005), the last major revision of the Felidae.
7. Future areas of taxonomic research have been highlighted in order to answer current areas of uncertainty.
8. This classification of the Felidae will be reviewed every five years unless a major new piece of research requires a more rapid revision for the conservation benefit of felid species at risk of extinction.

Introduction

The main task of the IUCN SSC Cat Specialist Group is the continuous review of the conservation status of all cat species and subspecies according to The IUCN Red List of Threatened Species process. A critical subject in this task is the systematic classification of the cat family, the Felidae. The taxonomy of cats has undergone considerable changes in the past, not only at the level of species and subspecies, but even at the level of genus. The classification presently used by the Cat Specialist Group was published in *Wild Cats – Status Survey and Conservation Action Plan* edited by K. Nowell and P. Jackson (published by IUCN 1996) and is based on the state of research in the early 1990s. Since then mainly studies using more advanced morphological, biogeographical and, foremost, molecular techniques have provided new insights into cat phylogeny and variation, suggesting several important changes with regard to species and subspecies, and the evolutionary relationships between genera and species. These changes may impact on the Red List process and on the listing of taxonomic units in international treaties and national legislation. Therefore the classification used by IUCN institutions has significance beyond the Red List. The Cat Specialist Group initiated a review of the present taxonomic system of the Felidae by an expert group, the Cat Classification Task Force CCTF. Their Terms of Reference were endorsed by Dr Simon Stuart, IUCN/SSC Chair 2008-2016.

Goal

The CCTF presents, on behalf of the Cat Specialist Group and the IUCN Red List Unit, and based on the best science and expert knowledge presently available, an updated and practical classification of the Felidae, including genera, species and subspecies, and the most likely geographical ranges of all taxa.

Principles

The starting point of the CCTF is the classification used by the Cat Specialist Group based on Nowell & Jackson (1996) and the classification (species, subspecies) used in the present version of The IUCN Red List of Threatened Species (www.iucnredlist.org), generally based on Wozencraft (2005). The CCTF has considered and reviewed all recent taxonomic reviews and scientific publications on the taxonomy of cats to propose an updated classification. The review was based mainly on new molecular and morphological research, but also considered general evolutionary, phylogenetic, palaeontological, biogeographical, behavioural and physiological evidence, especially in cases where molecular genetics and morphology are in disagreement. Conventional rules of zoological taxonomic nomenclature have to be respected, but traditions in the use of non-scientific names (from Jackson et al. 1996) – especially in cases where subspecies are merged – are also considered in order to produce a classification of cats useful for the practical work of the Cat Specialist Group and conservation in general. The CCTF has suggested a set of principles and criteria for decisions regarding the acceptance of proposed species and subspecies that can also be applied in future reviews. In case of uncertainty or lack of consensus,

Table 1: Members of the Cat Classification Task Force who have contributed to this report.

| | |
|--------------------------------|--|
| Core Group | |
| Andrew Kitchener (Chair CCTF) | National Museums Scotland, UK |
| Christine Breitenmoser-Würsten | Co-Chair IUCN/SSC Cat Specialist Group, Switzerland |
| Eduardo Eizirik | PUCRS, Porto Alegre, Brazil |
| Anthea Gentry | The Natural History Museum, London, UK |
| Lars Werdelin | Naturhistoriska riksmuseet, Stockholm, Sweden |
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| Nobuyuki Yamaguchi | University of Qatar |
| Expert Group | |
| Alexei Abramov | Zoological Institute, Russian Academy of Sciences |
| Per Christiansen | |
| Carlos Driscoll | Wildlife Institute of India, Dehradun, India |
| Will Duckworth | IUCN/SSC Cat Specialist Group, UK |
| Warren Johnson | Smithsonian Institution, USA |
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| Erik Meijaard | Borneo Futures, Jakarta, Indonesia |
| Paul O'Donoghue | University of Chester |
| Jim Sanderson | Small Wild Cat Conservation Foundation, USA |
| Kevin Seymour | Royal Ontario Museum |
| Review Group | |
| Mike Bruford | University of Cardiff, UK |
| Colin Groves | Australian National University |
| Mike Hoffmann | IUCN/SSC, UK |
| Kristin Nowell | IUCN/SSC Cat Specialist Group, USA |
| Zena Timmons | National Museums Scotland, UK |
| Shanan Tobe | Arcadia University, USA |

we use a conservative approach. Further cat specialists reviewed the proposals of the CCTF, especially in regard to the distribution of the taxa (e.g. the borders between neighbouring subspecies). Finally after a peer-review process, the proposals of the CCTF are published here and formally adopted as the current cat classification used by the IUCN/SSC Cat Specialist Group until the next revision. An important role of the CCTF was to identify key areas for future research in order to resolve current taxonomic uncertainties. We suggest future reviews every five years in order to keep pace with future research, but so as not to be too disruptive for legislators, field workers, captive breeding programmes, museums, educators and other cat workers, for whom an unstable and changing taxonomy could cause an enormous amount of work and may lead to inconsistent approaches.

The Cat Classification Task Force CCTF comprised three groups:

1. **Core Group** members set out general principles of the approach to be taken, reviewed current evidence, consulted with experts and drew up the proposed new classification of the felids.
2. **Expert Group** members provided specific and critical expert advice on species and subspecies, morphology, genetics, biogeographical areas, etc. to support the core group. Membership was not fixed and varied as specific expertise was required by the core group.
3. **Review Group** members provided a robust peer review of the proposed cat classification. Expert and Core Group members assumed also the role of reviewers at this stage.

The CCTF was chaired by Dr. Andrew Kitchener, Principal Curator of Vertebrates at the National Museums of Scotland, Edinburgh, UK.

Urs Breitenmoser and Christine Breitenmoser-Würsten

Stages in the development of the revised felid taxonomy

1. Establish general principles, definitions, and approach by Core Group
 - request input of Expert Group
 - invite Expert Group to submit any further evidence
2. Review of genera and likely included species
 - request input of Expert Group
 - invite Expert Group to submit any further evidence
3. Review of species focussing on those of key significance
 - request input of Expert Group
 - invite Expert Group to submit any further evidence
4. Review of subspecies focussing on those of key significance
 - request input of Expert Group
 - invite Expert Group to submit any further evidence
5. Core group assembles draft report
6. Draft report reviewed by Review and Expert Groups
7. Final report drafted and reviewed for publication

General principles for CCTF to consider including definition of terms

In order to overcome any misunderstandings of approach owing to different definitions of technical terms, the CCTF has defined these as used in the Task Force. This includes also the interrelationships between different technical terms and the taxonomic approaches that have been taken, e.g. naming of clines, relationship between species, subspecies, Evolutionary Significant Units ESUs, etc. and how to deal with the domestic cat.

Suggested required definitions and the relevant relationships between them in a hierarchical taxonomic order:

1. **Genera** – the CCTF has adopted an arbitrary cut-off date of the beginning of the Pliocene (5.2 Mya \pm 0.5 Mya) to define genera, following Hennig (1965). This is consistent with the major diversification of felid lineages during the late Miocene (Johnson et al. 2006).

2. **Species** – a group of individuals that share diagnostic morphological and molecular characteristics and distinct evolutionary lineages and biogeographical histories that allows them to be distinguished from other species. Species are generally expected to have had a most recent common ancestor with other species of at least 800,000 years ago based on the divergence times of Li et al. (2016). Species may hybridise with other species to a limited extent, but basic morphology, behaviour and ecology remain unaffected except in areas of introgression.

3. **Subspecies** – a group of individuals within a species that mostly share morphological and molecular characteristics that distinguish them from most other individuals within a species and that occupy a distinct part of the geographical range of the species. These distinguishing characters are not expected to be 100% diagnostic and gene flow is also expected between subspecies where ranges are contiguous.

4. Units

4.1. **Ecotypes** – Populations within a species that exhibit morphological and/or physiological adaptation to a particular environment or habitat that differs from the environment/habitat of neighbouring populations, but which display little or no genetic differentiation. These populations exhibit phenotypic plasticity in the face of varying environmental conditions.

4.2. **ESUs** – Evolutionary significant units are populations within a species that may not be morphologically distinct, but which exhibit a

distinct evolutionary history such that they may represent local long-term adaptation to environmental conditions or habitats. They may represent species or subspecies awaiting recognition.

4.3. **MUs** – Management units are populations within a species that are considered distinctive enough to warrant separate conservation management to that of the other populations. They may be equivalent to subspecies or to populations that are genetically differentiated but which are not taxonomically distinctive, but which may be locally adapted and considered worthy of separate conservation management.

5. **Clines** – Clines occur where species change gradually over geographical space, but all populations are genetically contiguous. Even though (particularly the end) populations along a cline may appear morphologically distinct, they do not represent distinct taxa.

6. **Domestic cat** – Following the ruling of the International Commission for Zoological Nomenclature (Opinion 2027; International Commission on Zoological Nomenclature 2003), the domestic descendant of the North African wildcat should be treated as a separate taxon, which here is regarded as a full species, *Felis catus*.

A system for indicating taxonomic certainty

Most scientific names for species and subspecies have little or no scientific basis. Many are based on one, a few or even no specimens, with few or no comparisons with related taxa and hence, in particular, many subspecies names are likely to be invalid. However, for many species and subspecies recent research based on more than one line of evidence is not available. Currently there is no system for indicating taxonomic certainty of particular taxa. Such a system would indicate to users of taxonomies the reliability and rigour behind classifications as well as highlighting areas where urgent research is needed.

Therefore, we propose a simple traffic-light system to indicate the likely reliability of species and subspecies given available evidence. At least three lines of correlated evidence are required for taxonomic certainty:

1. **Morphological** – taxa are diagnosably distinct on the basis of several characters (e.g. skull, pelage) in comparison with all other members of a species or genus (excluding hybrids) from throughout their respective geographical ranges. Average differences and size differences alone are not considered reliable indicators of taxonomic distinctiveness. Pelage characteristics may be especially variable within species and hence may be of poor diagnostic value. Care must also be taken that apparent differences are not clinal, especially where gaps in formerly contiguous distributions have occurred recently.

2. **Genetic** – taxa are genetically distinct based on a variety of genetic information, including mtDNA, Y-chromosome markers, Single Nucleotide Polymorphisms SNPs, etc., but care should be taken that alternative explanations, such as genetic drift, founder effects and population bottlenecks, could explain apparent genetic distinctiveness of no taxonomic significance.

3. **Biogeographical** – distinct taxa are more likely to be recognised where there are distinct geographical barriers relevant to the taxon, e.g. rivers, seas, mountains, deserts, or where geological events, such as sea-level changes, volcanic eruptions are broadly coincident with coalescence times, or where recolonisations following climate

change are consistent with former refugia. Phylogeographical patterns of similar species or those that occur in similar habitats in the same geographical range may be useful to infer probable taxa.

Care must be taken to avoid misinterpretation of all lines of evidence caused by recent anthropogenic impacts, which may have isolated populations by extirpation in intervening geographical areas. Ancient hybridisation between taxa may also give false indications of con(sub)specificity, leading to erroneous conclusions about taxonomic status. Clinal variation may be interpreted incorrectly as two or more apparently distinctive populations owing to poor or incomplete sampling. Other lines of supporting evidence may also be useful:

4. **Behavioural** – e.g. predisposition to taming
 5. **Ecological** – e.g. use of distinct habitats with appropriate adaptations
 6. **Reproductive** – e.g. seasonality or not of reproductive cycles.
- Therefore, we propose a simple traffic-light system:



- Three or more lines of correlated evidence as outline above.



- Two or more lines of correlated evidence as outlined above plus reasonable inferences based on data from closely related species; taxon likely to be distinct. Further research required.



- One or no lines of evidence; status of taxon currently unknown, but considered unlikely to be valid. Further research required.



- Despite recent research, no evidence for distinctiveness, which may have formerly been suggested, or based on incomplete or erroneous data, or alternatively con(sub)specificity demonstrated.

Below are two examples of the use of the traffic-light system. These summary tables are presented at the end of each species section to provide a quick-to-read summary to help in rapid assessment of taxonomic certainty of taxa within and between species. Key: ++ good evidence within category, e.g. skull/pelage; mtDNA/nDNA; + some evidence or reasonable, inference within category; - was investigated, but no evidence to support distinction; o has never been investigated. If the symbol is in brackets, the validity of evidence is considered uncertain.

Genus *Neofelis*

| Species | Subspecies | Morphology | Genetics | Biogeography | Certainty | Comments |
|--------------------------|-----------------------|------------|----------|--------------|-----------|--|
| <i>Neofelis nebulosa</i> | <i>nebulosa</i> | ++ | ++ | ++ | | |
| | <i>macrosceloides</i> | - | (-) | - | | Possible skull differences from <i>nebulosa</i> , but could be clinal |
| | <i>brachyura</i> | - | (-) | ?+ | | Genetically and morphologically similar to <i>nebulosa</i> |
| <i>Neofelis diardi</i> | <i>diardi</i> | ++ | ++ | ++ | | |
| | <i>borneensis</i> | + | ++ | ++ | | Skulls distinguishable between subspecies, but pelage variation poorly known |

Genus *Leptailurus*

| Species | Subspecies | Morphology | Genetics | Biogeography | Certainty | Comments |
|---------------------------|--------------------|------------|----------|--------------|-----------|--|
| <i>Leptailurus serval</i> | <i>serval</i> | ++ | ++ | ++ | | |
| | <i>brachyurus</i> | + | o | o | | |
| | <i>constantina</i> | + | o | ++ | | Possibly distinct, but could be synonym of <i>serval</i> |
| | <i>lipostictus</i> | + | o | ++ | | Possibly distinct, but could be synonym of <i>serval</i> |
| | <i>phillipsi</i> | + | + | + | | |
| | <i>togoensis</i> | + | o | o | | |

A short history of felid systematics

Today at least 38 species of cats are recognised throughout the world (excluding only Australasia and the polar regions), although recent morphological and molecular research suggests that there may be a few more. Traditionally cats have been classified into two main groups; the big cats, mostly of the genus *Panthera*, and the smaller cats, with the cheetah left as an odd afterthought, representing a very early divergence from the felid line (Pocock 1917). This basic classification stood the test of time throughout most of the twentieth century until new techniques and analyses became available. The key characteristic that was used to separate the big cats (Pantherinae) from the smaller cats (Felinae) is the presence in big cats of an elastic ligament in the hyoid apparatus below the tongue, which apparently allowed big cats to roar, but not purr. Conversely, the bony hyoid of smaller cats allowed them to purr but not roar. The other key characteristic, which allowed for the separation of the cheetah in its own subfamily, the Acinonychinae, was the absence of cutaneous sheaths to protect the retracted claws. However, recent studies of hyoid structure and vocal abilities of cats have found that this simple correlation does not hold. While it is true that some big cats roar (e.g. lion, leopard), not all are able or confirmed able to do so, despite having an elastic hyoid. It was found that the fundamental difference between the mostly roaring non-purring cats and the rest was the structure of the larynx (Hast 1989). Long, fleshy, elasticated vocal folds within the larynx of big cats resonate to produce a roar, whereas the smaller cats, including the cheetah, have simpler vocal folds that only allow purring.

Although the number of species of cats is fairly well known (with a handful of exceptions), the number of genera that have been recognised is very variable. From a proliferation of genera or subgenera during the 19th century, there was a lumping together into a handful during the middle of the 20th century, followed by a final flourish and re-recognition of many of the 19th century names towards the end of the 20th century. Therefore, at one extreme only two or three genera were used to classify all felids, whereas today there are varying opinions, with as many as 18 being recognised on the basis of several studies of morphology and genetics. This uncertainty is probably due to the high degree of similarity in basic body plan between all felid species, with the exception of the cheetah, and a lack of congruence between different sets of characters. Perhaps the recent radiation of the cat family as we know it today, coupled with the constraints of prey capture and the processing of a highly carnivorous diet, has resulted in a limited range of variation within the felids.

Two major developments towards the end of the 20th century have helped change our view of felid systematics. Firstly, the development of molecular techniques, including the polymerase chain reaction, has allowed the sequencing of mitochondrial genes and nuclear microsatellites, in particular, so that differences in the sequences of base pairs of DNA can be elucidated. Secondly, the advent of personal computers with powerful software coupled, with the use of advanced statistical methods, have allowed vast datasets of morphological and molecular characters to be analysed in order to produce dendrograms of relationships between species. By adding in a time element by correlating known evolutionary events with divergences between species, it has also been possible to calibrate phylogenies using the so-called molecular clock, for comparison with the fossil record. Encouragingly, in broad outline there is a high degree of agreement between the various morphological and molecular phylogenies, but inevitably some species have been difficult to pin down. Even a study of lipids from the anal

sacs of 16 cat species showed a high degree of agreement with more typical phylogenies (Bininda-Emonds et al. 2001).

To some extent the advent of molecular techniques, in particular, has helped overcome some of the taxonomic conundrums of the past. For example, on the basis of its highly specialised morphology for cursorial hunting, the cheetah was often placed in its own subfamily and regarded as representing a very early offshoot of the felid line. Another example is the caracal, which was often regarded as a close relative of the bobcat, Eurasian, Canadian and Iberian lynxes of the northern hemisphere, presumably on the basis of its tufted ears and short tail. However, molecular phylogenies based on a variety of techniques demonstrate that the cheetah is found within the main felid radiation (the pantherine lineage) and is closely related to the puma (Johnson et al. 2006, Li et al. 2016). The caracal was also found to have diverged from this pantherine lineage as part of its own lineage with the serval and African golden cat and is unrelated to the other lynxes, which do form a monophyletic clade, thus confirming Werdelin's (1981) earlier study based on morphology. Molecular techniques can also be used on some recent fossils of extinct taxa; a recent study (Barnett et al. 2005) showed that the sabre-toothed cats, *Smilodon* and *Homotherium*, are sister taxa to the crown group of modern felids and not in *Panthera* as previously shown.

The main Old World lineage of small cats comprises those species that belong to the genus *Felis* proper, including the wildcats, sand cat, jungle cat, and the domestic cat. The most recent molecular data suggest that the Felinae and Pantherinae diverged about 11.5 million years ago and that the eight felid lineages diverged sequentially from 5.67 to 10.67 million years ago (Li et al. 2016). *Felis* proper diverged from the Leopard cat lineage about 7.25 million years ago. The most basal lineage of the Felinae is the Caracal lineage, followed by the Ocelot lineage, the Lynx and Bay Cat lineages, and finally the Leopard Cat and Domestic Cat lineages. Some genera and species have been difficult to place in the felid phylogeny. For example, *Otocolobus* has been associated as a basal member of the Domestic Cat lineage, but in the latest phylogeny it is basal in the Leopard Cat lineage. The African and Asiatic golden cats were formerly considered to be close, but they occupy different lineages, i.e. the Asiatic golden cat and the bay cat form a distinct genus, *Catopuma*, in south east Asia, but the apparently morphologically similar African golden cat is closest to the caracal (both in the genus *Caraca*), which has no close relationship to the lynxes. The marbled cat (*Pardofelis*) is also found in the Bay Cat lineage, but is more distantly related to *Catopuma*. The once aberrant cheetah (genus *Acinonyx*) is in the same lineage as the puma (*Puma*) and jaguarundi (*Herpailurus*), although some include the jaguarundi in *Puma*. Fossil cheetahs (genus *Miracinonyx*) in North America that date back to three million years ago are very similar to pumas, supporting a close relationship between the lineages, although some palaeontologists regard the similarity between Old World and American cheetahs as being due to convergent evolution (Adams 1979). As defined here, *Miracinonyx* would be subsumed within *Puma*. The Puma lineage probably diverged more than eight million years ago on the basis of the molecular clock (Johnson et al. 2006, Li et al. 2016). As would be expected the lynxes form a coherent group (genus *Lynx*), supported by molecular and morphological analyses, which seems to have evolved to exploit the radiation of lagomorphs in the northern hemisphere. The molecular clock suggests a common ancestor dating back some 3.48 million years ago (Li et al. 2016).

A recent molecular phylogeny (Li et al. 2016) showed that the divergence and radiation of small South American cats occurred almost 10 million years ago, which was long before the Panama land bridge formed about 3–5 million years ago to join South and North America. Therefore, this radiation occurred in North America and indeed cats are not known from South America until a maximum of 1.8 million years ago. This isolation and radiation in the Americas is supported by differences in chromosome numbers between the two groups; the small South American cats of this group have two fewer chromosomes than the 38 of other lineages. These New World cats belong to the genus *Leopardus*, although more genera were recognised until recently, including *Oncifelis* (Geoffroy's cat and guigna), *Oreailurus* (Andean mountain cat) and *Lynchailurus* (pampas cat). However, natural hybridisation is frequent among some species of *Leopardus*, including Geoffroy's cat, pampas cat and tigrinas, emphasizing their close relationships (Li et al. 2016).

The big cats also form a monophyletic group comprising the clouded leopards (*Neofelis*) and the remaining big cats (*Panthera*). Molecular data suggest a common ancestor some 5.67 million years ago, which at first sight seems discordant with a fossil record that goes back only 2–3 million years ago (although a recent putative snow leopard ancestor, *Panthera blytheae* from Tibet has been dated to 4.4 million years ago and may be almost six million years old (Deng et al. 2011, Tseng et al. 2013). However, the clouded leopards represent the earliest divergence from this lineage and if the common ancestor of this group was also a rain forest inhabitant, it is unlikely that fossils will have survived, owing to poor preservation conditions. Therefore the fossil record of this group is likely to be deficient. Within the genus *Panthera*, recent molecular analyses have concluded that the snow leopard and tiger are sister species and diverged earlier from the ancestors of the jaguar, leopard and lion, of which the latter are also sister species (Davis et al. 2010, Li et al. 2015). Clearly more research needs to be done in all fields, not just the molecular side. The recent radiation of the Felidae and their conservative morphology will probably continue to give systematists trouble for some time to come and result in continuing instability in the classification of felid species at the generic level and above.

Bininda-Emonds et al. (1999) published the first attempt to combine carnivoran phylogenies from different molecular and morphological studies. In the case of the felids 40 part or whole phylogenies were combined. The combined phylogeny for felids still places the cheetah as a distinct lineage from the other cats, but puts the marbled cat back into the Pantherinae, the African golden cat into a group with Asiatic golden cat and bay cat, finds the Pallas' cat and serval as basal to the *Felis* group, but otherwise places species into the same groups as described above. All in all it demonstrates once more that although there are well-defined groups within the Felidae, their interrelationships are still uncertain. This was recently updated by Nyakatura & Bininda-Emonds (2012) with similar results.

As mentioned earlier there may still be some cat species waiting to be recognised and this review will highlight where there is clear or some evidence for this. The other contentious area concerning felid systematics is the number of felid subspecies that should be recognised.

There is a plethora of subspecies names associated with the cat species, but it must be remembered that almost in all cases these are not scientific designations, but have been used as handy labels for one or a handful of (often atypical) specimens from particular geographi-

cal locations. Putting aside questions of how we define and recognise subspecies, which are common to all animals, there is a clear need for taxonomic revisions (based on a variety of studies) of all species to determine whether geographical variation within species is present or not, and if so, whether it is clinal or discrete and of taxonomic significance. Many of the problems of lack of concordance between traditional classifications and molecular studies have arisen because of the misplaced assumption that these classifications have some basis in science. Where revisions have been made, there is a great deal of common ground.

In recent years there has been a growth in the application of the phylogenetic species concept (PSC) in taxonomic revisions, particularly in ornithology. The PSC defines species on the basis of populations, which have at least one unique diagnosable character. In ornithology the application of the PSC has seen many former subspecies raised to species level. Groves (2001) applied this concept to primates as the only feasible alternative to other species concepts and this has also resulted in a proliferation of primate species. There is concern that uncritical application of this species concept will lead to a huge rise in the number of recognised cat species, with implications for the conservation of many more endangered species (e.g. Zachos et al. 2013, but see also Meijaard & Rawson 2015). However, we have taken a conservative approach that relies on at least three independent lines of existing evidence to confirm the recognition of species and subspecies. While our review will not be the last word written on felid taxonomy, we hope the approach we have taken will provide a solid baseline against which future changes can be made and will offer taxonomic stability that will provide confidence for current and future conservation management of many endangered species.

A brief review of modern felid genera

The starting point for our discussion will be Johnson et al. (2006), in which 11 genera are recognised. We have followed Hennig (1965) in recognising as distinct genera those lineages that diverged in the late Miocene, c. 5 Mya. On this basis, the following genera are recognised.

1. ***Felis*** – there is a general consensus on this genus, although the number of included species is uncertain.
2. ***Otocolobus*** – this monotypic genus is retained for the unusual Pallas's cat, which is weakly aligned with *Prionailurus* or, more unlikely, with *Felis*.
3. ***Prionailurus*** – this genus is strongly supported, although there has previously been discussion about the inclusion of the rusty-spotted cat, which diverged early, but it does appear morphologically to be in this genus.
4. ***Puma*** – Johnson et al. (2006) include the puma and jaguarundi in this genus. Johnson et al. (2006) found the jaguarundi is the sister species to the puma and hence included it in the genus *Puma*, although Agnarsson et al. (2010) found that the jaguarundi was not a sister species to *Puma* and retained *Herpailurus*. There are distinct differences in morphology and behaviour between the two, and Segura et al. (2013) found that cranial development between *Puma* and *Acinonyx* was more similar to each other than between *Puma* and *Herpailurus*. Chimento et al. (2014) included the jaguarundi and *Puma pumoides* in the subgenus *Herpailurus* within the genus *Puma* in their morphological review of *Puma pumoides*. The problem in employing Hennig's (1965) criterion for generic recognition is that this depends on the dating of the divergence between the puma and

jaguarundi lineages, which in turn depends on which fossils are used to calibrate the molecular tree. For example, although Johnson et al. (2006) date this divergence more recently at a mean of 4.17 Mya, Barnett et al. (2005) found that the divergence date for the jaguarundi lineage varied from a mean of 5.03 Mya to a mean 7.42 Mya, depending on whether *Pseudaelurus* or *Proailurus* is used to calibrate the molecular tree. However, these dates fall within the late Miocene, which would lead to retention of *Herpailurus* as a distinct genus (but see Li et al. 2015). There is no clear resolution of this matter, in which case the CCTF has been asked to retain a conservative position, so that provisionally *Herpailurus* has been retained as a distinct genus until further evidence is available.

5. **Herpailurus** – see discussion under *Puma* above.

6. **Acinonyx** – there is general consensus on this genus, which is clearly defined.

7. **Lynx** – there is a general consensus on this genus, which is clearly defined.

8. **Leopardus** – in the recent past this genus has been further subdivided into four genera (*Leopardus*, *Oncifelis*, *Lynchailurus* and *Oreailurus*), but the recent radiation of these species, natural hybridisation and the close similarity in skull morphology between these species supports Johnson et al.'s (2006) conclusion of a single genus.

9. **Caracal** – formerly the African golden cat (*Profelis*) and serval (*Lepailurus*) were in separate genera. Using Hennig's (1965) criterion the serval would be retained in a separate genus, but *Profelis* is subsumed into *Caracal*.

10. **Pardofelis** – the marbled cat is morphologically very distinct from the Asiatic golden cat and bay cat (in a way that the margay is not distinct from the ocelot or other *Leopardus* spp.). Further based on Johnson et al. (2006), the marbled cat split from the Asiatic golden cat and the bay cat about 5.86 Mya. Therefore, applying Hennig's (1965) criterion together with the morphological differences, it is recommended separating the marbled cat from the latter two, thereby reinstating *Catopuma* for the bay cat and Asiatic golden cat.

11. **Catopuma** – see *Pardofelis*

12. **Neofelis** – there is a general consensus on this genus.

13. **Panthera** – there is a general consensus on this genus with the possible exception of the inclusion of the snow leopard, which has been separated into its own genus, *Uncia*. However, recent molecular studies show that the snow leopard is the sister species to the tiger (Davis et al. 2010; Li et al. 2015), so that either these two should be separated from the other *Panthera* spp. or all should be retained in *Panthera*, which would also be supported by Hennig's (1965) criterion and which we support.

Therefore, the CCTF recognises two genera, *Herpailurus* and *Catopuma*, in addition to the 11 recognised by Johnson et al. (2006), although this could be reduced to a total of 12 if further research supports the inclusion of *Herpailurus* in *Puma*.

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Species Accounts

The sequence of species below follows the phylogenetic tree of Li et al. (2016) from the most basal member of each lineage, starting with the domestic cat lineage. We provide maps based on the most recent Red List assessments (www.iucnredlist.org) with approximate locations of subspecies. For monotypic species we do not show a dis-

tribution map as they are available on the IUCN Red List website. We illustrate each species with at least one photograph.

Non-scientific names abbreviations

E – English; F – French; G – German; Sp – Spanish

Museum abbreviations

| | |
|-------|---|
| AMNH | American Museum of Natural History, New York, NY, USA |
| ANSP | Academy of Natural Sciences, Philadelphia, PA, USA |
| BMNH | Natural History Museum, London, UK |
| MACN | Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, |
| MCZ | Museum of Comparative Zoology, Cambridge, Massachusetts, USA |
| ZMB | Museum für Naturkunde, Berlin, Germany |
| MLP | Museo de La Plata, Buenos Aires, Argentina |
| MNCN | Museo Nacional de Ciencias Naturales, Madrid, Spain |
| MNHN | Museum national d'Histoire Naturelle, Paris, France |
| MNHNM | Museo Nacional Historia Natural, Montevideo, Uruguay Musacional de Natural |
| MSNM | Museo Civico di Storia Naturale, Milan, Italy |
| MZS | Musée zoologique de la ville de Strasbourg, Strasbourg, France |
| NMW | Naturhistorisches Museum Wien, Vienna, Austria |
| NRM | Naturhistoriska riksmuseet, Stockholm, Sweden |
| NSM | National Museum of Nature and Science, Tokyo, Japan |
| RMCA | Royal Museum for Central Africa, Tervuren, Belgium |
| RMNH | Naturalis Biodiversity Center, Leiden, The Netherlands |
| ROM | Royal Ontario Museum, Toronto, Canada |
| SMF | Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany |
| TM | Ditsong: National Museum of Natural History, Pretoria, Republic of South Africa |
| USNM | National Museum of Natural History, Smithsonian Institution, Washington DC, USA |
| ZFMK | Zoologisches Forschungsmuseum Alexander König, Bonn, Germany |
| ZMMU | Zoological Museum of Moscow State University, Moscow, Russia; |
| ZIN | Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia (each specimen from ZIN has two collection numbers – one for skin, and another for skull (skeleton)). |

Family Felidae Fischer, 1817; 372
Subfamily Felinae Fischer, 1817; 372

Genus *Felis* Linnaeus, 1758; 41

The genus *Felis* usually includes between four and six species. Here we provisionally recognise six species.

Felis chaus

E: Jungle cat, swamp cat; F: Chat de marais, chat de jungle, chaus; G: Rohrkatze, Sumpfluchs; Sp: Gato de la jungla, gato de los pantanos.

Up to 10 subspecies have been recognised (Wozencraft, 2005):

Felis chaus chaus Schreber, 1777a; 414 and 1777b; pl. 110B.

Locality from where species was first described: "... wohnt in den sumpfigen mit Schilf bewachsenen oder bewaldeten Gegenden der Steppen um das kaspische Meer, und die in selbiges fallenden Flüsse. Auf der Nordseite des Terekflusses und der Festung Kislar siehet man ihn selten, und gegen die Wolga hin gar nicht; desto häufiger aber bei der Mündung des Kur, und in den persischen Landschaften Gilan und Masanderan" [= lives in marshes overgrown with reeds or forested areas of the steppes around the Caspian Sea, and the same in the surrounding rivers. On the north side of the Terek River around the fortress Kislar it is rarely seen, and not at all towards the Volga; but more often at the mouth of the Kur River, and in the Persian provinces of Ghilan and Mazanderan], i.e. Terek River, Northern Caucasus, Dagestan, Russia.

Holotype: None designated, based on Gueldenstädt's (1776) Chaus.

Distribution: Turkestan, Caucasus, Iran and Baluchistan, Pakistan.

Felis chaus nilotica de Winton, 1898; 292.

Type locality: near Cairo [Egypt].

Holotype: BMNH 1898.6.5.1 adult male skin and skull.

Distribution: Egypt, the delta district extending westwards to Mersa Matruh, 155 miles W of Alexandria and S along Nile to Fayum, Quena Province and probably Mina Province.

Felis chaus furax de Winton, 1898; 293.

Type locality: Jericho.

Holotype: BMNH 1864.8.17.4 male skull.

Distribution: S Syria and Iraq.

Felis chaus prateri Pocock, 1939; 298.

Type locality: Jacobabad, on the Upper Sind Frontier [Pakistan].

Holotype: BMNH 1832.2.1.67 male skin and skull.

Distribution: Sind from upper frontier to Larkana and Karachi in the west to Thar Parkar in SE Pakistan.

Felis chaus kelaarti Pocock, 1939; 300.

Type locality: Cheddikulam, N.P., Ceylon [= Sri Lanka].

Holotype: BMNH 1932.2.1.58 young male skull and skin.

Distribution: Sri Lanka and S India, south of the Kistna River up to about 1500 metres.

Felis chaus oxiana Heptner, 1969; 1259.

Type locality: "Tigrovaya Balka" Nature Reserve in the lower Vakhsh flow (tributary of the Amu Darya river) [Tadjikistan].

Holotype: ZMMU S-77271 adult male skull and skin.

Distribution: Turkestan (= C Asia).



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Felis chaus affinis Gray, 1830; pl. 3.

Type locality: Gangootri, Tehri Garwhal, N India.

Syntypes: BMNH 1837.6.10.40 and BMNH 1837.6.10.41 skins and skulls.

Distribution: The Himalayas from Kashmir to Sikkim and probably the Naga Hills, Assam, at altitudes ranging from about 300-2300 metres or more.

Felis chaus kutas Pearson, 1832; 75.

Type locality: Midnapore, Bengal, c.70 miles W of Calcutta.

Holotype: Museum of the Asiatic Society Bengal mounted skin; lost?

Distribution: N Peninsular India from Bengal to Cutch and ranging from 460 metres in Darbhanga north of Ganges to 46 metres in Cutch.

Felis chaus fulvidina Thomas, 1928; 834.

Type locality: Originally given as "Kampong Tomb, Annam", but this was an error. Should be "Komphong Thom, Cambodia" (Duckworth et al. 2005).

Type: BMNH 1928.7.1.36 skin.

Distribution: Annam and probably Burma, up to 1500 metres in the Chin Hills.

Felis chaus maimanah Zukowsky, 1914; 139.

Type locality: Maimana, Afghanistan.

Holotype: Skin in Indian Museum, Kolkata, now lost (see Heptner & Sludskii 1972; 328).

Distribution: Afghanistan.

N.B. Heptner (1969) and Heptner & Sludskii (1972) identify this taxon as *F. lybica caudata=ornata*.

In addition the following subspecies is sometimes recognised from southern India, but would be included in *kelaarti* above:

Felis chaus valbalala Deraniyagala, 1955: 201.

Type locality: Karnool, [S India].

Holotype: BMNH 1932.2.1.58, adult male skin and skull.

Distribution: S India, S of the Kistna River.

Discussion

Until recently there had been no morphological or molecular study of geographical variation in jungle cats. Mukherjee & Groves (2007) examined the skull morphometrics of jungle cats from throughout their geographical range except SE Asia. They found that the skulls of western cats were much larger than those of eastern cats, such that all Indian populations were similar, but distinguishable from western ones. Mukherjee et al. (2010) examined variation in mitochondrial genes NADH5 and cytochrome b in Indian populations and found some degree of substructuring between northern and southern populations, but this was very recent and probably not sufficient to support subspecies distinctions. On the basis of these two studies it might be possible to infer two subspecies, with a possible additional subspecies in SE Asia, which has so far not been examined in detail:

Felis chaus chaus Schreber, 1777 (incl. *oxiana*, *nilotica*, *furax*).

Distribution: Egypt and the Middle East to Turkestan, Uzbekistan, Kazakhstan and Afghanistan.

Felis chaus affinis Gray, 1830 (incl. *prateri*, *kutas*).

Distribution: East Afghanistan, Indian subcontinent and Sri Lanka.

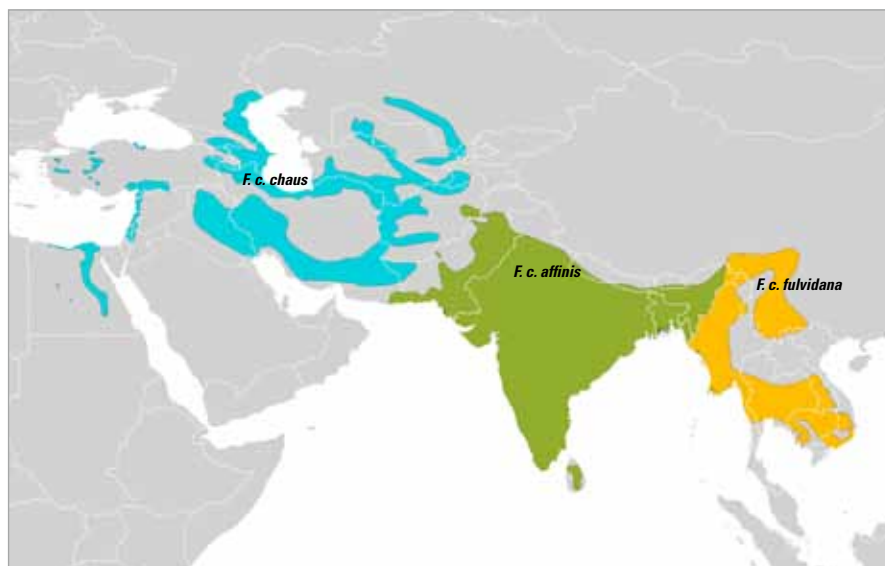
Felis chaus fulvidina Thomas, 1928.

Distribution: SE Asia, possibly including China.

Groves (pers. comm.) states that there are external characters as well as craniodental characters (Mukherjee & Groves 2007), which strongly distinguish those from the west (more or less, Iran westward) from those from the east, which he would be inclined to separate specifically. Their habitat requirements seem to be different as well – the western ones are riverine specialists, whereas the eastern ones are much more evenly spread.

A comprehensive phylogeographical study is required to understand better geographical variation in *Felis chaus*.

| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|------------------------------|------------|-----------|--------------|-----------|-----------------------------|
| <i>Felis chaus chaus</i> | ++ | ++ | ++ | | |
| <i>Felis chaus oxiana</i> | + | 0 | + | | Synonym of <i>chaus</i> ? |
| <i>Felis chaus maimanah</i> | + | 0 | | | Synonym of <i>chaus</i> ? |
| <i>Felis chaus nilotica</i> | + | 0 | + | | |
| <i>Felis chaus furax</i> | + | 0 | + | | Synonym of <i>chaus</i> ? |
| <i>Felis chaus affinis</i> | + | + | + | | |
| <i>Felis chaus prateri</i> | + | - | 0 | | Synonym of <i>affinis</i> ? |
| <i>Felis chaus kutas</i> | + | - | 0 | | Synonym of <i>affinis</i> ? |
| <i>Felis chaus kelaarti</i> | + | 0 | 0 | | Synonym of <i>affinis</i> ? |
| <i>Felis chaus valbalala</i> | + | - | + | | Synonym of <i>affinis</i> ? |
| <i>Felis chaus fulvidina</i> | + | 0 | + | | |



Distribution of tentative subspecies of the jungle cat. Borders between subspecies are speculative.

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Felis nigripes

E: Black-footed cat; F: Chat à pieds noirs; G: Schwartzfußkatze; Sp: Gato patinegro, gato de pies negros.

Felis nigripes is typically divided into two subspecies (Wozencraft 2005):

Felis nigripes nigripes Burchell, 1824; 592.

Type locality: the town of Litákun, [= Dithakong, near Kuruman, N Cape Province, South Africa].

Holotype: Incomplete skin seen by Burchell.

Distribution: Kalahari of Botswana, Namibia and northern Cape Province, South Africa (Sliwa 2013).

Distinguishing characters: Lighter in colour, tawny or off-white; bands running from nape often broken into spots or short stripes; spots brownish black or tawny (Sliwa 2013).

Felis nigripes thomasi Shortridge, 1931; 119.

Type locality: Thorn Kloof (Carlisle Bridge), C.P. (= Cape Province), [Eastern Cape, South Africa].

Holotype: Albany Museum no. 6333 adult male skin and skeleton.

Distribution: Karoo of central and southern South Africa (Sliwa 2013).

Distinguishing characters: Cinnamon-buff; bands from nape strongly developed and run unbroken to base of tail; three distinctive throat rings; spots are satiny black (Sliwa 2013).

Discussion

Pocock (1951) pointed out that variation in the pelage coloration of skins from the nominate race suggests the differences between these two subspecies are less than described. The supposed biogeographical barrier of the Orange River is also not consistent with



the distribution of the two supposed morphological types. Sliwa (2013) considered the two putative subspecies to represent the ends of a cline, with animals of the appearance of both subspecies occurring near Kimberley. Therefore, it seems likely that these subspecies are not valid and that this is a monotypic species, with some clinal variation:

Felis nigripes Burchell, 1824.

Distribution: Southern Africa.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|--------------------------------|------------|-----------|--------------|-----------|-----------------------------|
| <i>Felis nigripes nigripes</i> | ++ | ++ | ++ | | |
| <i>Felis nigripes thomasi</i> | + | 0 | 0 | | Included in <i>nigripes</i> |

Felis margarita

E: Sand cat; F: Chat des sables; G: Sandkatze, Saharakatze; Sp: Gato de las arenas, gato del Sahara.

Typically four subspecies are recognised (Wozencraft 2005):

Felis margarita margarita Loche, 1858; 49, pl.1.

Type locality: environs de Négonça (Sahara) [Algeria].

Holotype: No longer survives.

Distribution: North Africa.

Felis margarita harrisoni Hemmer, Grubb and Groves, 1976; 301.

Type locality: northern edge of Umm as Samin, Oman, 21°55' N / 55° 30' E.

Holotype: BMNH 1977.430 adult male skull and skin.

Distribution: Arabian Peninsula, Sinai, Israel.

Felis margarita thinobia (Ognev, 1927; 356).

Type locality: Repetek, Turkmenistan.

Holotype: ZMMU S-14226 adult male skull and skin.

Distribution: The deserts of Karakum and Kizilkum, Central Asia, and Iran (Lay et al. 1970).

Felis margarita scheffeli Hemmer, 1974; 32.

Type locality: Nushki-Wüste, Westpakistan [Nuski Desert, W Pakistan].

Holotype: SMF 38326 skull, skeleton and skin of an adult female imported alive in 1970-72.

Distribution: Pakistan.

Discussion

To date there have been no phylogeographical studies. There appear to be differences in pelage coloration and markings and skull size between North African sand cats and those from Pakistan (A. Kitchener, pers. obs.). The pelages of Arabian sand cats resemble that of some North African sand cats, and others resemble those of Pakistani and Turkmenian sand cats, which resemble each other, although the former tend to be greyer and the latter yellower. Preliminary genetic data (H. Senn, pers. comm.) support the distinctiveness of North African sand cats, albeit weakly. Therefore, it is possible that there are only two subspecies:



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Distribution of tentative subspecies of sand cat. Borders between subspecies are speculative.

Felis margarita margarita Loche, 1858.

Distribution: North Africa.

Distinguishing characters: Smaller size with yellowish pelage and often marked with spots and stripes.

Felis margarita thinobia (Ognev, 1927).

Distribution: Southwest Asia and the Arabian Peninsula.

Distinguishing characters: Large size, greyer pelage with fewer markings.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|----------------------------------|------------|-----------|--------------|-----------|---|
| <i>Felis margarita margarita</i> | ++ | ++ | ++ | | |
| <i>Felis margarita harrisoni</i> | + | 0 | + | | Synonym of <i>margarita</i> ? |
| <i>Felis margarita scheffeli</i> | + | 0 | + | | |
| <i>Felis margarita thinobia</i> | ++ | 0 | ++ | | Probably distinct and includes <i>scheffeli</i> |

Felis bieti

E: Chinese steppe cat, Chinese mountain cat, Chinese desert cat; F: Chat de Biet; G: Graukatze, Gobikatze; Sp: Gato de Biet, gato desierto de China.

Various subspecies have been described for *Felis bieti*, including (following Pocock 1951):

Felis bieti bieti Milne-Edwards, 1892; 671.

Type locality: Tengri-Nor à Batang, restricted to the environs de Tongolo et de Ta-tsien-lou [Central Sichuan, China] by Pousargues (1898; 357).

Diagnosis: Ears match coloration of back with red ear tufts, yellowish grey pelage, faint transverse stripes, whitish ventrally.

Holotype: MNHN-ZM-MO-1891-391 mounted skin and skull.

Distribution: Provinces of Qinghai, Sichuan and possibly Gansu, China (He et al. 2004, Webb et al. 2016).

Felis bieti chutuchta Birula 1917; 1.

Type locality: Nor locality, Goizso area, Gobi Desert, [China].

Holotype: Adult female skull (ZIN 9377) and skin (ZIN 9880).

Distribution: Gobi Desert, China.

Distinguishing characters: Redder and more distinctly striped than *bieti*.

Felis bieti vellerosa Pocock, 1943; 172.

Type locality: near Yu-Lin-fu, 4000 ft, on the borders of Ordos and NE Shensi [near Yulin, 1200 metres, on the borders of Ordos and NE Shaanxi, China].

Holotype: BMNH 1909.1.1.11 skin.

Distribution: Known only from type locality.

Distinguishing characters: Bicoloured ears (grey proximally, black distally) with long black ear tuft, black genal stripes, legs striped.



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Discussion

There has been no recent taxonomic study of this species since Groves (1980), although Driscoll et al. (2007) showed that *Felis bieti* was basal to *Felis silvestris* (*sensu lato*) according to mtDNA, but a sister taxon to *Felis lybica ornata* from microsatellites, which suggests that *Felis bieti* may have an ancient hybrid origin, possibly during the last glaciation when the distribution of *F. l. ornata* was apparently restricted to a very small area in Central Asia (Kitchener & Rees 2009). *F. bieti* is morphologically distinct and is supposedly sympatric with *F. l. ornata*, which would also preclude its recognition as a subspecies of *F. silvestris/lybica*. However, C. Driscoll (pers. obs.) maintains this species as a subspecies within *F. silvestris* (*sensu lato*).

The skull of putative subspecies *chutuchta* is similar to that of *lybica* (Groves 1980, A. Abramov, pers. obs.) and doubt has also been cast on *vellerosa*, although A. Kitchener (pers. obs.) believes that this specimen is a trade skin outside its geographical distribution or possibly a *Felis chaus*, while Groves (1980) believes it to be *F. catus*.

Therefore, given its restricted distribution and distinct morphology, *Felis bieti* is recognised here as a monotypic species.

Felis bieti Milne-Edwards, 1892.

Distribution: Provinces of Qinghai, Sichuan and possibly Gansu, China.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|------------------------------|------------|-----------|--------------|-----------|---|
| <i>Felis bieti bieti</i> | ++ | ++ | ++ | | |
| <i>Felis bieti chutchta</i> | ++ | 0 | 0 | | This is probably a form of <i>Felis lybica</i> |
| <i>Felis bieti vellerosa</i> | ++ | 0 | 0 | | This may be <i>Felis chaus</i> or <i>F. catus</i> |

Felis silvestris

E: European wildcat, Caucasian wildcat; F: Chat forestier, chat sauvage d'Europe, chat sylvestre; G: Europäische Wildkatze, Waldkatze; Sp: Gato montés, gato silvestre.

Felis silvestris, as defined here, includes only the forest cats of Europe. Many subspecies have been described, but there are no recent morphological and molecular studies of geographical variation in Europe and beyond. Wozencraft (2005) recognised the following subspecies:

Felis silvestris silvestris Schreber, 1777; 397 – conserved by Opinion 465 of the International Commission of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1957).

Locality from where the species was described: Unknown but fixed as "vielleicht Nordfrankreich" [perhaps N France] by Haltenorth, 1953 and "Germany" by Pocock (1951).

Holotype: None designated.

Distribution: Mainland Europe from Spain to eastern Europe, including Bulgaria, Rumania, southern Poland, western Russia.

Felis silvestris caucasica Satunin, 1905; 154.

Type locality: Borjomi, Georgia, Caucasus.

Type: Museum Tiflis [Georgia National Museum] female.

Distribution: Caucasus, Turkey.

Felis silvestris grampia Miller, 1907; 396.

Type locality: Invermoriston District, Inverness, Scotland.

Type: BMNH 1904.1.25.3 male skin and skull.

Distribution: N and C Scotland, formerly all of Britain.



Discussion

There is a cline in pelage flank stripes in Europe from distinctly striped animals in the west to faintly striped animals in the east (A. Kitchener, pers. comm.). This may reflect divergence in Pleistocene refugia in southern Europe followed by recolonisation and introgression following the end of the last glacial.

Based on current geographical isolation, it seems likely that there are two subspecies of *F. silvestris*:

Felis silvestris silvestris Schreber, 1777.

Distribution: Europe, including Scotland, Sicily and Crete.

Felis silvestris caucasica Satunin, 1905.

Distribution: Caucasus, Turkey.

However, C. Driscoll (pers. comm.) retains *lybica*, *cafra*, *ornata* and *bieti* within *Felis silvestris* as subspecies following Driscoll et al. (2007), while C. Groves (pers. comm.) regards all these as valid phylogenetic species.

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Satunin K. A. 1905. Die Säugetiere des Talyschgebietes und der Mughansteppe. *Mlekopitayushchie Talysha i Mugani. Mitteilungen des Kaukasischen Museums - Izvestiya Kavkazskago Muzeya* 2, 87-402.



Distribution of tentative subspecies of European wildcat. Borders between subspecies are speculative.

Schreber J. C. D. 1777. Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, vol. 3(23). Wolfgang Walther, Erlangen.

Wozencraft W. C. 2005. Order Carnivora. *In* *Mammal species of the world. A taxonomic and geographic reference* (3rd ed.). Wilson D. E. & Reeder D. M. (Eds). Johns Hopkins University Press, Baltimore, pp. 532-628.

| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|------------------------------------|------------|-----------|--------------|-----------|---------------------|
| <i>Felis silvestris silvestris</i> | ++ | ++ | ++ | | |
| <i>Felis silvestris grampia</i> | + | + | + | | Doubtfully distinct |
| <i>Felis silvestris caucasica</i> | ++ | 0 | ++ | | Probably distinct |

Felis lybica

E: African wildcat, Indian desert cat; F: Chat ganté, chat sauvage d'Afrique, chat orné, chat sauvage d'Asie ; G: Nubische Falbkatze, Asiatische Wildkatze; Sp: Gato silvestre, gato montés.

Felis lybica, as defined here, includes the steppe and bush cats of Africa and Asia. Very many subspecies have been described throughout the extensive geographical distribution of this species (Pocock 1951; distributions of subspecies below are taken from here). The subspecies listed by Wozencraft (2005) are as follows:

Felis lybica lybica Forster, 1780; 313.

Type locality: in der Gegend der alten Stadt Kapsa [= in the region of the ancient town of Gafsa, Tunisia].
Holotype: Based on "chat du desert from Capsa, Lybie" of Buffon (1776; 233) based on unpublished correspondence from Bruce.
Distribution: Semi-deserts of North Africa from Morocco, Algeria and Tunisia to Egypt and up the Nile to Sudan and eastwards to Suakin and Massowah and the E coast of Sinai.
Distinguishing characters: Light, buff or sandy coloration, pale with reddish spots ventrally, ochreous ears, whitish face.

Felis lybica ocreata Gmelin, 1791; 27 and 79.

Type locality: Ras el Feel, Abyssinia [= Ethiopia].
Holotype: Based on the booted lynx of Bruce (1790; 146).
Distribution: Ethiopia.

Distinguishing characters: Similar to *lybica*, but grey with more black speckling and reddish or yellow wash.

Felis lybica haussa Thomas and Hinton, 1921; 2.

Type locality: Zinder [about 300 miles south of Aïr, Niger].
Holotype: BMNH 1921.2.11.16 male skin and skull.
Distribution: Zinder, Niger and Franiso, near Kano, Nigeria.
Distinguishing characters: Similar to *lybica*, but smaller skull.

Felis lybica foxi Pocock, 1944a; 71.

Type locality: Kabwir, 7000 ft. on the slopes of the Panyam Plateau, [Bauchi Province, N Nigeria].
Holotype: BMNH 1912.11.7.5 male skin.
Distribution: Panyam Plateau, N Nigeria.
Distinguishing characters: Darker than *haussa*, similar to *sarda*, with reddish face, but less thick fur, spinal area and crown less black, and speckling on flanks buffy.

Felis lybica rubida Schwann 1904; 422.

Type locality: Monbuttu [Belgian Congo = Democratic Republic of Congo].
Holotype: BMNH 1887.12.1.6 young male skin and skull.
Distribution: Democratic Republic of Congo.
Distinguishing characters: Pale brown or cinnamon coloration, with almost no black speckling except dorsal line, spotted.

Felis lybica ugandae Schwann, 1904; 424.

Type locality: Mulema, Uganda.

Holotype: BMNH 1903.11.7.8 young adult male skin and skull.

Distribution: Mongalla in South Sudan, Garamba in Democratic Republic of Congo, Uganda, Kenya and possibly Tanzania.

Distinguishing characters: More black speckling than *rubida*, duller colouration, striping not always present.

Felis lybica tristrami Pocock, 1944b; 125.

Type locality: Ghor Seisaban, Moab [Palestine = Israel].

Holotype: BMNH 1893.1.29.3 female skin and skull.

Distribution: Israel, Jordan, Syria, Lebanon, W and S Arabia.

Distinguishing characters: Similar to *sarda*, but paler, less luxurious pelage, less black on back of metatarsus.

Felis lybica iraki Cheesman, 1921; 331.

Type locality: Koweit, Arabia [= Kuwait].

Holotype: BMNH 1920.1.19.2 male skin and skull.

Distribution: Kuwait and Iraq.

Distinguishing characters: Similar to *tristrami*, but pelage tawnier above, spinal band undifferentiated, face and feet whiter.

Felis lybica gordonii Harrison, 1968; 283.

Type locality: Wadi Suwera 6 miles west of Sohar, Batinah coast of Oman.

Holotype: BMNH 1968.608 female skin and skull.

Distribution: Oman and UAE.

Distinguishing characters: Compared with other Arabian *lybica*, very pale grey, lacking olivaceous tint of *tristrami*, brown spinal stripe from shoulders.

Felis lybica nesterovi Birula, 1917; 1.

Type locality: Nachr-Chazasch, Mesopotamia [= Iraq].

Holotype: Adult female ZIN 9374 (skull), ZIN 27643 (skin).

Distribution: Iraq and S Iran.

Distinguishing characters: Similar to *ornata*, but longer fur.

Felis lybica reyi Lavauden 1929; 1023.

Type locality: Forêt d'Aunes des bords de la lagune de Biguglia (Sud de Bastia) [Corsica].

Holotype: MNHN-ZM-MO-1932-3806 female skin and skull.

Distribution: Corsica.

Distinguishing characters: Compared with *sarda*, darker pelage, shorter tail, and backs of ears dark brown without a trace of red.

Felis silvestris cretensis Haltenorth, 1953; 29.

Type locality: Kanea auf Kreta [= Chania, Crete, Greece].

Holotype: BMNH 1905.12.2.14 skin.

Distribution: Crete.

Distinguishing characters: Similar to *lybica*, but with tail similar to *silvestris*.

Comments: C. Groves (pers. obs.) considers that this is probably *Felis catus*. *Felis silvestris* occurs also on Crete (Matschei 2015, A. Kitchener, pers. obs.).

Felis lybica jordansi Schwarz 1930; 223.

Type locality: Santa Margarita, Mallorca, Balearen [Majorca, Spain].

Holotype: ZFMK 83.186 male skull and skin.

Distribution: Balearic Islands.

Distinguishing characters: More strongly striped with brighter legs than *lybica*. C. Groves (pers. obs.) has measured the cranial volume of the holotype and it is *Felis catus*.

Felis lybica cafra Desmarest, 1822; 540.

Type locality: Kaffraria [South Africa].

Syntypes: MNHN-ZM-MO-2002-321 and MNHN-ZM-MO-2002-322 mounted skins (skulls inside).

Distribution: Originally S of the Orange River from Cape of Good Hope and Little Namaqualand in W to Eastern Cape and KwaZulu Natal and N to Transvaal. Now southern Africa.

Distinguishing characters: Similar to *ugandae*, but occurs in two colour phases (iron grey with black and whitish speckling, and tawny grey with less speckling), both of which have thicker coat, and development of black pigment on fore legs.

Felis lybica mellandi Schwann, 1904; 423.

Type locality: Mpika, NE Rhodesia [= Muchinga Province, Zambia].

Holotype: BMNH 1904.3.11.2 skin.

Distribution: Malawi, Zambia and S Democratic Republic of Congo.

Distinguishing characters: Similar to *ugandae*, but coloration above more uniform, brighter coloration on ears, and faint or absent striping on flanks.

Felis lybica griselda Thomas, 1926; 180.

Type locality: Fifty miles south of Dombe Grande, Benguela, Angola.

Holotype: BMNH 1925.5.16.1 skin.

Distribution: From S Angola and Namibia eastwards into Botswana.

Distinguishing characters: Similar to *cafra*, but paler, brighter ochreous ears, paler pelage, and coat pattern less distinct.

Felis lybica ornata Gray, 1830; pl.2.

Type locality: Nussurabad, Rajputana [India].

Holotype: BMNH 1848.8.14.3 skin.

Distribution: W and C India S of the Ganges.

Distinguishing characters: Greyish sandy cat covered in irregular black or brown spots.

Felis lybica caudata (Gray, 1874; 31).

Type locality: "Cocan", Bokhara; near the river Dyanan. Cocan, or Kho-kan, is situated on the Sir Daria; and I suppose that the Dyanan is a branch of the river Sir, which falls into the sea of Aral (Gray 1874: 31). Birula (1912; 226) clarified the type locality as "Jana Darya River, which is the south branch of Syr Darya River in its lower reach", neither Bukhara nor Kokand.

Holotype: BMNH 1873.7.22.12 skin and skull.

Distribution: Turkestan (C Asia) as far E as Tian Shan and S into Iran and Afghanistan.

Distinguishing characters: Similar to *ornata*, but larger and more luxuriant winter pelage, larger teeth.

Felis lybica chutuchta Birula 1917; 1.

Type locality: Nor locality, Goizso area, Gobi Desert [China].

Holotype: Adult female ZIN 9377 (skull), ZIN 9880 (skin).

Distribution: Gobi Desert, China.

Distinguishing characters: Reddish body and ears with distinct transverse stripes.

Discussion

Driscoll et al. (2007) identified three distinct clades within this species, which we identify tentatively as subspecies. However, it should be noted that samples were not available from some key areas throughout the geographical range, e.g. much of North, West and East Africa. In contrast, C. Groves (pers. comm.) recognises the three clades as representing distinct species, while C. Driscoll (pers. comm.) includes these, *silvestris* and *bieti* within *Felis silvestris*. We tentatively identify the following subspecies within *F. lybica*:

Felis lybica lybica Forster, 1780.

Distribution: E, W and N Africa, Arabian Peninsula, Middles East; probably intergrades with *ornata* in Iraq.



F. l. lybica in Saudi Arabia (Photo C. Barichirvy & T. Wachter).

Felis lybica cafra Desmarest, 1822.

Distribution: Southern Africa; exact boundary with *lybica* uncertain, but may lie in Mozambique or Tanzania.



F. l. cafra in Botswana (Photo P. Meier).

Felis lybica ornata Gray, 1830.

Distribution: SW and C Asia, Afghanistan, Pakistan, India, Mongolia and China.

Distinguishing characters: Light-coloured pelage with black spots.



F. l. ornata in India (Photo D. Khandal).

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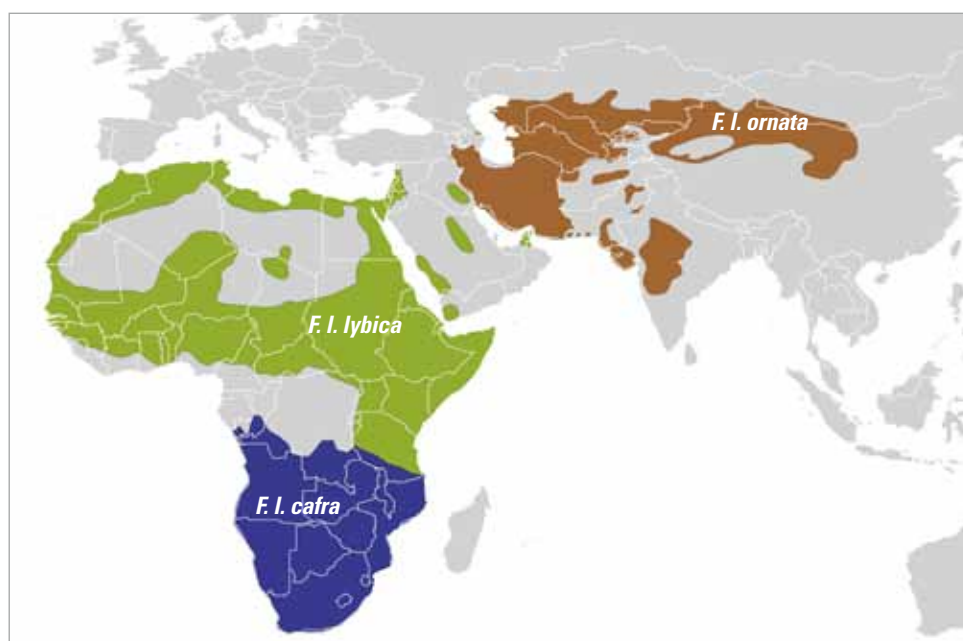
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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|-------------------------------|------------|-----------|--------------|-----------|---|
| <i>Felis lybica lybica</i> | ++ | ++ | ++ | | |
| <i>Felis lybica ocreata</i> | + | 0 | + | | Doubtfully distinct |
| <i>Felis lybica haussa</i> | + | 0 | 0 | | |
| <i>Felis lybica foxi</i> | + | 0 | 0 | | |
| <i>Felis lybica rubida</i> | + | 0 | 0 | | |
| <i>Felis lybica ugandae</i> | + | 0 | 0 | | |
| <i>Felis lybica tristrami</i> | + | 0 | + | | Doubtfully distinct |
| <i>Felis lybica iraki</i> | + | 0 | 0 | | |
| <i>Felis lybica gordonii</i> | + | 0 | + | | Doubtfully distinct |
| <i>Felis lybica nesterovi</i> | + | 0 | 0 | | |
| <i>Felis lybica reyi</i> | + | 0 | + | | Introduced by humans |
| <i>Felis lybica jordansi</i> | + | 0 | + | | Introduced by humans = <i>Felis catus</i> |
| <i>Felis lybica cretensis</i> | + | 0 | + | | Introduced by humans? |
| <i>Felis lybica cafra</i> | ++ | ++ | ++ | | |
| <i>Felis lybica mellandi</i> | + | 0 | 0 | | |
| <i>Felis lybica griselda</i> | + | 0 | 0 | | |
| <i>Felis lybica ornata</i> | ++ | ++ | ++ | | |
| <i>Felis lybica caudata</i> | + | 0 | 0 | | |
| <i>Felis lybica chutuchta</i> | + | 0 | 0 | | |



Distribution of tentative subspecies of steppe and bush cats of Africa and Asia. Borders between subspecies are speculative.

Felis catus

E: Domestic cat, feral cat; F: Chat domestique; G: Katze; Sp: Gato domestico.

Felis catus Linnaeus, 1758; 42

Locality from where species was first described: Sweden (Pocock 1951).

Holotype: None designated.

Distribution: Worldwide, except Antarctica.

Discussion

Domesticated mostly from a lineage of *Felis lybica lybica* from Mesopotamia (Driscoll et al. 2007). Following Opinion 2027 of the International Commission on Zoological Nomenclature (2003), the domestic cat is treated as a distinct taxon, *Felis catus*.

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Leopard Cat Lineage

Genus *Otocolobus* Brandt 1842; 38.

Otocolobus manul

E: Pallas's cat, manul; F: Manul, chat de Pallas; G: Manul; Sp: Gato manul, gato de Pallas.

Wozencraft (2005) recognised three subspecies of *Otocolobus manul*:

Otocolobus manul manul (Pallas, 1776; 692).

Locality from where the species was described: Frequens in rupetribus, apricis totius Tatariae Mongoliaeque desertae = Kulusutai, Borzya District, Chita Province, USSR [= Russia] (Heptner & Sludskii 1972).

Holotype: None designated.

Distribution: China (Gansu), Mongolia, Kazakhstan, southern Siberia (Altai, Tuva, Transbaikalia).

Otocolobus manul nigripectus (Hodgson, 1842; 276).

Type locality: from Tibet

Types: Three syntypes in Hodgson's possession.

Distribution: Tibet and Kashmir.

Distinguishing characters: Winter coat silvery-grey with more black in it, wool paler, head spotted thickly with black, back and tail stripes more distinct (Pocock 1951).



Otocolobus manul ferrugineus Ognev, 1928; 1013.

Type locality: from mountain ridge of Missanev, Kopet-Dag Mountains, Turkmenistan.

Holotype: Male skin (ZIN 28013) and skull (ZIN 15065).

Distribution: C Asia (Turkmenistan, Uzbekistan, Tadjikistan), N Iran, Afghanistan and Baluchistan.

Distinguishing characters: Reddish dorsally, black markings inconspicuous or red.

Discussion

There have been no recent molecular or morphological studies. The subspecies *ferrugineus* is variably rufescent (Pocock 1939, A. Kitchener, pers. obs.) and is said to intergrade with typical *manul*. It seems likely that this variability in erythrism is explained mostly by simple Mendelian inheritance, with completely orange animals (homozygous) and those with a mixture of orange and grey (heterozygous) for the O gene. Perhaps there is selection for more erythristic forms in the SW of the species' range? It is possible that this species is monotypic and shows clinal variation in pelage coloration.

Pocock (1951) found complete overlap in colouration between skins of all putative subspecies and it may turn out that variation is largely clinal.

We suggest the tentative recognition of only two subspecies:

Otocolobus manul manul (Pallas, 1776), including *ferrugineus*.

Distribution: China (Gansu), Mongolia, C Asia and Kazakhstan, S Siberia, Iran, Afghanistan and Pakistan.

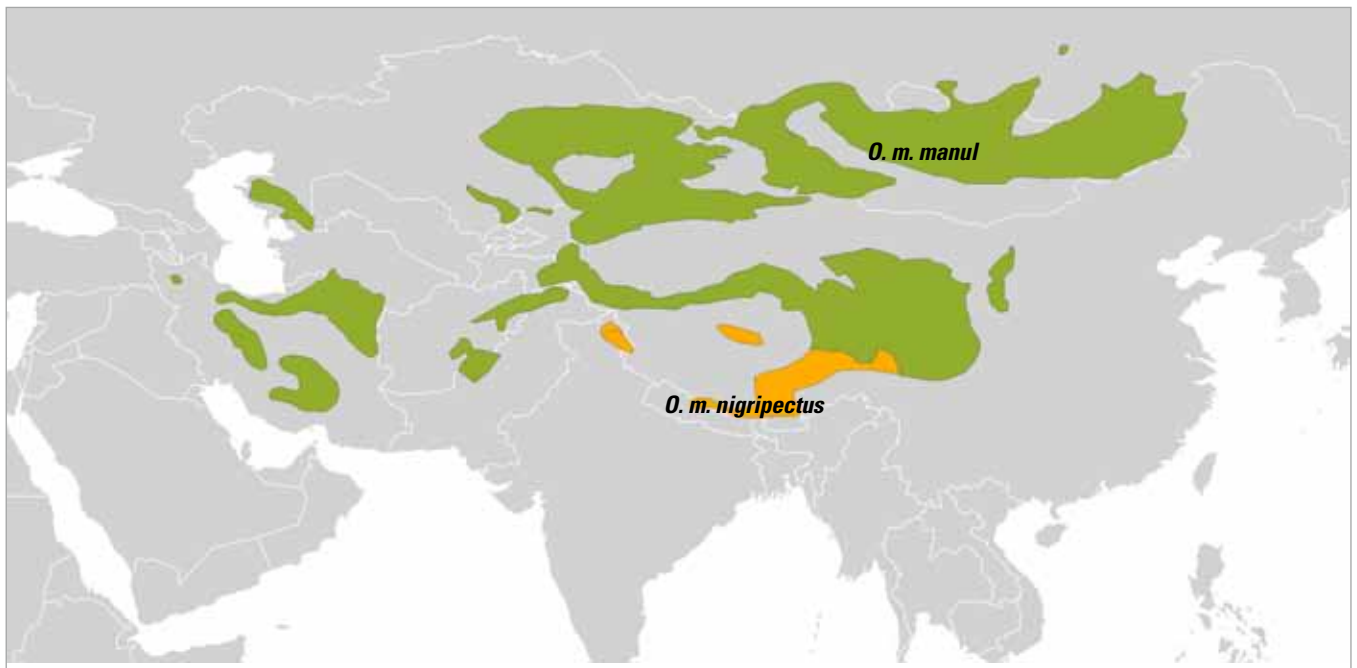
Otocolobus manul nigripictus (Hodgson, 1842).

Distribution: Tibet, Kashmir, Nepal and Bhutan.

Further research is required to understand geographical variation in *Otocolobus manul*.

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Distribution of tentative subspecies of Pallas's cat. Borders between subspecies are speculative.

| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|-------------------------------------|------------|-----------|--------------|-----------|---------------------|
| <i>Otocolobus manul manul</i> | ++ | ++ | ++ | | |
| <i>Otocolobus manul ferrugineus</i> | + | | | | Doubtfully distinct |
| <i>Otocolobus manul nigripictus</i> | + | | + | | Possibly distinct |

Genus *Prionailurus* Severtzov, 1858; 387.

This genus contains five species.

***Prionailurus rubiginosus*.**

E: Rusty-spotted cat; F: Chat rougâtre, chat rubigineux; G: Rostkatze; Sp: Gato rubiginosa, gato rojizo.

Wozencraft (2005) recognised two subspecies:

Prionailurus rubiginosus rubiginosus (l. Geoffroy Saint-Hilaire, 1831; 140).

Type locality: “les bois de lataniers qui couvrent une hauteur voisine de Pondichéry, connue sous le nom de Coteau”.

Holotype: MNHN-ZM-AC-A1791 juvenile incomplete skull.

Distribution: India, Nepal and ?Pakistan.

Distinguishing characters: Grey, darker and drabber on back, limbs paler than flanks; spots and stripes on back black, brownish black to brown on flanks, sometimes faint.

Prionailurus rubiginosus phillipsi Pocock, 1939; 278.

Type locality: Mousakanda, Gammaduwa, C.P., 3,000 ft [Sri Lanka].

Holotype: BMNH 1935.4.8.2 skin and skull.

Distribution: Sri Lanka.

Distinguishing characters: Darker, richer and less grey than *P. r. rubiginosus* with flank spots brownish to rusty brown. Pocock (1939) found no differences in skull measurements between *rubiginosus* and *phillipsi*.

However, a third subspecies is sometimes recognised:

Prionailurus rubiginosus koladivius Deraniyagala, 1956; 113.

Type locality: Kathiraveli (E. P.) [Sri Lanka].

Holotype: Colombo National Museum 384.

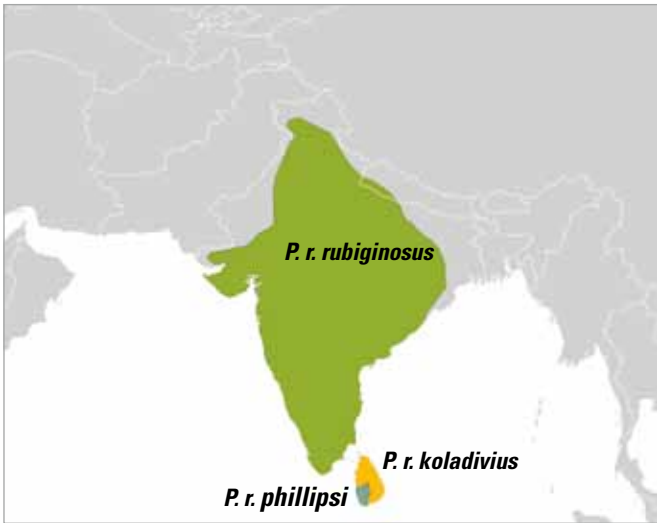
Distribution: Lowland dry zone of E Sri Lanka.

Distinguishing characters: Darker head than *P. r. phillipsi*, blue-grey; dorsal spots and stripes blackish, flank spots dark brown.

Discussion

Variation within subspecies is unclear. There appear to be two colour morphs both in India and Sri Lanka, i.e. typical pale brown or rusty spots, and dark brown to blackish spots. In Sri Lanka the dark-spotted form is said to inhabit the lowland dry zone, but it is unknown whether dark-spotted animals occupy drier habitats in India (Deraniyagala, 1956). There has been no phylogeographical study of *Prionailurus rubiginosus*.

We note several other taxonomic differentiations between Sri Lanka’s wet and dry zone. Groves (1998) argued that within Sri Lanka there are two species of *Loris*, one (*Loris tardigradus*) in the island’s wet



Distribution of tentative subspecies of the rusty-spotted cat. Borders between subspecies in Sri Lanka are speculative.

zone and the other (*Loris lydekkerianus*) in the dry country and medium altitudes of Sri Lanka and also in southern India. A similar, but not identical, pattern is also found in *Trachypithecus vetulus*, which has two subspecies in the wet zone, one in the dry zone and at medium altitudes, and one on the high mountains (Groves 2001). Groves & Meijaard (2005) found that chevrotains (genus *Moschiola*) from Sri Lanka’s wet zone were distinct in pelage, in body proportions, and in skull proportions, and differed more from both the Indian and dry zone Sri Lankan taxa than the two latter differed from each other. However, there is no such differentiation among carnivorans. In view of the uncertainties over whether dark-spotted and rusty-spotted forms represent colour morphs, ecotypes or subspecies, we retain three subspecies:

| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|---|------------|-----------|--------------|-----------|----------|
| <i>Prionailurus rubiginosus rubiginosus</i> | ++ | ++ | ++ | | |
| <i>Prionailurus rubiginosus phillipsi</i> | + | 0 | ++ | | |
| <i>Prionailurus rubiginosus koladivius</i> | + | 0 | + | | |

Prionailurus rubiginosus rubiginosus (L. Geoffroy Saint-Hilaire, 1831).

Distribution: India and Nepal

Prionailurus rubiginosus philipsi Pocock, 1939.

Distribution: Wet forest zone of Sri Lanka.

Prionailurus rubiginosus koladivius Deraniyagala, 1956.

Distribution: Lowland dry zone of E Sri Lanka.

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Prionailurus planiceps

E: Flat-headed cat; F: Chat à tête plate; G: Flachkopfkatz; Sp: Gato cabeciancho.

Prionailurus planiceps is a normally treated as a monotypic species:

Prionailurus planiceps (Vigors and Horsfield, 1827; 450, plate XII).

Type locality: Sumatra.

Holotype: BMNH 1855.12.24.247 skin and skull.

Distribution: Borneo, Sumatra, Malay Peninsula, Thailand.

Discussion

Kitchener (in Nowell & Jackson 1996) suggested that there may be subspecific differentiation between Sumatra/Malay Peninsula and Borneo, but so far no molecular or morphological data are available, which could support this view. Luo et al. (2014) reported molecular genetic variation with two individuals from the Malay Peninsula and Borneo respectively, which, based on mtDNA sequences, did not share haplotypes, sample sizes are too limited to support geographical subdivision.

Until such studies are completed, this species is treated here as monotypic.

Prionailurus planiceps (Vigors and Horsfield, 1827; 450, plate XII).

Distribution: Borneo, Sumatra, Malay Peninsula, Thailand, Burma



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| Species | Morphology | Molecular | Biogeography | Certainty | Comments |
|-------------------------------|------------|-----------|--------------|-----------|----------------------------|
| <i>Prionailurus planiceps</i> | ++ | ++ | ++ | | Distinct monotypic species |

Prionailurus viverrinus

E: Fishing cat; F: Chat pêcheur, chat viverrin; G: Fischkatze; Sp: Gato pescador

Wozencraft (2005) recognised two subspecies of the fishing cat:

Prionailurus viverrinus viverrinus (Bennett, 1833; 68).

Type locality: ...from the continent of India; probably the Malabar coast (Pocock 1939).

Holotype: BMNH 1855.12.24.252 skin and part skull.

Distribution: Pakistan, Sri Lanka, India E to Indochina.

Prionailurus viverrinus rhizophoreus Sody, 1936; 45.

Type locality: Pamanoekan, North coast of West Java.

Holotype: RMNH.MAM 33859 skull and skin.

Distribution: Java.

Distinguishing character: Shorter basal length of skull than *P. v. viverrinus* form Siam [=Thailand] (Sody 1936).

Discussion

Despite being commonly cited in the literature, there are no records that the fishing cat has ever occurred on Sumatra and there are only a few uncertain records from the Malay Peninsula (Sody 1949, Van Bree & Momin Khan 1992, Duckworth et al. 2009). Pocock (1939) was unable to discern any geographical differentiation based on pelage coloration and markings between fishing cats from throughout their range. Luo et al. (2014) decribed the phylogeographical pattern of fishing cats from northern Indochina based on multiple mitochondrial and nuclear markers, but specimens from other regions were lacking. This species needs urgent research into its geographical variation, because it is mostly intensely threatened throughout its geographical range.

Until a more comprehensive analysis becomes available, we recognise the following subspecies:

Prionailurus viverrinus viverrinus (Bennett, 1833).

Distribution: India, Sri Lanka, Pakistan, Bangladesh, Bhutan, Indochina and Nepal.

Prionailurus viverrinus rhizophoreus Sody, 1936.

Distribution: Java.

Distinguishing characters: Smaller basal length of skull than *P. v. viverrinus* from Siam [=Thailand] (Sody 1936).

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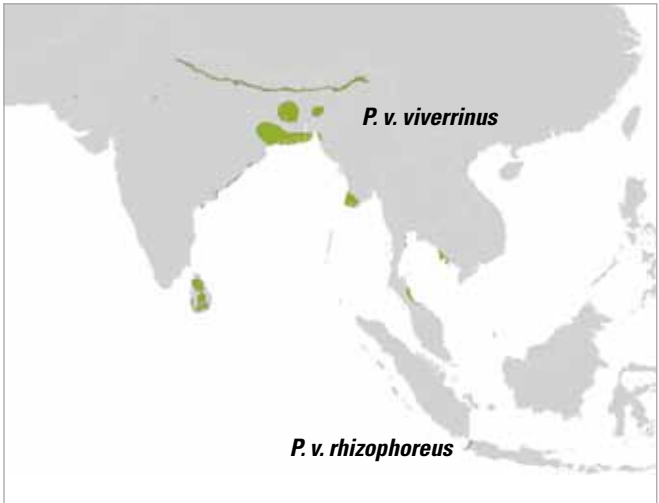
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Distribution of tentative subspecies of the fishing cat. Borders between subspecies are speculative.

| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|---|------------|-----------|--------------|-----------|----------|
| <i>Prionailurus viverrinus viverrinus</i> | ++ | ++ | ++ | | |
| <i>Prionailurus viverrinus rhizophoreus</i> | + | 0 | ++ | | |

Prionailurus bengalensis

E: Leopard cat; F: Chat-léopard du Bengale; G: Bengalkatze; Sp: Gato bengali, gato de Bengala

This widespread species is usually recognised as having several subspecies. Wozencraft (2005) recognised the following eleven subspecies:

Prionailurus bengalensis bengalensis (Kerr, 1792; 151).

Type locality: The coast of Bengal; restricted to S Bengal, India.

Holotype: From Pennant (1781; 164) a male that "swam on board a ship at anchor off the coast of Bengal and produced young afterwards with female cats in England". The specimen's remains were seen at Hammersmith. However Pocock (1939) noted: "Although the story hardly bears the impress of truth and Pennant's description agrees better with rich-coloured examples of the Sumatran race than with any Indian skins I have seen, I adhere to the traditional acceptance of Bengal as the locality and restrict it to the coast of that province to the west of the Ganges." A skin in the Natural History Museum (BMNH 1879.11.21.562) is labelled as a holotype, but originates from the Indian Museum, which seems unlikely since the specimen was last seen in Hammersmith, London.

Distribution: Peninsular India, Burma, Thailand, Indochina.

Distinguishing characters: Short, thin coat, tail slender in winter months. Ground colour ranges from ochreous buff to buffish white on flanks, but darker on head and back. Spots large and well spaced, sometimes solid and may run in chains.

Prionailurus bengalensis alleni Sody, 1949; 181.

Type locality: Nodda [= Dan Xian], Hainan Dao, China.

Lectotype: AMNH M-59961 skin and skull adult male (Goodwin 1956; 1).

Distribution: Hainan.

Distinguishing characters: Slightly smaller than those from the mainland (*P. b. chinensis*) and nasals of males seems to be a trifle shorter than in *P. b. chinensis* (Sody 1949).

Prionailurus bengalensis chinensis (Gray 1837; 577).

Type locality: China.

Holotype: BMNH GERM 120a skin and skull.

Distribution: China.

Distinguishing character: Yellowish grey.

Prionailurus bengalensis horsfieldii (Gray, 1842; 260).

Type locality: India, Bhotan [=Bhutan].

Holotype: BMNH 1879.11.21.285 adult male skin and skull.

Distribution: Kashmir, Kumaon, Nepal and Bhutan; limits to N and NE unknown.

Distinguishing characters: Larger skull than *bengalensis*, more luxuriant coat and bushy tail in winter. Ground colour paler and not so richly ochreous.

Prionailurus bengalensis euptilurus (Elliot, 1871; 761).

Type locality: Amur River, 60 km below mouth of Zeya River, Amur Province, Russia.

Holotype: BMNH 1873.11.20.1 skin. Based on *Felis undata* of Radde 1862; 106.

Distribution: Amur and Ussuri regions, Russia, NE China, Korean Peninsula.



P. b. euptilurus in the Russian Far East (Photo L. Kerley).

Distinguishing characters: Ground colour light brownish yellow mixed with grey. Spots reddish brown and rather oblong on flanks; darker and browner on hindquarters and back. Tail thick and bushy with incomplete rings.

Prionailurus bengalensis trevelyani Pocock, 1939; 273.

Type locality: Near Gilgit, Kashmir, 5000 feet.

Type: BMNH 1932.4.9.2 young adult male skin and skull.

Distribution: Northern Kashmir and the Upper Punjab in the drainage area of the Indus and Jhelum, approximately 74° longitude, also Baluchistan.

Distinguishing characters: Fuller longer coat (36-40 mm long) than *horsfieldii* and paler grey, sometimes nearly silvery ground colour, but buff tinge low on flanks and on limbs.

Prionailurus bengalensis javanensis (Desmarest 1816; 115).

Type locality: Java.

Holotype: MNHN-ZM-MO-2001-326 mounted skin.

Distribution: Java and Bali.

Distinguishing characters: Ground colour dark brownish grey; darker on midline of back than on flanks. Four dark longitudinal stripes on nape of neck are narrow and of equal width or inner ones wider than outer ones. Markings blackish brown and are elongate dark spots on midline of back and rounder on flanks.

Prionailurus bengalensis borneoensis Brongersma 1935; 26.

Type locality: Rantau, SE Borneo.

Holotype: RMNH.MAM 467 male skin.

Distribution: Borneo.

Distinguishing characters: Ground colour ferruginous to tawny, but darker than Sumatran animals. Nape stripes; inner pair narrower than outer ones. Spots very dark, almost black; fewer elongate spots on midline of back.

Prionailurus bengalensis sumatranus (Horsfield, 1821; pl. and text).

Type locality: Bencoolen, Sumatra [= Benkulu, Sumatra].

Holotype: BMNH GMCM 125a male skin.

Distribution: Sumatra.

Distinguishing characters: Ground colour ferruginous. Nape stripes; outer pair broad, inner pair narrow. Spots dark brown to blackish; spots on flanks elongate, but may be very small, roundish and numerous.

Prionailurus bengalensis heaneyi Groves, 1997; 377.

Type locality: Puerto Princesa, Palawan.

Holotype: FMNH 62896 subadult male skin and skeleton.

Distribution: Palawan.

Distinguishing characters: Grey-fawn with small dark brown flank spots.

Prionailurus bengalensis rabori Groves, 1997; 336.

Type locality: Canlaon, Negros Oriental.

Holotype: FMNH 74326 adult female skin and skull.

Distribution: Negros, Cebu and Panay, Philippines.

Distinguishing characters: Dark ochery to buffy fawn, but not as bright as *borneoensis*.

Discussion

In addition Wozencraft (2008) recognised the Iriomote cat as a distinct species:

Prionailurus iriomotensis (Imaizumi, 1967; 75).

Type locality: Haimida, Iriomote.

Holotype: NSM M 10890 adult male skin and almost complete skeleton.

Distribution: Iriomotejima, Ryukyu Islands, Japan.

However, recent molecular studies have clearly demonstrated that *P. iriomotensis* is a leopard cat, and its skull morphology confirms this (A. Kitchener, pers. obs.; *contra* Leyhausen & Pfeleiderer 1999), who considered its skull morphology unique and hence the taxon to be recognised as a distinct species. The pelage coloration is similar to that of leopard cats from northern China and this form has almost certainly arisen from a human introduction. Molecular studies confirm that *P. iriomotensis* is a leopard cat (Masuda et al. 1994, Masuda & Yoshida 1995, Suzuki et al. 1995), although estimated divergence times vary from 100,000 to 200,000 years ago.

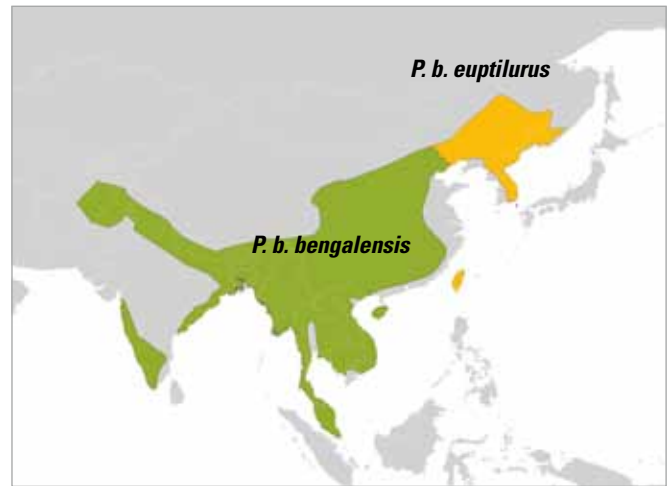
A recent molecular study, based on 1,792 bp of concatenated mtDNA haplotypes (spanning cytochrome b, ATPase8 and 16S ribosomal DNA), X-linked gene (*PLP*), 2,154 bp of concatenated Y-chromosome haplotypes of intronic regions of three genes (*DBY*, *SMCY3* and *UTY11*) and one Y-linked microsatellite *SMCY7-STR*, has demonstrated that there is a deep genetic divergence between Sundaland (the late Pleistocene land mass connecting the islands of Sumatra, Borneo and Java) and mainland leopard cats, with possible overlap in the Malay Peninsula (Luo et al. 2014, see also Tamada et al. 2008 for first demonstration of this deep split). Even more recently, Li et al. (2016) have shown a “species-level” difference between mainland and island leopard cats. However, it is unclear where the boundary between these two species occurs, although there appear to be clear morphological differences between the two; Sunda leopard cats have small solid spots while mainland leopard cats have larger blotches filled with a lighter coloration (A. Kitchener, pers. obs.).

Based on these recent molecular studies, coupled with clear morphological differences and biogeographical separation, we recognise two species:

Prionailurus bengalensis (Kerr, 1792).

E: Mainland leopard cat; F: Chat-léopard du Bengale; G: Bengalkatze; Sp: Gato bengali, gato de Bengala

Distribution: Mainland Asia from Pakistan to South East Asia, China and the Russian Far East, Tsushima Island and Iriomote Island, Japan.



Distribution of tentative subspecies of the mainland leopard cat. Borders between subspecies are speculative.



Mainland leopard cat in captivity (Photo A. Sliwa).

There is no comprehensive molecular review of mainland leopard cats and hence it is unclear how many subspecies to recognise. Luo et al. (2014) found no genetic differences between Chinese (*chinensis*) and Indochinese (*bengalensis*) leopard cats. Tamada et al. (2008) found two clades among mainland leopard cats; a northern clade comprising continental Far Eastern, Korean (*euphilurus*), Iriomote I. (*iriomotensis*), Tsushima I. and Taiwanese leopard cats and a southern clade of Indochinese cats. This dichotomy is reinforced by the inclusion of Indian leopard cats, which fall into the same clade as the Indochinese animals (Mukherjee et al. 2011).

Thus we tentatively recognise two leopard cat subspecies in mainland Asia:

Prionailurus bengalensis bengalensis (Kerr, 1792).

Distribution: S Asia from Pakistan to China and including probably the Malay Peninsula.

Synonyms: *horsfieldii*, *alleni*, *chinensis*, *trevelyani*.

Prionailurus bengalensis euphilurus (Elliot, 1871).

Distribution: Manchuria, Russian Far East, Taiwan, Iriomote Island, Tsushima Island.

Synonym: *iriomotensis*.

| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|--|------------|-----------|--------------|-----------|--|
| <i>Prionailurus bengalensis bengalensis</i> | ++ | ++ | ++ | | |
| <i>Prionailurus bengalensis alleni</i> | + | 0 | ++ | | |
| <i>Prionailurus bengalensis chinensis</i> | + | + | 0 | | Same genetic clade as <i>bengalensis</i> |
| <i>Prionailurus bengalensis horsfieldii</i> | + | + | + | | |
| <i>Prionailurus bengalensis euptilurus</i> | ++ | ++ | + | | Boundary with <i>bengalensis</i> uncertain |
| <i>Prionailurus bengalensis iriomotensis</i> | + | + | ++ | | More research required to determine distinctiveness on island; probably introduced by humans |

Prionailurus javanensis (Desmarest, 1816).

E: Sunda leopard cat; F: Chat-léopard de la Sonde; G: Sundakatze; Sp: Gato de las Islas de la Sonda.

Distribution: Java, Bali, Borneo, Sumatra, Palawan, Negros, Cebu and Panay, Philippines, possibly Malay Peninsula; probably introduced to Philippines with possible exception of Palawan.

Although clearly distinct from *P. bengalensis*, the status of the subspecies of *P. javanensis* is uncertain, owing to a lack of a phylogeographical study of this species. Javan animals appear to be distinct from Sumatran and Bornean animals, which are more similar to each other based on pelage coloration. It is possible that leopard cats from the Philippines are the result of human introductions, although it is more likely that those from Palawan are indigenous, having colonised from Borneo during glaciations when sea levels were lower. A genetic study is required. Until that time we recognise all five described subspecies.

Prionailurus javanensis javanensis (Desmarest, 1816).

Distribution: Java and Bali.

Prionailurus javanensis sumatranus (Horsfield, 1821).

Distribution: Sumatra.

Distinguishing characters: Ground colour ferruginous and not brownish grey as in those of *P. b. javanensis* (Brongersma 1935). Nape stripes; outer pair broad, inner pair narrow, but not so strongly marked as in *P. b. borneoensis* (Brongersma 1935). Spots dark brown to blackish; spots on flanks elongate, but may be very small, roundish and numerous. The specimen from Nias Islands showed similar skull measurements to those of Sumatran specimens, but skin seems to be more greyish and less heavily spotted (Brongersma 1935), indicating that this could be a distinct subspecies.

Prionailurus javanensis borneoensis Brongersma 1935.

Distribution: Borneo.

Distinguishing characters: Ground colour ferruginous to tawny, but darker than *P. b. sumatranus* specimens (Brongersma 1935), and not brighter than those from Sumatra as indicated by Gyldenstolpe (1919). Nape stripes; inner pair narrower than outer ones, which are very broad. This difference between the two sets of lines is much larger than in *P. b. sumatranus*. Spots very dark, almost black (even darker



Sunda leopard cat from Borneo (Photo Jo Ross and A. Hearn).

than in *P. b. sumatranus*). Spots on the back are elongate, large and darker and fewer than in *P. b. sumatranus*.

Prionailurus javanensis heaneyi Groves, 1997.

Distribution: Palawan.

Distinguishing characters: Colour grey-fawn with small dark brown spots on flanks; inner pair of nape-stripes always thinner than outer, both pairs reaching back to scapular level (Groves 1997). Skull small and even narrower than in *javanensis* though fairly broad across muzzle (Groves 1997). Upper carnassial smaller than in any other insular subspecies (Groves 1997).

Prionailurus javanensis rabori Groves, 1997.

Distribution: Negros, Cebu and Panay, Philippines.

Distinguishing characters: Dark ochery to buffy fawn in colour, less bright than *borneoensis* especially in median dorsal region (Groves 1997). Spots large (smaller than in *borneoensis*), dark (Groves 1997). Male skulls averaging larger than Indonesian forms, female skulls of similar size to *sumatranus* and *borneoensis* (Groves 1997). Skull somewhat narrower than latter two but not as narrow as *javanensis* (Groves 1997).

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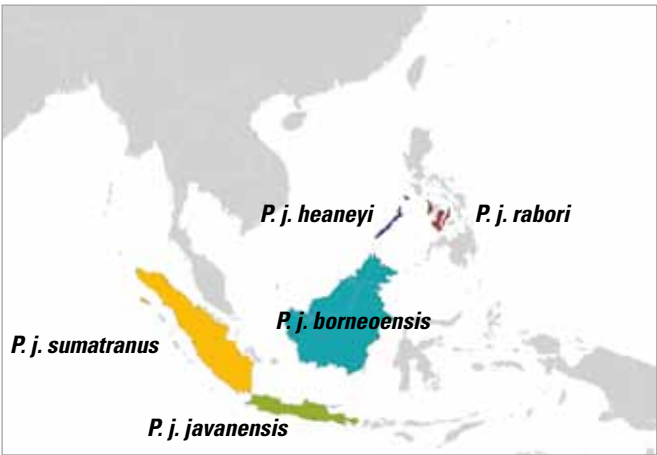
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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|--|------------|-----------|--------------|-----------|-------------------------------|
| <i>Prionailurus javanensis javanensis</i> | ++ | ++ | ++ | | |
| <i>Prionailurus javanensis sumatranus</i> | ++ | 0 | ++ | | |
| <i>Prionailurus javanensis borneoensis</i> | ++ | 0 | ++ | | |
| <i>Prionailurus javanensis heaneyi</i> | + | 0 | (+) | | Probably introduced by humans |
| <i>Prionailurus javanensis rabori</i> | + | 0 | + | | |

Puma lineage

The Puma lineage contains three monotypic genera.

Genus *Acinonyx* Brookes, 1828; 16, 33.

The genus *Acinonyx* contains a single species, *A. jubatus*, which is readily diagnosable from its distinctive morphology, including claws lacking cutaneous sheaths, elongated lower limbs and skull lacking diastema.

Acinonyx jubatus

E: Cheetah; F: Guépard; G: Gepard; Sp: Guepardo, chita.

Wozencraft (2005) recognised the following five subspecies:

Acinonyx jubatus jubatus (Schreber, 1775; pl. 105; 1777; 392).

Type locality: Das Vaterland dieses Thieres ist das südliche Afrika; man bekommt die Felle vom Vorgebirge der guten Hoffnung [The range of this mammal is southern Africa; the skin came from the Cape of Good Hope]. See Hollister (1911).

Holotype: Skin seen by Schreber.

Distribution: Southern Africa.

Acinonyx jubatus venaticus (Griffith, 1821; 93).

Type locality: India.

Holotype: From a sketch of a live animal by Mr Devis.

Distribution: SW Asia.

Acinonyx jubatus hecki Hilzheimer 1913; 288.

Type locality: Senegal.

Holotype: Live animal in Berliner Zoologisches Garten.

Distribution: W Africa.

Acinonyx jubatus soemmeringii (Fitzinger, 1855; 245).

Type locality: von den Steppen der Kababisch im Süden der Bajuda-Wüste [= from the steppes of the Kababish in the south of the Bayuda Desert, Sudan].

Holotype: Male living in the Menagerie at Schönbrunn, Vienna.

Distribution: Sudan, Ethiopia, Horn of Africa.

Acinonyx jubatus velox Heller 1913; 7.

Type locality: the Loita Plains, British East Africa [= Kenya].

Holotype: USNM 163096 adult male skin, skull and leg bones.

Distribution: E Africa.

Discussion

The most comprehensive phylogeographical study to date was by Charruau et al. (2011). This analysis of mtDNA (NADH5, cytb and control region) and 18 polymorphic nuclear microsatellites revealed a complex star-shaped pattern in the mtDNA haplotype network, with suggestions of geographical partitioning. For example, Asian, Arabian and north African cheetahs tended to group together as did those from north-east Africa, including Somalia, Sudan, Ethiopia and Djibouti. However, this was not exclusive. East African cheetahs diverged into two different lineages from those of southern Africa. C. Groves (pers. obs.) found that Saharan cheetahs are probably distinguishable morphologically from their small spots, but that Asian cheetahs did not seem to differ significantly from African cheetahs. Charruau et



al. (2011) concluded that the following subspecies can be recognised genetically, although no diagnostic morphological distinctions can be made currently:

Acinonyx jubatus jubatus (Schreber, 1775).

Distribution: Southern Africa.

Acinonyx jubatus soemmeringii (Fitzinger, 1855).

Distribution: NE Africa.

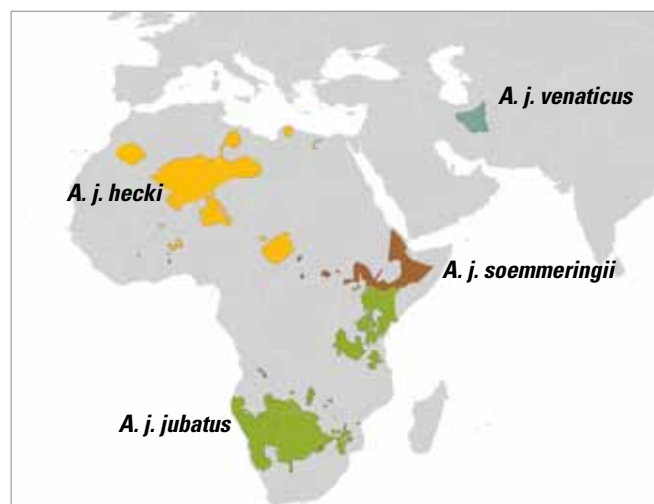
Acinonyx jubatus venaticus (Griffith, 1821).

Distribution: SW Asia and India.

Acinonyx jubatus hecki Hilzheimer 1913.

Distribution: W and N Africa.

However, the divergence times between these lineages are very recent (Charruau et al. 2011), e.g. 32,000-67,000 ya between *jubatus* and *venaticus*, and 16,000-72,000 ya between *jubatus* and *soemmeringii*, and the inclusion of ancient DNA samples from north Africa and south-west Asia blurred the distinction between north African and Asian cheetahs, suggesting isolation by distance. It is possible that there are only two subspecies of cheetah; northern (*venaticus*) and southern/eastern (*jubatus*), or perhaps none if further more comprehensive sampling of museum specimens is carried out.



Distribution of tentative subspecies of cheetah. Borders between subspecies are speculative.

| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|--------------------------------------|------------|-----------|--------------|-----------|--|
| <i>Acinonyx jubatus jubatus</i> | ++ | ++ | ++ | | |
| <i>Acinonyx jubatus venaticus</i> | + | ++ | ++ | | Possibly includes <i>hecki</i> and <i>soemmeringii</i> |
| <i>Acinonyx jubatus hecki</i> | + | + | + | | Possible synonym of <i>venaticus</i> |
| <i>Acinonyx jubatus soemmeringii</i> | + | + | + | | Possible synonym of <i>venaticus</i> |
| <i>Acinonyx jubatus velox</i> | + | - | - | | Synonym of <i>jubatus</i> |

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Genus *Herpailurus* Severtzov, 1858; 385.

As used here, this is a monotypic genus, but it may be included within *Puma*.

Herpailurus yagouaroundi

E: Jaguarundi; F: Jaguarondi; G: Jaguarundi, Wieselkatze, Eyra; Sp: Yaguarundi, onza, gato moro, gato eyra.

Wozencraft (2005) recognised eight subspecies of jaguarundi:

Herpailurus yagouaroundi yagouaroundi (É. Geoffroy Saint-Hilaire, 1803; 124).

Type locality: Paraguay, restricted to Cayenne, French Guiana by Hershkovitz (1951; 565).

Holotype: Based on l'yagouaroundi of Azara, who had two females (1801; 171).

Distribution: E Venezuela, the Guianas and NE Brazil.

Herpailurus yagouaroundi ameghinoi (Holmberg, 1898; 485).

Type locality: San Luis [Argentina].

Holotype: Skin in Turin Museum.

Distribution: Argentina.

Herpailurus yagouaroundi cacomitli (Berlandiere, in Baird, 1859; 12).

Type locality: Matamoros, Tamaulipas [Mexico].



A very red jaguarundi from Eastern Amazonia, Brazil (Photo Projeto Gatos do Mato - Brasil).

Holotype: USNM 1426 adult female skull.

Distribution: E Mexico as far north as S Texas.

Herpailurus yagouaroundi eyra (G. Fischer, 1814; 228).

Type locality: Paraguay.

Holotype: Based on a live animal in the possession of Azara, which he called l'eyra (1801; 177).

Distribution: S Brazil, Paraguay and N Argentina in Misiones and the Mediterranean and Chaco zones.

Herpailurus yagouaroundi fossata (Mearns, 1901; 150).

Type locality: Merida, Yucatán [Mexico].

Holotype: USNM 7036 adult skull.

Distribution: Honduras, Belize, Guatemala and Yucatan, Mexico.

Herpailurus yagouaroundi melantho (Thomas, 1914; 350).

Type locality: Pozuzo, departamento de Huánuco 800m [Peru].

Holotype: BMNH 1908.6.17.10 male skin and skull.

Distribution: Peru in the valleys of the Andes.

Herpailurus yagouaroundi panamensis (J. A. Allen 1904: 71).

Type locality: Boqueron, Chiriqui, Panama.

Holotype: AMNH M-18946 subadult female skin and skull.

Distribution: E of Colombia and possibly Ecuador extending N to Panama and Costa Rica.

Herpailurus yagouaroundi tolteca (Thomas 1898; 41).

Type locality: Tatemaes, Sinaloa [Mexico].

Holotype: BMNH 1898.3.2.17 male skin and skull.

Distribution: W Mexico as far N as S Arizona.

Discussion

This species is polymorphic with at least three common pelage colours. Da Silva et al. (2016) carried out ecological modelling of the two principal coat colours; dark/grey pelage is associated mostly with wet, dense forests, whereas the ancestral red coat colour is associated principally with dry, open habitats. A recent phylogeographical study by Ruiz-García & Pinedo-Castro (2013) based on three mitochondrial genes (ATP8, 16S rRNA and NADH5) found no evidence for subspecies. On the basis of this study we regard *Herpailurus yagouaroundi* as a monotypic species:

Herpailurus yagouaroundi (É. Geoffroy Saint-Hilaire, 1803).

Distribution: C and S America.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|--|------------|-----------|--------------|-----------|----------|
| <i>Herpailurus yagouaroundi yagouaroundi</i> | ++ | ++ | ++ | | |
| <i>Herpailurus yagouaroundi ameghinoi</i> | + | - | 0 | | |
| <i>Herpailurus yagouaroundi cacomitli</i> | + | - | 0 | | |
| <i>Herpailurus yagouaroundi eyra</i> | + | - | 0 | | |
| <i>Herpailurus yagouaroundi fossata</i> | + | - | 0 | | |
| <i>Herpailurus yagouaroundi melantho</i> | + | - | 0 | | |
| <i>Herpailurus yagouaroundi panamensis</i> | + | - | 0 | | |
| <i>Herpailurus yagouaroundi tolteca</i> | + | - | 0 | | |

Genus *Puma* Jardine, 1834; 266.

This is a monotypic genus, but may be revised to include *Herpailurus*.

Puma concolor

E: Puma, cougar, mountain lion; F: Puma, cougar; G: Puma, Silberlöwe; Sp: Puma, león americano, león bayo, león colorado, onza bermeja.

Traditionally this widespread species has been split into as many as 32 subspecies, most of which were of doubtful validity (Young & Goldman 1946). Culver et al. (2000) carried out a phylogeographical study of pumas throughout their range based on both contemporary and museum samples and analysis of three mitochondrial gene sequences (16S rRNA, ATPase-8, NADH-5) and composite microsatellite genotypes (10 feline loci).

One the basis of this study, six phylogeographical groups were claimed and designated as subspecies:

Puma concolor concolor (Linnaeus, 1771; 522).

Locality from where the subspecies was first described: Brassilia; restricted by Goldman (in Goldman & Young 1946) to Cayenne region, French Guiana.

Holotype: None designated.

Range: N and W South America.

Puma concolor puma (Molina, 1782; 295).

Locality from where the subspecies was first described: Chile; restricted to "in the vicinity of Santiago" by Nelson & Goldman (1929).

Holotype: None designated.

Range: S South America.

Puma concolor cougar (Kerr, 1792; 151).

Type locality: Pennsylvania, Virginia, Carolina and Georgia, in North America; restricted to Pennsylvania by Nelson & Goldman (1929).

Holotype: Based on Cougar de Pensilvanie of Buffon (1776; 222).

Range: North America.

Puma concolor capricornensis (Goldman, 1946; 246).

Type locality: Piracicaba, about 80 miles northwest of Sao Paulo, Brazil.

Holotype: USNM 100118 adult male skull.

Range: NE South America.

Puma concolor costaricensis (Merriam 1901; 596).

Type locality: Boquete, Chiriqui, Panama.

Holotype: MCZ 10118 female skin and skull.

Range: Costa Rica and Panama.

Puma concolor cabreræ (Pocock, 1940; 308).

Type locality: La Rioja, province of La Rioja, northern Argentina, altitude 968 metres.

Holotype: BMNH 1874.8.4.2 adult male skull.

Range: SE South America.

Wozencraft (2005) listed these subspecies, except for *capricornensis*, but added *anthonyi*, without explanation. This appears to be an error.



A puma in California (S. Kennerknecht/pumapix).

Discussion

A more recent study of mtDNA in pumas from throughout their range, although with lower sample sizes, supports only two main geographical groupings with North American populations having colonised since c. 8,000 years b.p. (Caragiulo et al. 2014).

On this basis, we tentatively recognise two subspecies within *Puma concolor*:

Puma concolor concolor (Linnaeus, 1771).

Distribution: South America, possibly excluding W of Andes in north.

Puma concolor cougar (Kerr, 1792).

Distribution: North and Central America, possibly N South America W of Andes.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|-----------------------------|------------|-----------|--------------|-----------|--|
| <i>P. c. concolor</i> | + | ++ | ++ | | |
| <i>P. c. cougar</i> | + | ++ | ++ | | |
| <i>P. c. anthonyi</i> | + | + | 0 | | Probably junior synonym of <i>P. c. concolor</i> |
| <i>P. c. capricornensis</i> | + | + | 0 | | Probably junior synonym of <i>P. c. concolor</i> |
| <i>P. c. costaricensis</i> | + | + | 0 | | Probably junior synonym of <i>P. c. cougar</i> |
| <i>P. c. cabreræ</i> | + | + | 0 | | Probably junior synonym of <i>P. c. concolor</i> |
| <i>P. c. puma</i> | + | + | 0 | | Probably junior synonym of <i>P. c. concolor</i> |

Bay cat lineage

Genus *Pardofelis* Severtzov, 1858; 387.

Pardofelis as defined here is usually regarded as a monotypic genus with the species, *P. marmorata* (Wozencraft 2005).

Pardofelis marmorata (Martin, 1837; 108).

E: Marbled cat; F: Chat marbré; G: Marmorkatze; Sp: Gato jaspeado. Type locality: Java or Sumatra; restricted to Sumatra by Robinson and Kloss (1919; 261).

Holotype: BMNH 1855.12.24.25 young male, skin and skull, from Sumatra

Distribution: Sumatra, Borneo, SE Asia as far N as Yunnan, N Burma, Assam to Nepal (Corbet & Hill 1992).

P. marmorata is usually divided into two distinct subspecies:

P. m. marmorata

Type: As above.

Distribution: Sumatra, Borneo, Mainland SE Asia excluding N Burma to India.

Distinguishing characters: Greyer with large distinct blotches.



A marbled cat in Borneo (S. Kennerknecht/Panthera).

P. m. charltonii (Gray, 1846; 211).

Type locality: Darjiling (= Darjeeling), North India.

Holotype: Female skin BMNH 1846.3.4.6 and skull BMNH 1846.3.17.23.

Distribution: Nepal to Assam, Bangladesh and N Burma.

Distinguishing characters: Rich ochreous brown, limited blotch-like markings.

Discussion

A preliminary analysis of pelage patterns confirmed the two basic pelage patterns, but their distributions are different from those above, with the greyer southern form restricted to the Sunda Islands and the Malay Peninsula as far north as the Isthmus of Kra, and the ochreous northern form ranging from throughout mainland SE Asia north of the Isthmus of Kra to Nepal. Preliminary analysis suggests that the pelages of these two forms are consistently distinct and geographically separated (A. Kitchener & E. Meijaard, pers. obs.; see also Brongersma 1935; 33).

A recent molecular study, based on mtDNA, X-linked and Y-linked nuclear genes supports this view (Luo et al. 2014), although this study was based on a limited number of samples, which did not cover the entire distribution range. Eleven samples from animals in Indochina showed a divergence time of about two million years compared with three Sunda animals, which were from the Malay Peninsula. Given the wider geographical distribution of the northern form, the earliest available name is *Felis longicaudata* based on a dried specimen collected by Diard probably from Cochinchina, from which the skeleton was extracted, but only the skull was figured (Blainville 1843).

The analysis of pelage patterns also suggested that there could be differentiation between Sumatra (greyer) and Borneo (brownier) populations (see also Brongersma 1935; 33), which may be recognised as distinct subspecies. If so, the Bornean subspecies would require a formal scientific description as a new subspecies.

The following taxonomic arrangement is tentative and awaits a more in-depth molecular and morphological study, which may show that there are two distinct species and a possible new subspecies on Borneo.

Pardofelis marmorata marmorata.

Distribution: Borneo, Sumatra, Malay Peninsula S of Isthmus of Kra and S Thailand.

Distinguishing characters: Greyer with large distinct blotches.

Pardofelis marmorata longicaudata (Blainville, 1843; 186, pl. X).

Type locality: del’Inde (Cochinchine?).

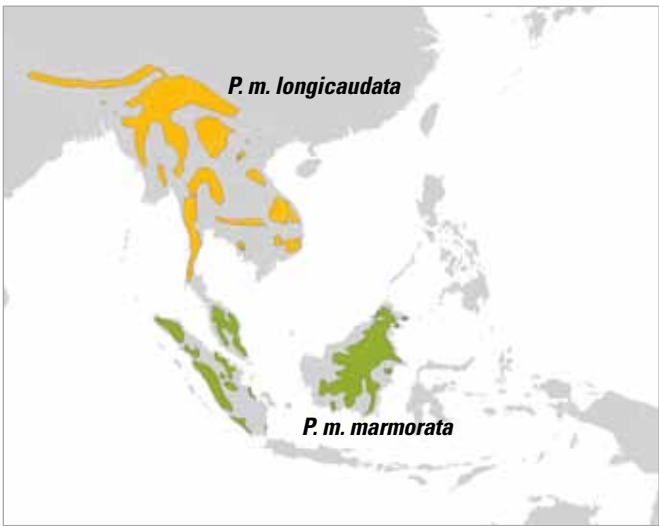
Holotype: MNHN-ZM-AC-A3424 articulated skeleton.

Distribution: Nepal to Assam, Bangladesh, SE Asia N of the Isthmus of Kra.

Distinguishing characters: Rich to pale ochreous brown, limited blotch-like markings.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|--|------------|-----------|--------------|-----------|---------------------------|
| <i>Pardofelis marmorata marmorata</i> | ++ | ++ | ++ | | |
| <i>Pardofelis marmorata longicaudata</i> | ++ | + | ++ | | Possibly distinct species |

Genus *Catopuma* Severtzov, 1858; 387.

The genus *Catopuma* contains two polychromatic species, the bay cat, *C. badia*, from Borneo and the Asiatic golden cat, *C. temminckii*, from Sumatra and the mainland of Asia.

Catopuma badia

E: Bay cat, Borneo bay cat; F: Chat bai; G: Borneo Goldkatze; Sp: Gato rojo de Borneo.

Although sometimes considered to be conspecific with *C. temminckii*, *C. badia* is a much smaller distinct monotypic species confined to Borneo (Wozencraft 2005). Like *C. temminckii*, it is polymorphic with reddish, greyish and mixed pelage colorations and there appears to be no geographical separation of these colour morphs and so we conclude that the species is monotypic.

Catopuma badia (Gray, 1874; 322).

Type locality: Sarawak, Borneo.

Holotype: BMNH 56.9.19.16 young male skin and skull.

Distribution: Borneo.

Diagnosis: Compared with *C. temminckii*, much smaller (head-and-body length (HB): 73-105 cm *C. temminckii*; 50-69 cm *C. badia* (Kitchener 1991) with reddish and greyish morphs.



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| Species | Morphology | Molecular | Biogeography | Certainty | Comments |
|-----------------------|------------|-----------|--------------|-----------|-------------------|
| <i>Catopuma badia</i> | ++ | ++ | ++ | | Monotypic species |

Catopuma temminckii

E: Asiatic golden cat, Temminck's golden cat; F: Chat de Temminck, chat doré d'Asie; G: Asiatische Goldkatze; Sp: Gato dorado asiático.

This polymorphic species is usually divided into two to three subspecies (Wozencraft 2005):

Catopuma temminckii temminckii (Vigors and Horsfield, 1827; 451).

Type locality: Sumatra.

Holotype: BMNH 1855.12.24.250 juvenile male skin and skull.

Distribution: Sumatra, Malay Peninsula, Indochina, Burma to Nepal.

Catopuma temminckii dominicanorum (Sclater, 1898; 2, pl. 1).

Type locality: Kuatun, Foochow, China.

Holotype: BMNH 1899.12.27.1 male skin and skull.

Distribution: S China.

Catopuma temminckii tristis (Milne-Edwards, 1872; 223, pl.31d).

Type locality: de l'intérieur de la Chine [from the interior of China].

Holotype: MNHN-ZM-MO-1867-535 adult male mounted skin.

Distribution: Tibet, Sichuan and Upper Burma.

Wozencraft (2008) suggested that SE Asian *C. temminckii* are probably distinct from those of Sumatra and those from Nepal, S Tibet and probably NW Yunnan and W Sichuan, thereby recognising two further subspecies:



Catopuma temminckii bainesi (Sowerby, 1924; 352).

Type locality: Tengueh, S.W. Yunnan China.

Holotype: Skin was in Royal Asiatic Society (North China Branch) Museum, Shanghai.

Distribution: Yunnan.

Catopuma temminckii moormensis (Hodgson, 1831; 177).

Type locality: Nepal.

Holotype: BMNH GERM 118a skull.

Distribution: Nepal, S Tibet and probably NW Yunnan and W Sichuan, China.

Discussion

This is a very variable species with a wide range of pelage colorations and markings, but northern populations seem to be particularly polymorphic. There is also a large difference in size between animals from Sumatra and the Malay Peninsula and those from SE Asia and China. Luo et al. (2014) carried out a first phylogeographical study on *C. temminckii* with specimens from China, Indochina and the Malay Peninsula. No samples from Sumatra or parts of the western distribution range were included. Based on mtDNA (spanning cytochrome b, AT-Pase8 and 16S ribosomal DNA), X-linked gene (PLP), Y-chromosome haplotypes of intronic regions of three Y-linked genes (DBY, SMCY3 and UTY11) and one Y-linked microsatellite SMCY7-STR *C. temminckii* populations showed a relatively recent divergence time with a separation between populations from the Malay Peninsula (n=7 plus one Sunda specimen of unknown locality) and, by inference, Sumatra from those north of the Isthmus of Kra (n = 36). Patel et al. (2016) carried out a comprehensive study of whole mitochondrial genomes and pelage coloration in *C. temminckii*. They found that this species has diversified since around the time of the Toba super-eruption in Sumatra c.74 kya. No geographical structure was found in the genetic data in mainland Asia, but there was a more or less distinct clade that included animals from the Malay Peninsula and Sumatra. This latter clade displays the least polychromatism compared with mainland populations.

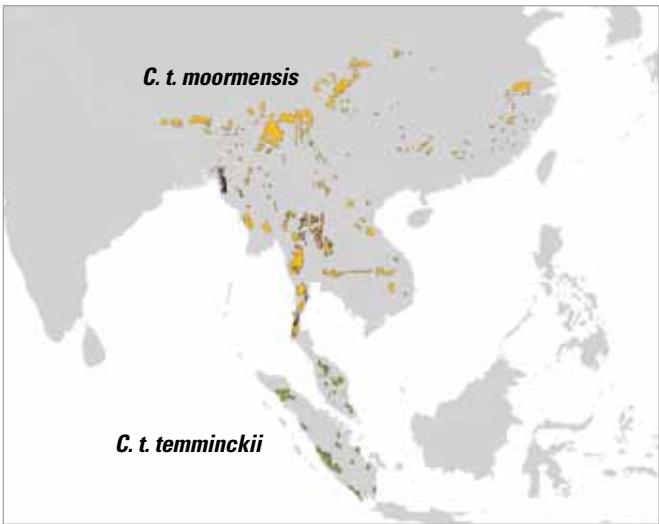
On the basis of this study, we suggest the recognition of two subspecies:

Catopuma temminckii temminckii (Vigors and Horsfield, 1827).
Distribution: Sumatra and the Malay Peninsula.
Distinguishing characters: Relatively small, typical reddish coloration (melanistic morphs also).

Catopuma temminckii moormensis (Hodgson, 1831).
Distribution: From Nepal to N Burma, China, Tibet and SE Asia.
Distinguishing characters: Relatively large, pelage very variable ranging from blotches and spots to dark grey, blackish, brown and reddish morphs.

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Distribution of tentative subspecies of Asiatic golden cat. Borders between subspecies are speculative.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|--|------------|-----------|--------------|-----------|-------------------------------------|
| <i>Catopuma temminckii temminckii</i> | ++ | ++ | ++ | | |
| <i>Catopuma temminckii dominicanorum</i> | + | 0 | 0 | | Colour variant of <i>moormensis</i> |
| <i>Catopuma temminckii tristis</i> | ++ | 0 | 0 | | Colour variant of <i>moormensis</i> |
| <i>Catopuma temminckii bainesi</i> | + | 0 | 0 | | Colour variant of <i>moormensis</i> |
| <i>Catopuma temminckii moormensis</i> | + | + | ++ | | |

Lynx lineage

Genus *Lynx* Kerr 1792; 157.

Monophyletic group with four species, recognised from morphology (Nowak 1999) and DNA-based analyses (Johnson et al. 2004).

Lynx rufus

E: Bobcat; F: *Lynx roux*, *lynx bai*; G: Rotluchs, Luchskatze; Sp: Lince rojo.

Wozencraft (2005) recognized twelve subspecies of *Lynx rufus* following Larivière and Walton (1997), Hall (1981) and Anderson (1987):

Lynx rufus rufus (Schreber 1777a; pl. 109B, 1777b; 412).

Locality from where the species was first described: der Provinz Neu York in America [= the Province of New York in America].

Holotype: None designated. Based on Pennant's (1781; 281) Bay Lynx (Allen 1920).

Distribution: E and midwestern USA.

Lynx rufus baileyi (Merriam 1890; 70, pl. 11).

Type locality: Moccasin Spring, Arizona [USA].

Holotype: USNM 186519 adult female skin and skull.

Distribution: SW arid zone from California to W Texas and Utah, and S to Durango, Mexico.

Lynx rufus californicus (Mearns 1897; 458).

Type locality: San Diego, California [USA].

Holotype: USNM 1588 adult female skin and skull.

Distribution: Nevada to C and S California.

Lynx rufus escuinapae J. A. Allen 1903; 614.

Type locality: Escuinapa, Sinaloa, Mexico.

Holotype: AMNH M-14326 adult female skin and skull.

Distribution: C Mexico extending north along W coast to Sonora.

Lynx rufus fasciatus (Rafinesque 1817; 46).

Locality from where the subspecies was first described: North-West coast [USA].

Holotype: None designated. Based on Lewis and Clark's description of specimens obtained near the mouth of the Columbia, on Netul River (now Lewis and Clark River) near Astoria, Oregon on 13 December 1805 (Allen 1814; 96, Bailey 1936, Young 1958; 137).

Distribution: Coastal forests from SW British Columbia, Canada to N California, USA.

Lynx rufus floridanus (Rafinesque 1817; 46).

Locality from where the subspecies was first described: Florida, Georgia and Louisiana, restricted to Florida by Stark (1828; 103).

Holotype: None designated.

Distribution: SE USA.

Lynx rufus gigas (Bangs 1897; 50, plate II).

Type locality: from fifteen miles back of Bear River, Nova Scotia [Canada].

Holotype: MCZ 4951 male skin and skull.

Distribution: Maine and adjacent SE Canada, including Nova Scotia.



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Lynx rufus oaxacensis Goodwin 1963; 1.

Type locality: Los Nanches, San Pedro Jilotepec, District of Tehuantepec, Oaxaca, Mexico.

Holotype: AMNH M-189300 female skin and skull.

Distribution: Uplands of C and S Oaxaca, from the districts of Tlaxiaco and Ixtlan S to the districts of Yautepec and Tehuantepec; not known to occur E of the Isthmus of Tehuantepec.

Lynx rufus pallascens (Merriam 1899; 104).

Type locality: south base of Mount Adams, near Trout Lake, Washington [USA].

Holotype: USNM 76585 adult male skin and skull.

Distribution: Rocky Mountains from British Columbia, Canada to New Mexico.

Lynx rufus peninsularis (Thomas 1898; 42).

Type locality: Santa Anita, Lower California, Mexico.

Holotype: BMNH 1898.3.1.51 adult male skin and skull.

Distribution: Baja California, Mexico.

Lynx rufus superiorensis (Peterson and Downing 1952; 1).

Type locality: McIntyre Township, near Port Arthur, Ontario [Canada].

Holotype: ROM 20947 male skin and skeleton.

Distribution: S Ontario, SE Manitoba to Wisconsin and Minnesota, USA.

Lynx rufus texensis (Allen 1895; 188); renaming of *Felis maculata* Horsfield & Vigors 1829; 381, pl. 13; type locality: Mexico (which is preoccupied by *Felis (Lynx) vulgaris maculatus* Kerr 1792; 157) and *Lynx rufus* var. *maculatus* Audubon and Bachman (1851; 295).

Type locality: Castroville, on the head waters of the Medina, in Texas [USA].

Holotype of *maculata*: BMNH 1856.12.24.275 skin and skull.

Distribution: W Louisiana to E Texas and NE Mexico.

Discussion

Young (1958) identified 12 subspecies based on pelage coloration. Hall & Kelson (1959) described 11 subspecies. Samson (1979) confirmed 11 of Young's 12 subspecies (*L. r. oaxacensis* was not included), using multivariate analyses of cranial characters. Hall (1981) refined boundaries for all 12 subspecies. Werdelin (1981) found that skulls of *floridanus* are morphometrically distinct from those of *pallascens*, *baileyi* and *californicus*, but no other eastern subspecies were sampled in this study. At the same time Read (1981) came to a much

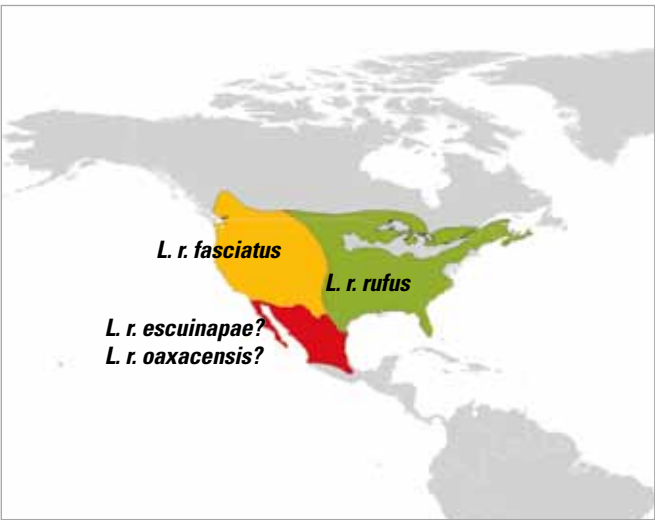
different conclusion, suggesting that there were far fewer valid sub-species.

Recently, studies on the phylogeography and population history of bobcats on a continental scale with genetic analyses have been performed (Croteau 2009, Reding 2011). Reding (2011) analysed 1700 samples with 15 microsatellites and 1 KB of mtDNA sequence. The primary signature involves a longitudinal cline with a transition or suture zone along the Great Plains in the central USA. This divergence was evident in both marker types. Significantly negative FS values and unimodal mismatch distributions support a scenario of post-glacial expansion from two disjunct Pleistocene refugia, which were probably separated by the aridification of the Great Plains during interglacial periods. Under the conservation criterion of reciprocal monophy on a DNA sequences-based tree (Moritz 1994), the findings of Reding (2011) support two historically independent units representing eastern and western bobcats. There were some unique haplotypes found in the few Mexican samples that were analysed. To clarify the status of Mexican bobcats, more rigorous sampling is required.

Croteau (2009) came to a very similar conclusion with a much smaller sample size. She identified, based on mtDNA analyses, two phylogeographical groups, western versus mid-western/eastern bobcats. Loveless et al. (2016) modelled the geographical distribution of the bobcat during the LGM and today and confirmed an east-west division with the Great Plains being devoid of bobcats during the late Pleistocene and acting as an ecological barrier even today along with the Rocky Mountains. Skull morphometrics supported two glacial refugia with longer, thinner skulls in the northwest and shorter, broader skulls in the southeast (Loveless et al. 2016).

We recognise the following subspecies:

Lynx rufus rufus (Schreber 1777), including *L. r. rufus*, *L. r. superiorensis*, *L. r. floridanus*, *L. r. gigas*.
Distribution: E of the Great Plains, North America.



Distribution of tentative subspecies of bobcat. Borders between subspecies are speculative.

Lynx rufus fasciatus (Rafinesque 1817) including *L. r. pallescens*, *L. r. baileyi*, *L. r. fasciatus*, *L. r. californicus*, *L. r. peninsularis*, *L. r. texensis*.
Distribution: W of the Great Plains, North America.

The status of bobcats in Mexico (*L. r. escuinapae* and *L. r. oaxacensis*) needs to be clarified.

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| Species | Morphology | Genetics | Biogeography | Certainty | Comments |
|---------------------------------|------------|----------|--------------|-----------|-----------------------------------|
| <i>Lynx rufus rufus</i> | ++ | ++ | ++ | | |
| <i>Lynx rufus baileyi</i> | + | - | - | | |
| <i>Lynx rufus californicus</i> | + | - | - | | |
| <i>Lynx rufus escuinapae</i> | + | + | ? | | Needs further research |
| <i>Lynx rufus fasciatus</i> | ++ | ++ | ++ | | Distinctive western genetic clade |
| <i>Lynx rufus floridanus</i> | + | - | - | | |
| <i>Lynx rufus gigas</i> | + | - | - | | |
| <i>Lynx rufus oaxacensis</i> | + | + | ? | | Needs further research |
| <i>Lynx rufus pallescens</i> | + | - | - | | |
| <i>Lynx rufus peninsularis</i> | + | ? | - | | |
| <i>Lynx rufus superiorensis</i> | + | - | - | | |
| <i>Lynx rufus texensis</i> | + | - | - | | |

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A bobcat in California (S. Kennerknecht/pumamix).

Lynx canadensis

E: Canada lynx; F: Lynx du Canada, loup-cervier; G: Kanadaluchs; Sp: Lince de Canada.

Wozencraft (2005) recognised three subspecies of *Lynx canadensis*:

Lynx canadensis canadensis Kerr 1792; 157.

Locality from where the species was first described: Canada; restricted by Miller (1912) to Eastern Canada.

Holotype: None designated.

Distribution: Mainland Canada.

Lynx canadensis mollipilosus Stone 1900; 48.

Type locality: Wainwright Inlet, Pt. Barrow [Alaska].

Holotype: ANSP 141 male skin and skull.

Distribution: Alaska.

Distinguishing characters: Browner and less grey than true *Lynx canadensis*, with a very dense, soft, woolly pelage. Skull decidedly narrower, higher and more arched than *L. canadensis*, and much more constricted across the frontals and between the orbits, the postorbital processes are conspicuously more slender. Measurements: -Total length 1,040 mm; tail vertebra 130 mm; hind foot ca. 260 mm (Stone 1900).

Lynx canadensis subsolanus Bangs 1897; 49.

Type locality: Codroy, Newfoundland [Canada].

Holotype: MCZ 1190 male skin and skull.

Distribution: Newfoundland, Canada.

Distinguishing characters: Differs from *L. c. canadensis* in darker and richer colour, and some cranial characters.

Discussion

Van Zyll de Jong (1975) measured skulls of Canada lynx from across the range, including Newfoundland. He found that zygomatic width, mastoid width, interorbital width, postorbital width and width between the postorbital processes were significantly greater relative to condylobasal length in *L. c. subsolanus*. But there was an overlap in many other measures. He concluded that the separation was of relatively recent date and that the subspecies status was questionable, which means that the species would be monotypic. Based on genetics, no evidence for isolation in different glacial refugia within North America was found (Rueness et al. 2003). It seems that Canada lynx is genetically structured following ecological differentiation due to large scale climatic factors (Stenseth et al. 1999). Canada lynx are known to disperse over very large distances, even up to 1,100 km (Poole 1997). This creates a high level of gene flow (Schwartz et al. 2002). This was confirmed by Row et al. (2012). They analysed samples from across mainland North America and Newfoundland and found only little genetic differentiation among mainland Canada lynx, but large differentiation between the mainland and Newfoundland. This is to be expected for an island population. There is currently a



study going on which also looks into slower mutating genetic markers and includes an attempt to estimate divergence time with different markers (J. Row, pers. comm.).

There has been a lot of speculation about the colonization of Newfoundland by Canada lynx. Cameron (1958) said that they arrived early in the post-glacial period, and Dodds (1960) concluded that they arrived as late as 1861 in Newfoundland. Cameron's hypothesis is very unlikely to be true as lynx arrived late in North America and did not make it south of the large ice sheet during the Pleistocene (Guthrie 1990, Pielou 1991) and cannot have arrived on Newfoundland early in the post-glacial period.

Therefore we conclude that *Lynx canadensis* is a monotypic species:

Lynx canadensis Kerr 1792.

Distribution: Canada, Alaska and northern USA.

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| Species | Morphology | Genetics | Biogeography | Certainty | Comments |
|-------------------------------------|------------|----------|--------------|-----------|-----------------------------|
| <i>Lynx canadensis canadensis</i> | ++ | ++ | ++ | | |
| <i>Lynx canadensis mollipilosus</i> | + | - | - | | |
| <i>Lynx canadensis subsolanus</i> | + | - | + | | Probable human introduction |

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Lynx lynx

E: Eurasian lynx; F: Lynx commun, lynx boréal; G: Luchs; Sp: Lince.

Wozencraft (2005) recognised five subspecies of *Lynx lynx*.

Lynx lynx lynx (Linnaeus, 1758; 43).

Locality from where the species was first described: Europae sylvis & desertis; restricted by Thomas (1911; 136) to Wenersborg, S. Sweden.

Holotype: None designated.

Distribution: From W Europe through the boreal forests of Scandinavia and Russia.

Lynx lynx isabellinus (Blyth 1847; 1178).

Type locality: Tibet.

Holotype: An imperfect skin collected by Blyth.

Distribution: Central Asian mountains (Pamir, Hindukush, Tian Shan), Tibetan Plateau and south slopes of the Himalayas.

Distinguishing characters: Fur dense and soft, colour monochromatic, grayish or white-brownish without spots or only faintly visible spots. Size comparable to European lynx and therefore smaller than the other lynx in Asia. The border between *L. l. isabellinus* and *L. l. wardi* is not clear. It seems to be around the Irtysh Valley.

Lynx lynx kozlovi Fetisov 1950; 21.

Type locality: Barun-Burinkhan, Selenginskiy region, Buryatskaya ASSR, USSR [=Russia].

Holotype: Adult male skull No.80 in collection of Zoological Museum, Irkutsk State University.

Distribution: C Siberia, from the Yenissei River to Lake Baikal.

Distinguishing characters: Somewhat smaller than Altai lynx, fur very dense. Winter coat extremely diverse in general colour and degree of spottiness.

Lynx lynx neglectus Stroganov, 1962; 408.

Heptner (1969; 1260) renamed *Felis neglecta* as *Felis stroganovi*, because this name was preoccupied by *Felis neglecta* Gray (1838; 27; holotype BMNH 1838.4.16.325) = *Caracal aurata*. However, now



that this species is in the genus *Lynx*, the original name is available. Type locality: Glazkovka, Suputinskiy Nature Reserve, Primorsk Territory, USSR [= Russia].

Holotype: ZMMU S-41310 adult male skull.

Distribution: Russian Far East, Ussuri and Amur territories, North Korea, NE China (Manchuria).

Distinguishing characters: Characterized mainly by size and to a lesser extent craniological features. It occupies an intermediate position between the Baikal lynx and the Siberian lynx.

The subspecies status of *stroganovi* was challenged by Matjuschkin (1978).

Lynx lynx sardiniae Mola 1908b; 48.

Type locality: Nuoro, Sardinia.

Syntypes: Zoology Institute, Sassari University two mounted skins; both now lost.

Distribution: Sardinia.

In 1908 Mola published two short articles in the Bollettino della Società Zoologica Italiana describing, firstly, *a problematico incrocio di Felidi* (Mola 1908a), then a *Lince della Sardegna* (Mola 1908b). Both descriptions were clearly and doubtlessly related to two Sardinian wildcats (*Felis lybica lybica*). In November 1979, during his survey for the preparation of the monograph on *Felis lybica* in Italy (Ragni 1981), B. Ragni saw and examined one of Mola's two mounted specimens in

the zoological collection of the Zoology Institute of Sassari University; the animal was in a poor state of preservation, but was obviously *Felis lybica* and not *Lynx lynx* (see photo). The other specimen was lost and the cited one was destroyed a few years after his visit (G. Delitala, curator of zoological collections, Sassari University, pers. comm.). Both specimens were without skulls. A few years after Mola's "discovery" Prof. Alessandro Ghigi, a famous Italian zoologist, assessed the major lapsus of the Sardinian student, affirming that the described Sardinian lynx was, effectively, a Sardinian wildcat (Ghigi 1911).



The Sardinian wildcat, described by Mola (1908) as a lynx (Photo G. M. Dalitalia).

Discussion

However, there is no broad consensus on the number of recognized subspecies of *Lynx lynx* and their geographical distributions. Other subspecies that have been recognised in recent years include:

Lynx lynx balcanicus Bureš 1941; 51; junior synonym *L. l. martinoi* Mirić 1978.

Type locality: Šara Mts., the Republic of Macedonia.

Holotype: Skull in Zoo Skopje.

Distribution: The Balkan lynx is distributed in the south west Balkans. Albania, Macedonia, Kosovo, Montenegro and potentially Greece are countries that are sharing this scattered and fragmented population.

Lynx lynx carpathicus Heptner (in Heptner and Sludskii, 1972; 408). Originally described by Kratochvíl & Štollmann (1963) in Štollmann (1963; 315) as *Lynx lynx orientalis carpathicus*, which is not available as a valid subspecific name.

Type locality: Turie, Žilina District, Low Tatras, [Slovakia].

Holotype: No.131-62 adult male skull and skin, kept in Povázie museum, Žilina, Slovakia.

Distribution: Carpathian Mountains.

Distinguishing characters: Significantly larger skull size than other lynx in Europe (Štollmann 1963, Hell 1980). Reddish and highly spotted fur with little variability.

Lynx lynx dinniki Satunin, 1915; 391; Renaming of *Lynx pardina orientalis* Satunin (1905; 165, 323), preoccupied by *Felis orientalis* Schlegel (1857; 23) = *Panthera pardus orientalis*.

Type locality: Designated by Heptner & Sludskii (1972; 385) as "Psebai, north-western parts of Greater Caucasus Range", [Psebai, Krasnodar Territory, Russia].

Lectotype: Skin from collection of N.Ya.Dinnik (Dinnik 1914) selected by Heptner & Sludskii, 1972; 385.

Distribution: Caucasus Mountains S to Turkey, Iraq and Iran, formerly also in the Kopet-Dag, Turkmenistan.

Distinguishing characters: Intermediate in size between Carpathian and Balkan lynx. Fur short and sparse, which leaves a very slender impression. Reddish fur with bright pattern of spots and stripes predominate. It was formerly considered to be a member of the species *Lynx pardina* based on the spotted coat pattern.

Lynx lynx wardi (Lydekker 1904; 576).

Type locality: Altai Mountains.

Holotype: BMNH 1904.10.14.1 skin.

Distribution: Altai Mountains (Russia, Kazakhstan, China and Mongolia).

Distinguishing characters: Much larger in size than the neighbouring *L. l. kozlovi*, *L. l. lynx* and *L. l. isabellinus*.

Lynx lynx wrangeli Ognev 1928; 22.

Type locality: Valley of River Adycha, Hotan-Haia, Verkhoyansk District, Yakutia, Russia.

Holotype: ZIN 12692 male skull.

Distribution: from the Yenisei River E to the Pacific, S to the Stanovoy Mountains.

Distinguishing characters: Skull larger than in any other group or subspecies with the zygomata markedly broader, frontal region flat and without longitudinal depression. Fur colour light and monochromatic almost entirely without spots, only a few spots on the legs.

Lynx lynx melinus Kerr 1792; 157.

Locality from where subspecies first described: on the banks of the Volga, below Casan [= Kazan, Russia]

Holotype: None designated. Based on Pennant (1781; 279).

Distribution: Finland, European Russia, W Siberia (Ratkiewicz et al. 2014).

Despite the number of supposed subspecies a comprehensive phylogeography and morphological analysis has not been carried out, although some regional studies have been conducted.

L. l. balcanicus is significantly smaller than other European lynx (Mirić 1978), and has less dense fur with shorter hair (Mirić 1981). Preliminary genetic analyses have shown that the Balkan lynx is different from other European lynxes (Gugolz et al. 2008).

There has been much debate about the taxonomic status of *L. l. carpathicus*. While Vasiliu & Decei (1964) and (1993) did not recognise this subspecies, Matjuschkin (1978) and Heptner & Sludskii (1972) had no doubt about its distinctiveness, which they considered as one of the most distinctive forms in Eurasia. Hemmer (1993) argued that the name *carpathicus* was not available as the subspecies had been incorrectly described. There is increasing evidence for extra-Mediterranean ice-age refugia in Europe (Schmitt 2007), including the Carpathian Mountains, which were a forest refugium (Burga & Perret 1998) and very likely occupied by lynx. Recent genetic analyses have shown that Carpathian lynx are isolated from the other lynx populations and have low variability in the mtDNA Control Region (Breitenmoser-Würsten et al. 2003, Gugolz et al. 2008).

Matjuschkin (1978) and Heptner & Sludskii (1972) considered *L. l. dinniki* as a very morphologically distinct form, which has been geographically isolated for a long time. During the last Ice Age lynx lived south of the Caucasus Mountains, which were covered by ice. Sea levels were much lower, including that of the Black Sea, so that the Dardanelles, Bosphorus and Marmara, were dry, creating a land bridge

| Species | Morphology | Genetics | Biogeography | Certainty | Comments |
|------------------------------|------------|----------|--------------|-----------|---|
| <i>Lynx lynx lynx</i> | ++ | ++ | ++ | | |
| <i>Lynx lynx balcanicus</i> | + | ++ | + | | Possibly part of <i>dinniki</i> |
| <i>Lynx lynx carpathicus</i> | ++ | ++ | + | | |
| <i>Lynx lynx dinniki</i> | ++ | ++ | ++ | | |
| <i>Lynx lynx isabellinus</i> | ++ | 0 | ++ | | |
| <i>Lynx lynx kozlovi</i> | + | 0 | 0 | | |
| <i>Lynx lynx neglectus</i> | + | 0 | ?+ | | May be distinct subspecies? |
| <i>Lynx lynx wardi</i> | + | 0 | 0 | | |
| <i>Lynx lynx wrangeli</i> | ++ | + | ++ | | |
| <i>Lynx lynx melinus</i> | + | 0 | 0 | | |
| <i>Lynx lynx sardiniae</i> | - | - | - | | Misidentified; actually <i>Felis lybica</i> |

between Asia Minor and the Balkans (Hewitt 1999). The geographical distribution of *L. l. dinniki* may have reached southeastern Europe and preliminary genetic analyses have shown that *L. l. balcanicus* and *L. l. dinniki* share haplotypes (Gugolz et al. 2008) and are perhaps consubspecific.

The taxonomic status of the Asian lynxes is still poorly understood. *L. l. wrangeli* is the largest form and shows the greatest sexual dimorphism. Only 12% of *L. l. wardi* lack a metaconid on m1, whereas 75% of *L. l. isabellinus* individuals lack a metaconid on m1, which is much higher than in any other population. The taxonomic status of lynx in the Altai, the Baikal region and the Amur region needs further investigation and clarification. C. Groves (pers. comm.) considers *L. l. neglectus* as distinct because this area of the Russian Far East and northern Manchuria is biogeographically distinct.

Rueness et al. (2014) have carried out a phylogeographical analysis of lynx throughout Eurasia excluding the Himalayas. Based on both mtDNA and microsatellites, they identified three main clades (western, eastern and southern), which do not appear to correspond to putative subspecies. There is clearly more research required with more extensive sampling in order to elucidate the phylogeography and subspecific variation of *Lynx lynx*.

On the basis of current evidence we propose the following six subspecies, although this number may be further reduced in the future:

Lynx lynx lynx (Linnaeus 1758), including *melinus*.

Distribution: Scandinavia, Finland, Baltic States, Belarus, European part of Russia E to the Yenissei River.

Lynx lynx balcanicus (Bureš 1941).

Distribution: The Balkans and possibly Greece; possibly a synonym of *L. l. dinniki*.

Lynx lynx carpathicus Heptner, 1972.

Distribution: E and C Europe.

Lynx lynx dinniki Satunin 1915.

Distribution: The Caucasus, Asia Minor, Iran, Iraq.

Lynx lynx isabellinus (Blyth, 1847), including *kamensis*.

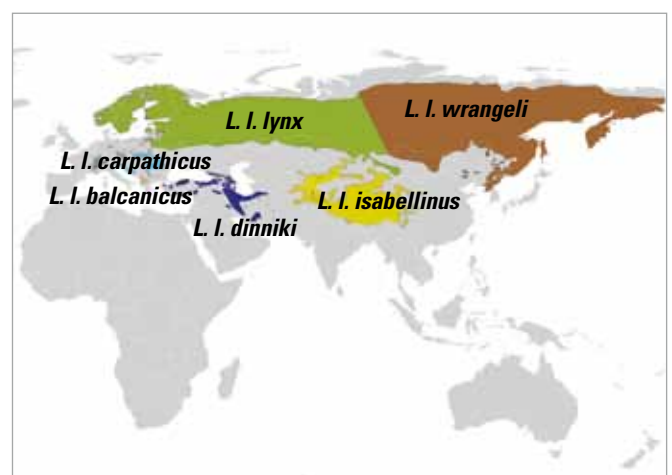
Distribution: C Asia including the Himalayas and Tibet.

Lynx lynx wrangeli Ognev 1928, including *kozlovi*, *neglectus*, *wardi*?

Distribution: E of the Yenissei River to China??

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Lynx pardinus

E: Iberian lynx; F: Lynx pardelle, lynx d’Espagne; G: Pardelluchs; Sp: Lince iberico.

Lynx pardinus (Temminck, 1827; 116).

Type locality: Portugal, puisque le commerce reçoit des peaux prepares de Lisbonne, et que M. le baron de Vionénil tua, en 1818, sur les bords du Tage, à dix lieues de Lisbonne [= on the banks of the River Tagus {Portugal}, ten leagues from Lisbon].

Holotype: MNHN-ZM-MO-2001-325 mounted skin (skull inside; Al-maça 1992).

Distribution: Iberian Peninsula.

Discussion

This is a monotypic species, which was formerly included in *Lynx lynx* (Johnson et al. 2004). No subspecies are recognised.

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| Species | Morphology | Molecular | Biogeography | Certainty | Comments |
|----------------------|------------|-----------|--------------|-----------|----------------------------|
| <i>Lynx pardinus</i> | ++ | ++ | ++ | | Distinct monotypic species |

Genus *Leopardus* Gray, 1842; 260.

This genus comprises eight species that represent an adaptive radiation in South and Central America. Characterised by a chromosome count of $2n=36$ compared with $2n=38$ in other felids. Hybridisation between species has been documented (Trigo et al. 2008, 2013).

Leopardus jacobita

E: Andean mountain cat; F: Chat des Andes; G: Bergkatze; Sp: Chinchay, gato andino, gato lince.

This species is regarded as monotypic (Wozencraft 2005):

Leopardus jacobita (Cornalia, 1865; 1).

Type locality: Bolivia, circa Potosí et Humacuaca in montibus sat elevatis; further defined by Cabrera (1958; 297) as "Sur del departamento boliviano de Potosí, cerca de la frontera argentina, entre Potosí y Humahuaca" [= southern Bolivian province of Potosí, near the Argentinian border, between Potosí and Humahuaca].

Holotype: MSNM Ma 143 mounted skin; specimen lost to bombing in 1943 (Mann 1945; Gippoliti 2005).

Distribution: S Peru, NE Chile, SW Bolivia and NW Argentina.

Discussion

Genetic analysis of mitochondrial DNA (459 bp control region, 789 bp ND5, ATP-8 and 16S mitochondrial genes) and 11 nuclear microsatellites revealed two Evolutionary Significant Units ESUs that are separated between latitudes 26° and 35° S (Cossío et al. 2012), with the possibility that the northern ESU can be split into two Management Units. With a greatly enhanced number of samples Ruiz-García et al. (2013) found that four populations of *L. jacobita* (northern Peru; southern Peru – northern Bolivia; southern Bolivia – northern Argentina; Mendoza, Argentina) were more genetically isolated from each other on the basis of microsatellites than between putative subspecies of *L. colocolo*. However, morphological samples were not sufficient to confirm whether these populations represent distinct subspecies. Further research is urgently required, owing to the endangered status of this species.

Therefore, we continue to recognise *L. jacobita* as a monotypic species until further evidence is available:

Leopardus jacobita (Cornalia, 1865).

Distribution: Andes from N Argentina and Chile to S Peru.

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| Species | Morphology | Molecular | Biogeography | Certainty | Comments |
|---------------------------|------------|-----------|--------------|-----------|--|
| <i>Leopardus jacobita</i> | ++ | ++ | ++ | | May comprise four or more subspecies or even species |

Leopardus pardalis

E: Ocelot; F: Ocelot; G: Ozelot; Sp: Ocelote, gato onza, gato tigre, manigordo, pumilio, tigrillo, cunaguaro.

Wozencraft (2005) listed the following subspecies:

Leopardus pardalis pardalis (Linnaeus, 1758; 42).

Locality from where species was first described: America, restricted to State of Vera Cruz, Mexico by Allen (1919).

Holotype: None designated.

Distribution: Mexico to Panama.

Leopards pardalis aequatorialis (Mearns, 1903; 246).

Type locality: Paramba, northern Ecuador.

Holotype: USNM 113267 adult female skin and skull.

Distribution: NE South America

Leopardus pardalis albescens (Pucheran, 1855; 149).

Type locality: Arkansas [USA].

Holotype: MNHN-ZM-MO-2001-323 male mounted skin.

Distribution: E Texas, USA S to Tamaulipas, Mexico.

Leopardus pardalis melanurus (Ball, 1844; 128).

Type locality: Unknown, but probably British Guiana [= Guyana] (Pocock 1941b; 328-333).

Holotype: BMNH 1855.12.24.251 adult probably male skin and skull.

Distribution: Venezuela, Guyana, Surinam and probably Trinidad.

Leopardus pardalis mitis (F. G. Cuvier, 1820; 221).

Type locality: Unknown, but restricted to Rio de Janeiro [Brazil] by Jardine (1834; 194).

Syntypes: MNHN-ZM-MO-2001-319 and MNHN-ZM-MO-2001-320 mounted skins.

Distribution: C and E Brazil, Paraguay and N Argentina.

Leopardus pardalis pseudopardalis (Boitard, 1842; 263).

Type locality: Mexique et la baie de Campêche?, emended to Cartagena [Colombia] by Cabrera (1958; 284).

Holotype: MNHN-ZM-AC-A1753 juvenile part skull.

Distribution: N Colombia and Venezuela.

Leopardus pardalis pusaeus (Thomas, 1914; 347).

Type locality: Congon, 15 miles W. of Guayaquil, Ecuador.

Holotype: BMNH 1899.8.1.29 male skin and skull.

Distribution: SE Ecuador to NE Peru.

Leopardus pardalis sonoriensis (Goldman, 1925; 123).

Type locality: Camoa, Rio Mayo, Sonora, Mexico.

Holotype: USNM 96216 adult male skin and skull.

Distribution: Arizona, USA and Sonora, Mexico.

Leopardus pardalis steinbachi (Pocock, 1941a; 235).

Type locality: Buenavista, Santa Cruz, Bolivia.

Holotype: BMNH 1928.2.9.15 adult male skin and skull.

Distribution: C Bolivia.



Discussion

Wozencraft (2005) followed the arrangement by Cabrera (1958) and Murray & Gardner (1997). Eizirik et al. (1998) examined the mitochondrial control region in ocelots throughout their range and identified four phylogeographical groups in Central America, northwestern South America, northeastern South America and southern South America south of the Amazon.

Ruiz-Garcia et al. (2013) examined craniometric variation and microsatellite diversity in ocelots from throughout their range, except for the southern most part of the range, most samples were from Colombia. Microsatellite differentiation identified three groups; Texas, Central America and South America (excluding eastern Brazil), whereas craniometric variation revealed that animals from Bolivia were significantly smaller.

Nascimento (2010) carried out a traditional morphological study of ocelots and concluded that there are two species. The Central American ocelot, *Leopardus pardalis*, is smaller and has a greyer pelage than the South American ocelot, *Leopardus mitis*, which is larger and has a brighter, yellower pelage. Nascimento (2010) suggests that these two species are sympatric in Nicaragua and Costa Rica, supporting their distinction as separate species. However, given high individual morphological variability within populations, this situation needs to be examined in more detail including more detailed morphological molecular analyses.

Following Eizirik et al. (1998), up to four subspecies can be differentiated:

Leopardus pardalis pardalis

Leopardus pardalis ssp. [traditionally part of *L. p. mitis*]

Leopardus pardalis pseudopardalis

Leopardus pardalis mitis

Following Ruiz-Garcia et al. (2013), up to four different subspecies can be differentiated:

Leopardus pardalis pardalis

Leopardus pardalis albescens

Leopardus pardalis steinbachi

Leopardus pardalis mitis

However, the geographic delimitation of different genetic clades is not completely congruent between these two molecular studies. The morphological differentiation between Central and South American forms is clear and supported partly by molecular data as well as a clear biogeographical barrier, the Andes.

Provisionally, two subspecies are recognised:

Leopardus pardalis pardalis (Linnaeus, 1758).

Distribution: from Texas and Arizona south to Costa Rica.

Distinguishing characters: Smaller and greyer than *mitis*.

Leopardus pardalis mitis (Cuvier, 1820).

Distribution: South America as far south as northern Argentina; limit of range with respect to *L. p. pardalis* is unclear.

Distinguishing characters: Larger and yellower than *pardalis*.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|--|------------|-----------|--------------|-----------|--|
| <i>Leopardus pardalis pardalis</i> | ++ | ++ | ++ | | |
| <i>Leopardus pardalis albescens</i> | + | + | 0 | | |
| <i>Leopardus pardalis sonoriensis</i> | 0 | 0 | 0 | | |
| <i>Leopardus pardalis mitis</i> | ++ | ++ | ++ | | mtDNA suggests might be two subspecies |
| <i>Leopardus pardalis melanurus</i> | + | - | 0 | | |
| <i>Leopardus pardalis aequatorialis</i> | + | - | 0 | | |
| <i>Leopardus pardalis pseudopardalis</i> | + | ++ | 0 | | |
| <i>Leopardus pardalis pusaeus</i> | + | 0 | 0 | | |
| <i>Leopardus pardalis steinbachi</i> | + | 0 | 0 | | |

Leopardus wiedii

E: Margay; F: Margay; G: Langschwanzkatze, Margay; Sp: Tigrillo, margay, caucal, gato tigre.

Wozencraft (2005) recognised 11 subspecies, following de Oliveira (1998):

Leopardus wiedii wiedii (Schinz, 1821; 235).

Type locality: Brasilien [= Brazil]; Brasil, restringida al Morro de Arará, sobre el río Mucurí, estado de Baía [= Brazil, restricted to the Morro de Arara, on the Mucuri river, state of Baía] by Cabrera (1958; 290) and to northern Espírito Santo, Brazil by Allen (1919; 357), both of which are based on Wied (1826; 378).

Lectotype: RMNH.MAM 17695 (original register no. c) skin (Avila-Pires 1965).

Distribution: S Brazil W to S Colombia.

Leopardus wiedii amazonicus (Cabrera, 1917; 28).

Type locality: Tabatinga [Amazonas, Brasil].

Holotype: MNCN 774 adult female skin and skull.

Distribution: Amazonas, Brazil.

Leopardus wiedii boliviae Pocock, 1941; 237.

Type locality: Buena Vista, Santa Cruz, Bolivia, 300 m. alt.

Holotype: BMNH 1926.1.5.4 adult male skin and skull.

Distribution: Bolivia to N Argentina.

Leopardus wiedii pirrensis (Goldman, 1914; 4).

Type locality: Cana (altitude 2,000 feet), eastern Panama.

Holotype: USNM 179162 adult female skin and skull.

Distribution: Panama.

Leopardus wiedii vigens (Thomas, 1904; 192).

Type locality: Igarapé-Assu, near Pará [Brazil]. Alt. 50 m.

Holotype: BMNH 1904.7.4.43 & 1904.7.4.43a adult male skin and skull.

Distribution: Lower Amazon, Brazil, Guianas.

Leopardus wiedii glauculus (Thomas, 1903; 235).

Type locality: Beltran, Jalisco, Mexico.

Holotype: BMNH 1890.1.4.1 adult female skin and skull.

Distribution: Jalisco, Sinaloa and N Yucatan, Mexico.

Leopardus wiedii nicaraguae (Allen 1919; 357).

Type locality: Volcan de Chinandego, Nicaragua.

Holotype: AMNH M-28957 adult male skin and skull.

Distribution: Nicaragua.

Leopardus wiedii oaxacensis (Nelson and Goldman 1931; 303); pre-dated by *Felis mexicana* Saussure 1860; 3, but name preoccupied by *F. mexicana* Desmarest 1816.

Type locality: Cerro San Felipe, Oaxaca, Mexico (altitude 10,000 feet).

Holotype: USNM 68169 adult male skin and skull.

Distribution: High mountains of Oaxaca, Mexico.

Leopardus wiedii salvinia Pocock, 1941; 239.

Type locality: Vera Paz, Guatemala.

Holotype: BMNH 1875.2.27.1 adult male skin and skull.

Distribution: Guatemala and perhaps Belize.

***Leopardus wiedii yucatanicus*** (Nelson and Goldman 1931; 304).

Type locality: Merida, Yucatan.

Holotype: USNM 8612 subadult female skin and skull.

Distribution: Yucatan Peninsula and N Chiapas, Mexico.

Leopardus wiedii cooperi (Goldman, 1943; 384).

Type locality: Eagle Pass, Texas.

Holotype: USNM 25 adult male skin.

Distribution: Texas, USA and NE Mexico.

Discussion

A study of mtDNA among margays by Eizirik et al. (1998) revealed three phylogeographical groups; South America, south of the Amazon; South America, north of the Amazon; and Central America. However, a more recent analysis of skins and skulls by Nascimento (2010) failed to find any significant geographical variation, although Central American margays appear to be smaller and greyer compared with South American animals. A more comprehensive molecular and morphological study is required. Until then, we recognise three subspecies as an interim conservative arrangement based on Eizirik et al. (1998):

Leopardus wiedii wiedii Schinz, 1821.

Distribution: South America S of the Amazon.

Leopardus wiedii vigens (Thomas, 1904).

Distribution: South America N of the Amazon.

Leopardus wiedii glauculus (Thomas, 1903).

Distribution: C America.

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Distribution of tentative subspecies of margay. Borders between subspecies are speculative.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|-------------------------------------|------------|-----------|--------------|-----------|----------|
| <i>Leopardus wiedii wiedii</i> | ++ | ++ | ++ | | |
| <i>Leopardus wiedii amazonicus</i> | + | 0 | 0 | | |
| <i>Leopardus wiedii boliviae</i> | + | 0 | 0 | | |
| <i>Leopardus wiedii pirrensis</i> | + | 0 | 0 | | |
| <i>Leopardus wiedii vigens</i> | + | + | + | | |
| <i>Leopardus wiedii glauculus</i> | + | ++ | ++ | | |
| <i>Leopardus wiedii nicaraguae</i> | + | 0 | 0 | | |
| <i>Leopardus wiedii oaxacensis</i> | + | 0 | 0 | | |
| <i>Leopardus wiedii salvinia</i> | + | 0 | 0 | | |
| <i>Leopardus wiedii yucatanicus</i> | + | 0 | 0 | | |
| <i>Leopardus wiedii cooperi</i> | + | 0 | 0 | | |

Leopardus colocola

E: Pampas cat; F: Chat des pampas; G: Pampaskatze; Sp: Gato pajero, gato de los pajonales, gato de pajonal, osio.

The taxonomic history of pampas cats is quite complex, owing to previous misidentifications. For example, there has been confusion with the Andean mountain cat, *L. jacobita*, and Hamilton Smith (1827; 479-480) gave the name *L. colocola* to a cat from Guyana (García-Perea 1994), which cannot now be identified.

In 1782, Molina (p. 295) twice mentioned the cat “Il Colocolo” but he also twice used the specific name *Felis colocola* (on p. 295 and in the list of new species described in *Saggio sulla storia naturali del Chili* on p. 341). We suspect that *colocola* was the name that he intended for the species and that it was not a spelling or typing error by Molina or the printer. In his later publication (1788: 322), Molina maintained the spelling *colocola*, but by the time of the English translation of this work in 1808, the name appeared as *Felis colocolo* in the text (pp. 206-207), but remained as *colocola* in the list of new species (p. 239). In Edition 2 of the *Saggio* (1810: 245) the specific name appears as *colocolo*.

It seems that Molina’s name *colocola* has been “corrected” to *colocolo* by subsequent authors. As noted above, there is nothing in the original 1782 work to indicate that *colocola* was a mistake and therefore that *colocolo* can be accepted as a “justified emendation”. According to Article 33.2.2 of the Code notes “The correction of an incorrect original spelling ... is a “justified emendation”, and the name thus corrected retains the authorship and date of the original spelling”. This Article is followed by Article 33.2.3: “Any other emendation is an “unjustified emendation”; the name thus emended is available and it has its own author and date and is a junior objective synonym of the name in its original spelling; it enters into homonymy and can be used as a substitute name, but Article 33.2.3.1 when an unjustified emendation is in prevailing usage and is attributed to the original author and date it is deemed to be a justified emendation”. Therefore *colocolo* could be maintained as being the correct spelling with the original authorship and date (Molina 1782). However, this is dependent on interpretation of “prevailing usage”. A quick search on Google Scholar reveals at least 19 references which use the name *colocola* dating from 1782 to 2013, although interestingly these were mostly published in South American countries. Members of the CCTF have agreed to revert to Molina’s original spelling of *colocola* for this species.

Until the mid-1990s there was a consensus that the pampas cat comprised a single species, but García-Perea (1994) carried out a comprehensive review of skull and pelage characters on 86 specimens from throughout the species’ range. This review concluded that the pampas cat actually comprises three species and 10 subspecies as follows:

Leopardus colocola colocolo (Molina, 1782; 295).

Locality from where the species was first described: “Chili” [= Chile]; restricted to “province of Valparaiso”, Chile by Osgood (1943; 79).

Holotype: None designated.

Distribution: C Chile from Coquimbo to Concepción.

Leopardus colocola wolffsohni (García-Perea, 1994; 30).

Type locality: Río Camarones, provincia Tarapacá, between 2000 and 4000 m, Chile.

Holotype: USNM 391853 skin and skull.

Distribution: Tarapacá Province, N Chile on W slopes of Andes.



Pampas cat, northern Argentina (Photo A. Seguin).

Leopardus pajeros pajeros (Desmarest, 1816; 114).

Locality from where the species was first described: “las pampas de Buenos Ayres, entre los 35 y 36 grados” (Azara 1802; 160), Argentina. Holotype: None designated. Based on account by Azara (1802; 160) of the “gato pajero”.

Distribution: La Pampa Province, C Argentina.

Distinguishing characters: Larger and yellower than *pardalis*.

Leopardus pajeros budini (Pocock, 1941; 263).

Type locality: Mount Sola, 2500 m, in Salta, northern Argentina [= Argentina].

Holotype: BMNH 1934.11.4.5 adult male skin and skull.

Distribution: Mountains of NW Argentina on E side of Andes.

Leopardus pajeros crespoi (Cabrera, 1957; 71).

Type locality: Aguaray, provincia de Salta, [Argentina].

Holotype: MACN 36.230 female skin and skull.

Distribution: Known only from type locality.

Leopardus pajeros crucinus (Thomas, 1901; 247).

Type locality: Santa Cruz, Argentina.

Holotype: BMNH 1855.12.24.261 skin and skull.

Distribution: S half of Argentina and Chilean Patagonia.

Leopardus pajeros garleppi (Matschie, 1912; 259).

Type locality: von Cuzco in Südost-Peru, im Gebiet des Apurimac, der durch den Ucayali zum oberen Amazonas abwässert [from Cuzco in SE Peru, in the region of Apurimac, {Peru}, from the Ucayali to the Upper Amazon].

Holotype: ZMB Mam 21244 adult male skin and skull.

Distribution: Highland steppes of E side of Peruvian Andes.

Leopardus pajeros steinbachi (Pocock, 1941; 264).

Type locality: Tiraque, Cochabamba, western Bolivia, 4000 m.

Holotype: BMNH 1934.9.2.31 adult female skin and skull.

Distribution: Highland steppes of E slopes of Bolivian Andes.

Leopardus pajeros thomasi (Lönnberg, 1913; 7).

Type locality: Near Quito, [Ecuador].

Holotype: NRM A621386 male skin and skull.

Distribution: Highland steppes of E side of Peruvian Andes.

Leopardus braccatus braccatus (Cope, 1889; 144).

Type locality: The province of Rio Grande do Sul, or in Matto Grosso; restricted to "Chapada dos Guimaraes, Matto Grosso", Brazil by Allen (1919; 378).

Holotype: AMNH MO-354 adult male skin and skull.

Distribution: SW Brazil and Paraguay.

Leopardus braccatus munoai (Ximénez, 1961; 3).

Type locality: Arroyo Perdido, Departamento de Soriano, [Uruguay].

Holotype: MNHN 884 female skin and skull.

Distribution: S Brazil, Uruguay.

Discussion

Undoubtedly, there is considerable morphological variation in this taxon, but so far genetic studies do not appear to support conclusively the differentiation of more than one species. Molecular data do indicate the existence of genetic differentiation (i.e. phylogeographical structure) among present-day populations, but these partitions are rather recent, at the same level as intra-specific partitions observed in other felids. Therefore, based on evolutionary depth (i.e. time of divergence), there is no support for species-level partitions. However, it is still possible that the group comprises a complex of very recently diverged species, whose current genetic connectivity and ecological differentiation is still not conclusively settled. Here is a summary of recent studies:

Johnson et al. (1999) examined the phylogeography of a limited sample of pampas cats using mtDNA. Genetic divergence among geographical groups was significant but shallow in terms of evolutionary time, and thus they considered that it did not support the recognition of three species, although three subspecies could be supported:

Leopardus colocolo colocolo incl. *pajeros*, *budini*, *crespoi*.

Leopardus colocolo garleppi incl. *thomasi*.

Leopardus colocolo braccatus incl. *munoai*.

Nascimento (2010) recognised six species based on studies of skins and skulls from throughout the range:

Leopardus colocolo

Leopardus pajeros

Leopardus braccatus

Leopardus garleppi

Leopardus budini

Leopardus munoai

Ruiz-García et al. (2013) investigated microsatellite and mtDNA diversity in the largest sample of pampas cats to be investigated so far, but even so, some putative subspecies were not sampled. Their results support those of Cossíos et al. (2009) and can be summarised briefly as follows:

The pampas cat is a single species comprised of several subspecies, including:

Leopardus colocolo colocolo

Leopardus colocolo pajeros incl. *crucinus*

Leopardus colocolo budini

Leopardus colocolo garleppi incl. *wolffsohni*

Leopardus colocolo braccatus

?*Leopardus colocolo steinbachi*

?*Leopardus colocolo thomasi*



Distribution of tentative subspecies of pampas cat. Borders between subspecies are speculative.

There is significant morphological and genetic variation in *L. colocola sensu lato*, but it is difficult to evaluate what this variation means taxonomically. While molecular studies suggest that there is only one species of pampas cat, there is a fundamental difference in rhinarium structure between some forms, which might indicate a species difference between western Chilean populations (a small rhinarium) compared with that of others (large ovate rhinarium). Perhaps introgression with other *Leopardus* species has influenced rhinarium morphology in some pampas cats, although currently there is no evidence of introgression of *L. tigrinus* or any other species into *L. colocola*.

C. Groves (pers. comm.) has suggested the following provisional classification:

Leopardus garleppi: While this has a colour pattern not all that different from *L. wolffsohni*, it has the skull features typical for *colocola*, and is mtDNA clade A, which is different from all the others whose DNA is known. The smaller size of *thomasi*, mentioned by García-Perea (1994), is not all that cogent as in her Table 1 the skull sizes overlap. *Leopardus steinbachi*: This seems to differ, but not greatly, in colour pattern from *garleppi*, but has mtDNA clade C, shared with some northern populations of *budini*.

Provisional species: *Leopardus budini*: Colour pattern is distinctive, its mtDNA is polymorphic, but mostly clade C; this taxon may actually be of hybrid origin, or indeed, that which García-Perea (1994) thought was a single taxon might actually be a mixture of two or more, or indeed that at least the northern end of it could be a hybrid swarm? There is a possibility that *crespoi* could be a synonym.

Provisional species: *Leopardus pajeros*: Again, there is a possibility that this taxon could actually be, at least in part, a hybrid swarm or a mixture of two or more: García-Perea (1994) says that it shows colour pattern types 2B and 2C, but at the same time has its own colour tone; it has predominantly mtDNA clade D, but with some individuals falling into clade C and some in clade B.

Leopardus crucinus: This one really is different from any other in colour pattern and apparently in skull. It has mtDNA clade D.

Leopardus wolffsohni: Distinctive in colour pattern and skull features, and mtDNA clade C, which also occurs as a minority in neighbouring *budini*.

Leopardus colocola: Distinctive in all sorts of features. DNA unknown.

Leopardus braccatus: Classed correctly as a distinct species by García-Perea (1994).

Leopardus munoai: Colour pattern type is different from *braccatus*, but otherwise not said to be very different.

Overall the taxonomy of *Leopardus colocola* remains confused, although it is commonly viewed by molecular biologists as comprising a single species, but the date of the main split between the two main mitochondrial clades of northern and southern populations is more than 800kya (Cossíos et al. 2009), which would support the recognition of at least two species based on our species definition above. However, there is a lack of congruity between morphological and genetic studies, so that further data and analyses are required to elucidate this confused picture.

We propose the following subspecies based mainly on Cossíos et al. (2009) and Ruiz-García et al. (2013), but recognise that this is likely to change as more information becomes available, including the possible recognition of some of these as full species:

Leopardus colocola colocola (Molina, 1782).

Distribution: Central Chile W of Andes.

Leopardus colocola wolffsohni (García-Perea, 1994).

Distribution: Tarapacá province, N Chile W of Andes.

Leopardus colocola pajeros Desmarest 1816, including *crucinus*.

Distribution: C, NC and S Argentina.

Leopardus colocola budini (Pocock, 1941), including *steinbachi*.

Distribution: NW Argentina and Bolivia E of Andes.

Leopardus colocola garleppi (Matschie, 1912), including *thomasi*.

Distribution: S Colombia, Ecuador, Peru E of Andes.

Leopardus colocola braccatus (Cope, 1889).

Distribution: SW and C Brazil, Paraguay.

Leopardus colocola munoai (Ximénez, 1961)

Distribution: Uruguay.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|--------------------------------------|------------|-----------|--------------|-----------|---|
| <i>Leopardus colocola colocola</i> | ++ | ++ | ++ | | |
| <i>Leopardus colocola braccatus</i> | ++ | ++ | ++ | | |
| <i>Leopardus colocola budini</i> | + | + | + | | Possibly includes <i>steinbachi</i> |
| <i>Leopardus colocola crespai</i> | + | + | + | | |
| <i>Leopardus colocola crucinus</i> | + | - | + | | Probable synonym of <i>pajeros</i> |
| <i>Leopardus colocola garleppi</i> | + | + | + | | Includes <i>thomasi</i> |
| <i>Leopardus colocola munoai</i> | + | ++ | + | | Probably distinct from <i>braccatus</i> |
| <i>Leopardus colocola pajeros</i> | ++ | ++ | ++ | | Includes <i>crucinus</i> |
| <i>Leopardus colocola steinbachi</i> | + | + | + | | Possible synonym of <i>budini</i> |
| <i>Leopardus colocola thomasi</i> | + | 0 | + | | Probable synonym of <i>garleppi</i> |
| <i>Leopardus colocola wolffsohni</i> | + | + | ++ | | Status uncertain |

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Leopardus guttulus

E: Southern tigrina; F: Oncille du sud, chat-tigre du sud; G: Südliche Tigerkatze; Sp: Sp: Tigrillo, tirica, gato tigre, caucel.

Leopardus guttulus (Hensel, 1872; 73).

Type locality: Rio Grande do Sul, Brasilien [= Brazil].

Syntypes: ZMB Mam 21229 and Mam 21231 skulls only.

Distribution: SE and S Brazil, N Argentina and probably Paraguay.

Discussion

Although described originally as a new species, *Felis guttula* (Hensel 1872), this species was commonly treated as a subspecies of *Leopardus tigrinus* until 2013 (Wozencraft 2005, Trigo et al. 2013). However, despite this apparent consensus, others had suggested that *Leopardus tigrinus* may well comprise two or even three distinct species (e.g. Leyhausen 1963). In the fur trade, two kinds of tigrina fur were recognised, the typical kind and the Ceara kind.

Trigo et al. (2013) demonstrated with a comprehensive molecular study that *Leopardus tigrinus* and *L. guttulus* are clearly distinct species. *L. guttulus* hybridises with *L. geoffroyi* in Rio Grande do Sul, which is the type locality. The syntypes of *L. guttulus* should be investigated in order to check whether they are hybrids or not.

Further research is required to establish whether northwestern tigrinas comprise a third species, *L. pardinoides*, or even a fourth species, *L. onchilla*, in Costa Rica (Johnson et al. 1999, Trigo et al. 2008, Nascimento 2010, Li et al. 2016). Also the distribution and morphology of *L. guttulus* need to be better defined. Until then *L. guttulus* is recognised as a monotypic species.

Leopardus guttulus (Hensel, 1872; 73).

Distribution: SE and S Brazil, N Argentina and probably Paraguay.

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| Species | Morphology | Molecular | Biogeography | Certainty | Comments |
|---------------------------|------------|-----------|--------------|-----------|--|
| <i>Leopardus guttulus</i> | ++ | ++ | + | | Distinct species from <i>L. tigrinus</i> |

Leopardus tigrinus

E: Northern tigrina, oncilla; F: Oncille du nord, chat-tigre du nord; G: Nordliche Ozelotkatze, Nördliche Tigerkatze; Sp: Tigrillo, tirica, gato tigre, caucel.

Wozencraft (2005) recognised a single species with four subspecies:

Leopardus tigrinus tigrinus (Schreber, 1775; pl.106, 1777; 396).

Type locality: südlichen Amerika, restricted to Cayenne by Allen (1919).

Holotype: Based on le margay in Buffon (1765; 248).

Distribution: NE Brazil and French Guiana to E Venezuela.

Leopardus tigrinus guttulus (Hensel, 1872; 73).

Type locality: Rio Grande do Sul, Brasilien [= Brazil].

Syntypes: ZMB Mam 21229 and Mam 21231 skulls only.

Distribution: SE and S Brazil, N Argentina and probably Paraguay.

Leopardus tigrinus pardinoides (Gray, 1867; 400).

Type locality: India, revised to Bogotá, Colombia by Gray (1874).

Holotype: BMNH 1855.12.24.185 skin and skull.

Distribution: W Venezuela, Colombia and Ecuador.

Leopardus tigrinus oncilla (Thomas, 1903; 237).

Type locality: Volcan de Irazu, Costa Rica.

Holotype: BMNH 1878.7.6.3 skin, skull lost.

Distribution: Costa Rica and ?Panama.

Discussion

The taxonomy of South American small spotted cats was highly unstable during the 19th and early 20th centuries, with particular confusion between *L. wiedii* and *L. tigrinus*. This issue has mostly been settled, i.e. little confusion remains regarding the distinctiveness between these two species. However, there has been an emerging realisation that *L. tigrinus* may in fact represent a species complex, whose exact composition is still not completely clear. This concept is a paradigm shift relative to the modern consensus supporting a single species of *L. tigrinus*, in spite of earlier suggestions that this species actually comprised two or three species (Allen 1919, Leyhausen 1963).

Johnson et al. (1999) examined variation in mtDNA (16S rDNA, ATP8 and ND5) in four *L. t. oncilla* from Costa Rica and 28 *L. (t.) guttulus* from SE Brazil. There was a 4.9% mtDNA sequence divergence between animals from these different populations, suggesting species-level distinction. The same pattern was again observed by Trigo et al. (2008), also with mtDNA data. The limited sample size and the use of only a matrilineal marker (mtDNA) in those studies, precluded a more confident conclusion that *L. t. oncilla* was indeed a distinct species. A recent study (Li et al. 2016), based on genome-wide nuclear markers, supported the distinctiveness of the single individual from Costa Rica. This provides strong support for the recognition of *L. oncilla* as a separate species, although additional analyses, including more individuals, should be performed to further confirm this conclusion and establish its relationship with neighbouring populations in NW South America. Based on a morphological analysis of skulls and pelages, Nascimento (2010) proposed that this species actually comprises four species, *L. tigrinus*, *L. guttulus*, *L. pardinoides* and *L. oncilla*.

Trigo et al. (2013) demonstrated with a comprehensive molecular study that tigrinas occurring in Brazil comprise two species, *Leopardus tigrinus* and *L. guttulus*, which may not even be sister species. *L. guttulus*



hybridises with *L. geoffroyi* in Rio Grande do Sul, which is the type locality.

Further research is required to establish whether northwestern South American tigrinas comprise yet another species, *L. pardinoides*. Li et al. (2016) suggest that tigrinas from Central America may represent a distinct species, *L. oncilla*, but it is unclear whether this would be part of *pardinoides*. Also the distribution and morphology of *L. guttulus* and *L. tigrinus* need to be better defined. Tigrinas appear to be absent from the core of the Amazon, which would pose a significant biogeographical barrier between these known and potential species. Until then *L. tigrinus* is recognised as having two subspecies:

Leopardus tigrinus tigrinus (Schreber, 1775), including *pardinoides*.

Distribution: N South America possibly as far S as Bolivia and N Argentina.

Leopardus tigrinus oncilla (Thomas, 1903).

Distribution: Costa Rica and possibly Panama.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|---------------------------------------|------------|-----------|--------------|-----------|--|
| <i>Leopardus tigrinus tigrinus</i> | ++ | ++ | + | | Distinct from <i>L. guttulus</i> |
| <i>Leopardus tigrinus pardinoides</i> | + | 0 | + | | Possibly distinct or even a distinct species |
| <i>Leopardus tigrinus guttulus</i> | ++ | ++ | + | | Distinct species from <i>L. tigrinus</i> |
| <i>Leopardus tigrinus onchilla</i> | + | ++ | ++ | | Needs further assessment; may be a distinct species. |

Leopardus geoffroyi

E: Geoffroy's cat; F: Chat de Geoffroy; G: Geoffroy Katze; Kleinfleckkatze, Salzkatze; Sp: Gato de mato, gato montés.

Wozencraft (2005) recognised four subspecies of *L. geoffroyi* based on Ximenez (1975):

Leopardus geoffroyi geoffroyi (d'Orbigny and Gervais, 1844; 40).

Type locality: des rives du Rio Negro, en Patagonie [the banks of the Rio Negro, Patagonia].

Syntypes: MNHN-ZM-MO-2001-298 mounted skin (skull inside), MNHN 2001-299 mounted skin (skull inside) and MNHN 2001-300 mounted skin (skull inside).

Distribution: C to S Argentina and Chile.

Leopardus geoffroyi salinarum (Thomas, 1903; 239).

Type locality: Cruz del Eje, Cordova, Argentina, altitude 600m.

Holotype: BMNH 1902.2.5.10 female skin and skull.

Distribution: NW Argentina.

Leopardus geoffroyi paraguayae (Pocock 1940; 351).

Type locality: Paraguay.

Holotype: BMNH 1871.3.3.6 adult female skin and skull.

Distribution: Paraguay, Uruguay, NE Argentina and SE Brazil.

Leopardus geoffroyi euxanthus (Pocock, 1940; 352).

Type locality: Tiragui, Cochabamba district in the western Bolivian highlands, 3,300 m.



Holotype: BMNH 1934.9.2.27 adult male skin and skull.

Distribution: Bolivia and far N of Argentina.

Discussion

Johnson et al. (1999) examined the phylogeography of *L. geoffroyi* based on 38 specimens from throughout their range. They examined variation in mtDNA (16S rDNA, ATP-8 and ND5) and among 20 microsatellite loci. No phylogeographical structure was present, so that no subspecies could be supported, despite some degree of morphological differentiation.

A recent morphological study of skull morphometrics by Rojo Gómez & García-Perea (in review) showed that while *L. g. salinarum* has a

small distinct skull, there is considerable overlap between *L. g. geoffroyi* and *L. g. paraguayae*, suggesting that the latter are consubspecific. However, this analysis did not remove the effect of size and hence it is not possible to be certain whether the skull shape of *L. g. salinarum* is significantly different from that of *L. g. geoffroyi* or represents a scaled-down version as part of clinal variation.

Nascimento (2014) examined geographical variation in skull morphometrics and pelage coloration and markings from all putative subspecies. He found that there was no evidence for distinct groups, but only clinal variation with latitude; diagnostic characters for one putative subspecies occurred in individuals of another putative subspecies.

Until further genetic data are available, it is probably best to treat *L. geoffroyi* as a monotypic species, which displays a morphological cline in relation to differences in habitat throughout its range.

Leopardus geoffroyi (d’Orbigny and Gervais, 1844).

Distribution: S South America from Bolivia to Patagonia.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|---------------------------------------|------------|-----------|--------------|-----------|----------|
| <i>Leopardus geoffroyi geoffroyi</i> | ++ | ++ | ++ | | |
| <i>Leopardus geoffroyi salinarum</i> | - | - | - | | |
| <i>Leopardus geoffroyi paraguayae</i> | - | - | - | | |
| <i>Leopardus geoffroyi euxanthus</i> | - | - | - | | |

Leopardus guigna

E: Guiña, kod-kod; F: Guigna, chat du Chili, kodkod; G: Kodkod, Chil-enische Waldkatze, Nachtkatze; Sp: Guiña, huiña.

Traditionally two subspecies of *Leopardus guigna* are recognised (Wozencraft 2005):

Leopardus guigna guigna (Molina, 1782; 295).

Locality from where the species was first described: Chili; restricted by Thomas (1903; 240) to Valdivia in Chile based on Philippi (1873).

Holotype: None designated.

Distribution: S Chile (38° to 48° S) and SW Argentina (39° to 46° S).

Distinguishing characters: Darker and smaller than *tigrillo*; often melanistic.

Leopardus guigna tigrillo (Schinz, 1844; 470).

Locality from where the subspecies was first described: Chili; restricted to Talcahuano, Prov. Concepcion, Chile based on Pöppig (1829; 7), following Cabrera (1958), who pointed out that Osgood’s (1943; 85) *molinae* is a junior synonym of *tigrillo*.

Holotype: None designated.

Distribution: N and C Chile (30° to 38° S).

Distinguishing characters: Larger and paler than *guigna*.



Discussion

A molecular study by Napolitano et al. (2014) of mtDNA and microsatellites identified a phylogeographical pattern that showed moderate separation between northern and southern populations, thereby supporting the two recognised subspecies.

Therefore, we recognise two subspecies:

Leopardus guigna guigna (Molina, 1782).
Distribution: S Chile (38° to 48° S) and SW Argentina (39° to 46° S).

Leopardus guigna tigrillo (Schinz, 1844).
Distribution: N and C Chile (30° to 38° S).

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Distribution of tentative subspecies of guña. Borders between subspecies are speculative.

| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|----------------------------------|------------|-----------|--------------|-----------|-----------------|
| <i>Leopardus guigna guigna</i> | ++ | ++ | ++ | | |
| <i>Leopardus guigna tigrillo</i> | ++ | + | + | | Weakly distinct |

Caracal lineage

Genus Leptailurus Severtzov, 1858; 389.

A monotypic genus confined to Africa, recognisable from its elongated legs and large mobile pinnae. The single species is highly polymorphic in coat pattern, which has resulted in taxonomic confusion.

Leptailurus serval

E: Serval; F: Serval; G: Servalkatze, Serval; Sp: Serval.

Wozencraft (2005) apparently followed Smithers (1971) in listing 18 subspecies, but in fact he probably followed Allen (1939) and Smithers (1971) has no synonymy. However, Smithers (1975, 1978) only listed six:

Leptailurus serval serval Schreber, 1776; pl. 108; 1777; 407.

Type locality: Ostindien und Tibet in gebirgegen Gegenden, vielleicht auch am Vorgebirge der guten Hofnung und dem heissern Afrika; restricted to Cape region of South Africa by Allen 1924; based on Buffon (1765; 233).

Holotype: Animal shown in plate 34 in Buffon (1765).

Distribution: Southern Africa as far N as S Democratic Republic of Congo and S Tanzania.



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Leptailurus serval brachyurus (Wagner, 1841: 547, para (b)).

Type locality: Sierra Leone, a substitute for *F. servalina* Ogilby (1839; 94).

Holotype of *servalina*: BMNH 1855.12.24.412 skin.

Distribution: W Africa, including southern Mauritania, Senegal, Gambia and Sierra Leone.

Leptailurus serval constantina (Forster, 1780; 313).

Type locality: Konstantine im algerischen Gebiet [= vicinity of Constantine, Algeria], based on Buffon (1765; 233).

Holotype: An animal in la Ménagerie du Roi, Paris.

Distribution: Morocco and Algeria.

Leptailurus serval lipostictus (Pocock, 1907; 666, pl. 38, Fig. 4).

Type locality: Mombasa, [Kenya].

Holotype: BMNH 1913.4.14.1 female skin [and skull].

Distribution: E Africa.

Comment: For some reason Smithers (1975) recognised this as the valid subspecies for E Africa, even though *pantastica* (Pocock 1907; 665) has a more certain provenance.

Leptailurus serval phillipsi (G. M. Allen, 1914; 337).

Type locality: El Garef, Blue Nile, Anglo-Egyptian Sudan [= Sudan].

Holotype: MCZ 14908 adult male skin and skeleton.

Distribution: Sudan.

Leptailurus serval togoensis (Matschie, 1893; 109).

Type locality: Bismarckburg, Togo.

Syntypes: Five described originally (only one located): ZMB Mam 105791 skin is here selected as lectotype.

Distribution: Togo, Dahomey, Nigeria.

Discussion

It is not credible that in a savanna species that all these subspecies actually exist, but there have been no recent morphological and molecular studies to examine geographical variation in this species. However, Lorenzen et al. (2012) have recently reviewed phylogeographical studies of savanna ungulates in Africa to explore patterns of differentiation within different species. For those species (e.g. *Syncerus caffer/nanus*, *Hippotragus equinus*, *Kobus ellipsiprymnus/defassa*) that show a general African distribution, they differentiate generally into a western and northern clade and a southern and eastern one.

Charruau et al. (2011) examined the phylogeography of the cheetah and found that northern and southern populations were differentiated, but that there was also some differentiation between eastern and southern populations. Dehghani et al. (2008) found a similar pattern in the white-tailed mongoose, *Ichneumia albicauda*, and Bertola et al. (2011) found differentiation between western and central African lions and those from southern and eastern Africa.

If these phylogeographical patterns apply also to *Leptailurus*, perhaps three subspecies could be distinguished, but no diagnoses are currently available:

Leptailurus serval serval (Schreber, 1777).

Distribution: Southern Africa.

Leptailurus serval constantina (Forster, 1780).

Distribution: W and C Africa.

Leptailurus serval lipostictus (Pocock, 1907).

Distribution: E Africa.

Further research is required to understand geographical variation in *Leptailurus serval*.



Distribution of tentative subspecies of serval. Borders between subspecies are speculative.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|---------------------------------------|------------|-----------|--------------|-----------|--|
| <i>Leptailurus serval serval</i> | ++ | ++ | ++ | | |
| <i>Leptailurus serval brachyura</i> | + | 0 | 0 | | |
| <i>Leptailurus serval constantina</i> | + | 0 | ++ | | Possibly distinct; could be synonym of <i>serval</i> |
| <i>Leptailurus serval lipostictus</i> | + | 0 | ++ | | |
| <i>Leptailurus serval phillipsi</i> | + | + | + | | |
| <i>Leptailurus serval togoensis</i> | + | 0 | 0 | | |

Genus *Caracal* Gray 1843; 46.

The genus *Caracal* contains two species, the caracal, *C. caracal*, and the African golden cat, *C. aurata*, which was formerly included in the monotypic genus *Profelis*.

Caracal aurata

E: African golden cat; F: Chat doré africain; G: Afrikanische Goldkatze; Sp: Gato dorado.

The African golden cat is typically divided into two subspecies (e.g. Smithers 1975, Ray & Butynski 2013), although which ones are recognised may vary. Wozencraft (2005), following Allen (1939), recognised:

Caracal aurata aurata (Temminck, 1827; 120).

Type locality: Unknown; restricted to the coastal region of Lower Guinea (between the Cross River and the River Congo) by van Mensch & Van Bree (1969).

Holotype: RMNH.MAM 19.633 (formerly d).

Distribution: W and C Africa.

Caracal aurata cottoni (Lydekker, 1906; 992, pl. 70, Fig. 1).

Type locality: the Ituri Forest, Central Equatorial Africa, in the Mawambi District.

Holotype: BMNH 1906.12.22.2 skin.

Distribution: E and C Africa.

However, van Mensch & van Bree (1969) carried out a comprehensive review of variation in this species and recognised:

Caracal aurata aurata (Temminck, 1827; 120).

Type locality: Unknown; restricted to the coastal region of Lower Guinea



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ea (between the Cross River and the River Congo) by van Mensch & Van Bree (1969).

Holotype: RMNH.MAM 19.633 (formerly d).

Distribution: E and C Africa as far W as the River Congo.

Caracal aurata celidogaster (Temminck, 1827; 140).

Type locality: Originally des côtes du Chili et Pérou [= the coasts of Chile and Peru], but Temminck (1853; 88) revised this to la côte de Guinée [the coast of Guinea], which van Mensch & van Bree (1969) restricted to Dabocrom between Secondi (4°59'N / 1°43'W) and Butry (4°50' N / 1°56' W).

Holotype: RMNH.MAM 19.632 (formerly c).

Distribution: W Africa, W of the Cross River.

Discussion

There is a large area of west Central Africa where these two subspecies intergrade between the Cross and Congo Rivers. Van Mensch &

van Bree (1969) have selected a type locality for *aurata* in this intergrade zone, so that we propose that a revised type locality east of the River Congo is designated for *Felis aurata* Temminck 1827, if it is proven that the current type locality falls within a zone of intergradation between subspecies. Van Mensch & van Bree (1969) suggested that in due course that these two subspecies may represent the ends of a cline, in which case no subspecies should be recognised. Unfortunately there have been no molecular studies (despite the potential abundance of study skins as a source of DNA) or skull morphometrics studies (skulls are rare in museums in comparison with skins). We conclude that there are probably two subspecies based on the biogeographical patterns among other rainforest species, especially the Cross River. However, a molecular study is required to confirm this probable taxonomic arrangement and if there is a wide area of intergradation should two or more subspecies be recognised.

Caracal aurata aurata (Temminck, 1827).

Distribution: E and C Africa as far W as the River Congo.
Distinguishing characters: Spotted pattern almost completely absent from back, nape and shoulders, distinct spots on lower half of flanks or spotting almost completely absent except ventral surface and indistinct spots on thigh.

Caracal aurata celidogaster (Temminck, 1827).

Distribution: W Africa W of Cross River.
Distinguishing characters: Distinctly spotted all over, with 5-6 rows of small spots on nape, 3 rows of small spots or stripes on back, many small spots arranged transversely on shoulders, circular or rosette-like spots on flanks becoming bigger on belly, or not distinctly spotted on nape and back, few spots on neck, dorsal median stripe, shoulder spots less distinct.

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Distribution of tentative subspecies of African golden cat. Borders between subspecies are speculative.



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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|------------------------------------|------------|-----------|--------------|-----------|--|
| <i>Caracal aurata aurata</i> | ++ | ++ | ++ | | |
| <i>Caracal aurata celidogaster</i> | + | 0 | + | | Possibly distinct, but possible wide area of intergradation; could be cline. |

Caracal caracal

E: Caracal; F: Caracal; G: Wüstenluchs, Karakal; Sp: Caracal, lince africano.

Wozencraft (2005) recognised eight subspecies of *Caracal caracal* based on Smithers (1975):

Caracal caracal caracal (Schreber, 1776; pl. 110; 1777; 413).

Type locality: Vom Vorgebirge der guten Hofnung [from the Cape of Good Hope], restricted by Allen (1924; 281) to Table Mountain, near Cape Town, South Africa.

Holotype: A skin brought to Schreber by Herr Hauptmann Bodenschaz.

Distribution: S Africa.

Caracal caracal algira (Wagner, 1841; 76).

Type locality: Algeria.

Holotype: Juvenile live animal in pl. IV Wagner 1841.

Distribution: N Africa from Morocco to E Libya.

Caracal caracal damarensis (Roberts, 1926; 248).

Type locality: Quickborn, Okahandja, SW Africa [= Namibia].

Holotype: TM 3841 adult male skin and skull.

Distribution: Southern Africa from N Cape Province to Namibia, Botswana, Angola and Zimbabwe.

Caracal caracal limpopoensis (Roberts, 1926; 248).

Type locality: Njelle River, north of Zoutpansberg, and near the Limpopo River [South Africa].

Holotype: TM 3180 adult male skin and skull.

Distribution: SE Africa including Transvaal, Mozambique, S Tanzania, Malawi, Zambia, S Democratic Republic of Congo and E Angola.

Caracal caracal lucani (Rochebrune, 1885; 87).

Type locality: Landana, [northern Angola, north of the River Congo's mouth].

Holotype: Museo Bouvieri.

Distribution: Gabon, N Angola, SW and W Democratic Republic of Congo.

Caracal caracal nubicus (J. B. Fischer, 1829; 210).

Locality from where the subspecies was first described: Nubia [= Sudan].

Holotype: None designated.

Distribution: From Egypt to N Tanzania.

Caracal caracal poecilotis Thomas and Hinton, 1921; 3.

Type locality: Mt. Baguezan, Asben, 5200 feet [= Mt. Bagzane, Asben, Air, Niger, 1,600 m].

Holotype: BMNH 21.2.11.19 adult female skin and skull.

Distribution: S Mauritania, N Niger, N Senegal as far E as W borders of Sudan.

Caracal caracal schmitzi (Matschie, 1912; 64).

Type locality: Ain ed Dschuheijir nordwestlich des Toten Meeres, [Ain Dcherer, northwest of the Dead Sea, Palestine = Israel].

Holotype: ZMB Mam 14347 adult male skull and skin.

Distribution: Middle East, Arabian Peninsula to Turkmenistan and India.

**Discussion**

It is not credible that so many subspecies exist in a savanna species, but there have been no recent morphological and molecular studies to examine geographical variation in this species.

However, Lorenzen et al. (2012) have recently reviewed phylogeographical studies of savanna ungulates in Africa to explore patterns of differentiation within different species or species groups. For those species (e.g. *Syncerus caffer/nanus*, *Hippotragus equinus*, *Kobus ellipsiprymnus/defassa*) that show a general African distribution, they differentiate generally into a western and northern clade and a southern and eastern one.

Charruau et al. (2011) examined the phylogeography of the cheetah and found that northern and southern populations were differentiated, but that there was also some differentiation between eastern and southern populations. Dehghani et al. (2008) found a similar pattern in the white-tailed mongoose, *Ichneumia albicauda*, and Bertola et al. (2011) found differentiation between western and central African lions and those from southern and eastern Africa.

If these phylogeographical patterns apply also to *Caracal caracal*, perhaps three subspecies could be distinguished:

Caracal caracal caracal (Schreber, 1776).

Distribution: Southern and E Africa.

Caracal caracal nubicus (J. B. Fischer, 1829).

Distribution: N and W Africa.

Caracal caracal schmitzi (Matschie, 1912).

Distribution: Middle East to India.

Further research is required to establish the geographical variation of *Caracal caracal*.

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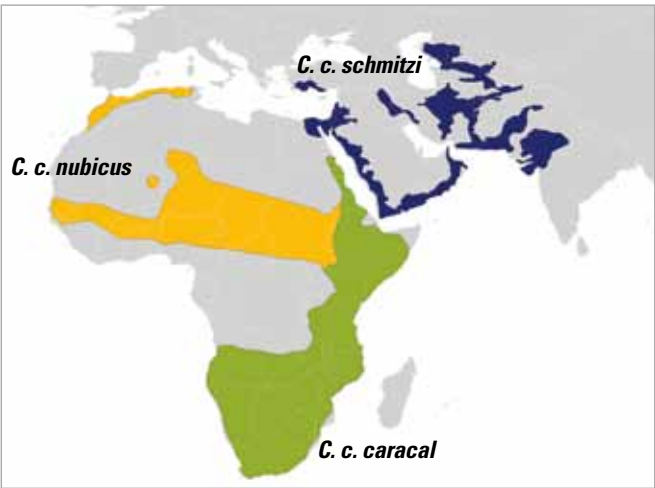
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Distribution of tentative subspecies of caracal. Borders between subspecies are speculative.

| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|-------------------------------------|------------|-----------|--------------|-----------|---------------------|
| <i>Caracal caracal caracal</i> | ++ | ++ | ++ | | |
| <i>Caracal caracal nubicus</i> | ? | ? | + | | Possible subspecies |
| <i>Caracal caracal algira</i> | + | 0 | 0 | | |
| <i>Caracal caracal lucani</i> | + | 0 | 0 | | |
| <i>Caracal caracal poecilotis</i> | + | 0 | 0 | | |
| <i>Caracal caracal damarensis</i> | + | 0 | 0 | | |
| <i>Caracal caracal limpopoensis</i> | + | 0 | 0 | | |
| <i>Caracal caracal schmitzi</i> | + | 0 | + | | Possible subspecies |



Caracal in Yemen (Photo S. Kennerknecht/pumapix).

Subfamily Pantherinae Pocock, 1917; 332.**Panthera lineage.****Genus *Neofelis* Gray 1867; 265.**

Until recently, *Neofelis* was regarded as a monotypic genus. For example, Wozencraft (2005) recognised a single species with four subspecies:

***Neofelis nebulosa nebulosa* (Griffith, 1821; 37).**

Original type locality: Unknown, possibly Canton, China.

Holotype: An animal in the Exeter 'Change, London; skin made into hats and now lost.

Neotype locality: Taran, Chumpawn, peninsular Siam [= Taran, Chumphon, peninsular Thailand].

Neotype: BMNH 1955.1644 male skin and skull designated by Christiansen & Kitchener (2011).

Distribution: China, SE Asia, Hainan.

***Neofelis nebulosa diardi* (Cuvier, 1823; 437).**

Original type locality: Java; corrected to Sumatra by Temminck (1827) as *Felis macrocelis*.

Holotype: Based on a skin and drawing by Diard sent to Cuvier in MHNH. Specimen now lost.

Neotype locality: Palembang, Sumatra.

Neotype: RMNH.MAM 1981 adult male mounted skin and skull designated by Christiansen (2009).

Distribution: Sumatra, Borneo.

***Neofelis nebulosa macrosceloides* (Hodgson in Gray, 1853; pl. 38).**

Type locality: [Nepal].

Holotype: BMNH 1845.1.8.211b skin and skull.

Distribution: Nepal, NE India, Bhutan.

***Neofelis nebulosa brachyura* (Swinhoe, 1862; 352, pl. 43).**

Type locality: Formosa [= Taiwan].

Holotype: BMNH 1862.12.24.25 skin and skull.

Distribution: Taiwan; probably extinct.

Discussion

Recent morphological and molecular studies have confirmed that there are two species of *Neofelis* (Buckley-Beason et al. 2006, Kitchener et al. 2006, Wilting et al. 2007, Christiansen 2008).

***Neofelis nebulosa* (Griffith, 1821).**

E: Mainland clouded leopard; F: Panthère longibande, panthère nébleuse; G: Festlands Nebelparder; Sp: Pantera longibanda, pantera nebulosa.



Mainland clouded leopard. (Photo J. Sanderson).

Distribution: Mainland Asia from Nepal, NE India, China, SE Asia, Taiwan and Hainan.

Diagnosis: Large cloud-like markings with generally fewer spots inside them.

The subspecific classification of *Neofelis nebulosa* needs further analyses. Hodgson described the subspecies *N. n. macrosceloides* based on a specimen from Nepal, but did not provide any description or diagnosis (Kitchener et al. 2006). Kitchener et al. (2006) did not find any support to distinguish *N. n. macrosceloides* from other mainland clouded leopards based on pelage characters. Further a very short mtDNA sequence (138 bp of ATPase 8) of Buckley-Beason et al. (2006) also showed no clear differences from that of other mainland clouded leopards. However, the length of the sequence was too short to draw robust conclusions. In contrast Christiansen's (2008) analysis of skull morphology of clouded leopards found significant differences for 13 of the 136 computed ratio variables. He concluded that these distinct morphological differences support the recognition of *N. n. macrosceloides*. However, his sample size for *macrosceloides* was very small, just three males and four females. Additional, especially molecular data, are needed here to evaluate the validity of *N. n. macrosceloides*. The distinctiveness of *N. n. brachyura* was also not supported by Kitchener et al. (2006) or by analysis of the short mtDNA fragment of Buckley-Beason et al. (2006). In addition Kitchener et al. (2006) pointed out that the original diagnosis of *brachyura* was made on the basis of a shorter tail, which is an unreliable characteristic (Pocock 1939, Kuroda 1940), especially as the holotype was a traded specimen with an incomplete tail (Kitchener et al. 2006). Therefore, the data currently available do not support the distinction of the subspecies *N. n. brachyura*.

So we propose to keep *N. nebulosa* as monotypic until we have further evidence for subspecification.

| Species | Morphology | Molecular | Biogeography | Certainty | Comments |
|---|------------|-----------|--------------|-----------|---|
| <i>Neofelis nebulosa nebulosa</i> | ++ | ++ | ++ | | |
| <i>Neofelis nebulosa macrosceloides</i> | - | (-) | - | | Possible skull differences from <i>nebulosa</i> , but could be sampling error or clinal |
| <i>Neofelis nebulosa brachyura</i> | - | (-) | + | | |

Neofelis diardi (Cuvier, 1823).

E: Sunda clouded leopard; F: Panthère longibande, panthère nébleuse;

G: Sunda Nebelparder; Sp: Pantera longibanda, pantera nebulosa.

Distribution: Sumatra, Borneo, Batu Islands.

Diagnosis: Small cloud-like markings with generally many small spots inside them.

A recent molecular and morphological analysis of *N. diardi* showed that Bornean and Sumatran animals are sufficiently distinct to warrant recognition as separate subspecies, and hence a new subspecies was described from Borneo (Wilting et al. 2011). The name *borneensis* for this new subspecies had been previously published as a *nomen nudum* (Wilting et al. 2007). However, no such variation was detected among mainland animals including those from Taiwan.

Neofelis diardi diardi (Cuvier, 1923).

Distribution: Sumatra and Batu Islands.

Distinguishing characters: See *N. d. borneensis*.

Neofelis diardi borneensis Wilting, Christiansen, Kitchener, Kemp, Ambu and Fickel, 2011; 327.

Type locality: Baram, Sarawak, Borneo.

Holotype: BMNH 1903.4.9.2 female skin and skull.

Distribution: Borneo.

Distinguishing characters: Differs from nominal subspecies, *N. d. diardi*, in the following craniomandibular and dental characters; greater width across the nasal aperture and mastoid processes, and shorter pterygoid palate relative to condylobasal skull length; pterygoid palate narrow; shorter paracone length and narrower across the protocone relative to P4 length than in *N. d. diardi*; and longer and taller p4 protoconid relative to p4 length than *N. d. diardi*. Pelage diagnosis is provisional; more frequent and bolder, cloud spots, larger, more angular cloud-like blotches than in *N. d. diardi*, which particularly in shoulder region are intermediate in size between those of *N. d. diardi* and *N. nebulosa*. Cloud-like blotches tend to have thicker black borders, and neck and shoulder stripes tend to be thicker than in *N. d. diardi*. Ground colour tends towards grey with yellowish tinge, whereas Sumatran animals have a tendency towards tawny too. A few fixed nucleotide differences distinguish it from *N. d. diardi* (Wilting et al. 2011).

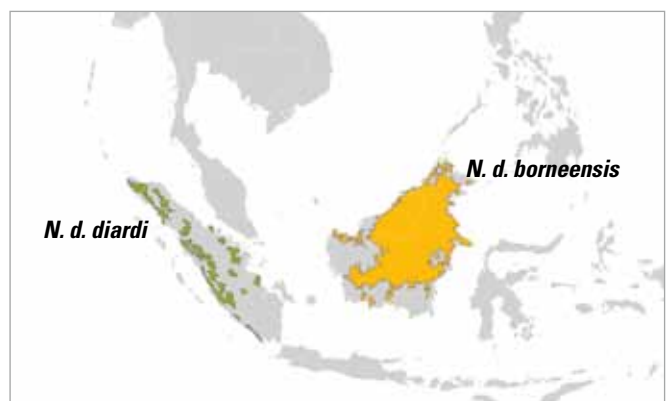
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Distribution of subspecies of Sunda clouded leopard.

| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|-----------------------------------|------------|-----------|--------------|-----------|--|
| <i>Neofelis diardi diardi</i> | ++ | ++ | ++ | | |
| <i>Neofelis diardi borneensis</i> | + | ++ | ++ | | Skulls distinguishable between subspecies, but pelage variation poorly known |

Genus *Panthera* Oken, 1816; 1052.

This genus contains five species, including the largest known felid species.

Panthera tigris

E: Tiger; F: Tigre; G: Tiger; Sp: Tigre.

Few species have received so much scientific attention regarding subspecific taxonomy as the tiger. Wozencraft (2005) recognised eight subspecies:

Panthera tigris tigris (Linnaeus, 1758; 41).

Locality from where the species was first described: Asia; restricted by Thomas (1911) to Bengal [India].

Holotype: None designated.

Distribution: India, Pakistan, Bangladesh, Bhutan, Nepal.

Panthera tigris virgata (Illiger, 1815; 90, 98).

Locality from where the subspecies was first described: in Persien und am Kaspischen Meere [in Persia and the Caspian Sea]; restricted by Harper (1940) to the Province of Mazanderan, northern Persia [= Iran].

Holotype: None designated.

Distribution: Caspian region (Turkmenistan, south Azerbaijan, northern Iran), Uzbekistan, Tadjikistan, Afghanistan, China (Tarim Basin, Lobnor). Extinct.

Panthera tigris altaica (Temminck, 1844; 43).

Type locality: la Corée (Korai) [= Korea].

Holotype: RMNH.MAM f or 13.

Distribution: Russian Far East, NE China, Korea.

Panthera tigris sondaica (Temminck, 1844; 43).

Type locality: Java.

Lectotype: RMNH.MAM c or 39216 female mounted skin.

Distribution: Java (extinct).

Panthera tigris amoyensis (Hilzheimier, 1905; 598).

Type locality: Hankau in China [= Hankou, China].

Syntypes: MZS Mam03305, Mam03306, Mam03307, Mam03308, Mam0311 five skulls.

Distribution: China (extinct in wild).

Panthera tigris balica (Schwarz, 1912; 325).

Type locality: Bali.

Holotype: SMF 2576 female skull and skin.

Distribution: Bali (extinct).



Panthera tigris sumatrae Pocock, 1929; 535, pl. H (live animal), pls. 1C and 1D (skull).

Type locality: Deli in Sumatra.

Holotype: BMNH 1912.11.10.1 male skin and skull.

Distribution: Sumatra.

Panthera tigris corbetti Mazák, 1968; 105.

Type locality: Quang-Tri, Annam [= Vietnam].

Holotype: BMNH 1933.4.1.203 male skin and skull.

Distribution: Indochina, S China.

A further molecular study, based on 4kb of mtDNA sequences and 30 nuclear microsatellites markers, apparently distinguished a further subspecies from the Malay Peninsula (Luo et al. 2004), which was named:

Panthera tigris jacksoni Luo et al., 2004: 2275.

Type locality: Melaka, Malaysia.

Holotype: Zoo Melaka #12 live male.

However, there is no description or definition (genetic or morphological distinction) of the subspecies *Panthera tigris* "jacksoni" that makes the name available (Article 13 of the International Code of Zoological Nomenclature) and, indeed, the authors state "the taxonomic diagnosis will be described elsewhere".

Under the Code, a holotype or syntypes must be fixed for a new name to be available (Article 72.3). However, it is not absolutely necessary for there to be (an) existing specimen(s) (Article 73.1.4). Thus, a live animal would be acceptable as the type.

Therefore, this subspecies has not been named in accordance with the rules of the ICZN and is a *nomen nudum*.

Discussion

There have been several molecular and morphological studies of tigers, which have come to different conclusions regarding numbers of subspecies, which vary from two to three up to eight or nine (Cracraft et al. 1998, Kitchener 1999, Kitchener & Dugmore 2000, Luo et al. 2004, 2010, Driscoll et al. 2009, Wentzel et al. 1999, Mazák & Groves 2006, Mazák 2010, Kitchener & Yamaguchi 2010, Xue et al. 2015, Wilting et al. 2015). The most significant of these is Driscoll et al. (2009) who demonstrated a 1 bp fixed difference between *virgata* and *altaica* across a total of 1,257 bp of five partially sequenced mtDNA genes, and tentatively suggested that they should be treated as consubspecific.

Luo et al. (2010) provide a comprehensive review of tiger phylogeography, but there were no data available for the extinct Javan and Balinese tigers, although it seems likely that based on skull and pelage morphology that these are consubspecific (Kitchener & Yamaguchi 2010, Mazák 2009). The taxonomic status of tigers in Indochina and the Malay Peninsula is still unclear; “*jacksoni*” is diphyletic, based on mtDNA, and must have originated very recently from *corbetti*. Subspecies *corbetti* shows further genetic structure which does not appear to have geographical significance (Luo et al. 2004). However, we should be wary of conclusions based only on living tiger populations. Mondol et al. (2013) showed that modern Indian tiger populations show increased population structure compared with historical samples, indicating a loss of mtDNA and microsatellite diversity, owing to local extirpation and genetic drift.

Recently, two studies have elucidated the relationships between Sunda Island tigers. Xue et al. (2015) showed that *balica*, *sondaica* and *sumatrae* share the same genetic clade but found slight differences (similar to the differences between *virgata* and *altaica*) between the islands. A comprehensive study by Wilting et al. (2015) showed that there is no geographical structure amongst these island populations and that they even share haplotypes, and concluded that Sunda Island tigers should be considered consubspecific. Furthermore, Wilting et al. (2015) failed to find support from multiple lines of evidence for mainland subspecies (morphological, molecular and ecological data), but did support the differentiation of Sunda Island tigers. However, owing to the morphological and ecological distinctiveness of northern tigers (formerly *altaica* and *virgata*), which is due to the large gap in the geographical distribution caused by ancient to modern exploitation of tigers by humans. Wilting et al. (2015) retained these as a MU distinct from a southern (mainland) MU. Following this comprehensive study, we revise the subspecific taxonomy of the tiger as follows:

Panthera tigris tigris (Linnaeus, 1758).

Distribution: Mainland Asia, including India, Pakistan, Nepal, Bhutan, Sikkim, China, Russia, Indochina and the Malay Peninsula (includes *virgata*, *altaica*, *amoyensis*, *corbetti* and “*jacksoni*”).

Distinguishing characters: Larger size, paler pelage with fewer stripes.

Panthera tigris sondaica (Temminck, 1844).

Distribution: Sumatra and formerly Java and Bali (includes *balica*, *sumatrae*).

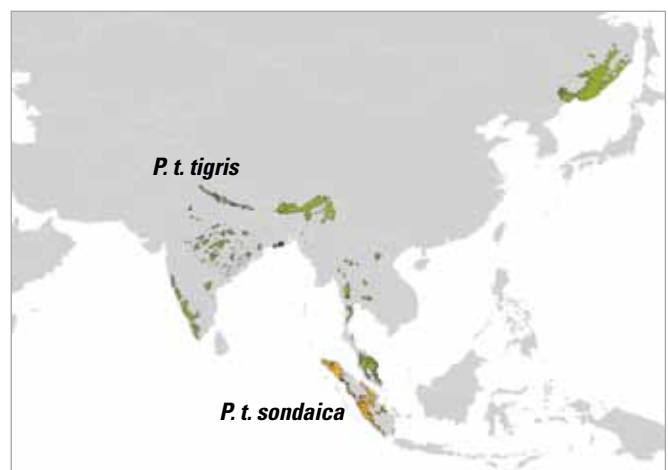
Distinguishing characters: Smaller size, darker pelage with more frequent stripes.

In contrast, Luo and Driscoll (pers. comm.) retain the classification of Wozencraft (2005) for *amoyensis*, *tigris* and *corbetti*, while recognising also *jacksoni* (Luo et al. 2004; 2010) and synonymising *altaica* with

virgata (Driscoll et al. 2009). They maintain the subspecific status of *sumatrae*, *balica* and *sondaica* (Xue et al. 2015), at least provisionally. While Xue et al. (2015) showed that *balica*, *sondaica* and *sumatrae* form a monophyletic clade that is distinctive and equidistant from all other subspecies, the authors found no shared mtDNA haplotype across the three island populations, indicating a lack of detectable gene flow among tigers on these islands, perhaps as a result of prehistoric isolation by rising sea levels. Mazák & Groves (2006) meanwhile suggested separation of the Sunda Islands tigers into two species: *sumatrae* and *sondaica*, including *balica*, based on skull morphology. Subspecies differentiation in the tiger would have resulted from geographical isolation, genetic drift and local adaptation associated with repeated restriction and expansion of habitats in the last 100,000 years. However, Kitchener (1999) and Wilting et al. (2015) showed that skull characters, such as a narrow occipital region, are shared by other putative tiger subspecies and there is complete overlap in skull morphology amongst Sunda tigers.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|-----------------------------------|------------|-----------|--------------|-----------|--|
| <i>Panthera tigris tigris</i> | ++ | ++ | ++ | | |
| <i>Panthera tigris virgata</i> | + | - | ++ | | Genetically closely related to <i>altaica</i> |
| <i>Panthera tigris altaica</i> | ++ | - | + | | Genetically closely related to <i>virgata</i> |
| <i>Panthera tigris sondaica</i> | ++ | ++ | ++ | | Genetically closely related to <i>sumatrae</i> and <i>balica</i> |
| <i>Panthera tigris amoyensis</i> | + | ?++ | | | Unique mtDNA haplotype |
| <i>Panthera tigris balica</i> | + | - | ++ | | Included in <i>sondaica</i> |
| <i>Panthera tigris sumatrae</i> | + | - | ++ | | Included in <i>sondaica</i> |
| <i>Panthera tigris corbetti</i> | + | - | - | | |
| <i>Panthera tigris 'jacksoni'</i> | + | - | + | | Diphyletic |

Panthera uncia

E: Snow leopard, ounce; F: Once, panthère de neige; G: Schneeleopard, Irbis; Sp: Leopardo nival, pantera de las nieves.

The snow leopard is usually treated as a monotypic species, *Panthera uncia*:

Panthera uncia (Schreber, 1775; pl.100; 1777; 386).

Type locality: Barbarey, Persien, Ostindien, und China; Unknown, but fixed as the Altai Mountains by Pocock (1930; 332)

Holotype: Based on specimen in Buffon (1761; 151).

Distribution: C Asia from Mongolia, Altai Mountains, Tian Shan Mountains, to Tibet, the Himalayas and Afghanistan.

Discussion

Kitchener (in Nowell & Jackson 1996) suggested that owing to its montane habitat, there may have been isolation between populations. However, there have been no phylogeographical studies of *Panthera uncia* so far. If there are sufficient concordant morphological and genetic differences between these regions, the earliest available name for the Himalayan population is:

Panthera uncia uncioides (Horsfield, 1855; 105).

Type locality: Nepal.

Holotype: Specimens in Museum of the East India Company from Hodgson

Distribution: Himalayas and Tibetan Plateau.

However, uncioides is a *nomen nudum* and the next available name for the Himalayan and Tibetan population is:

Panthera uncia schneideri Zukowsky, 1950; 213.

Type locality: Sikkim.

Holotype: A painting!

Medvedev (2000) described a new subspecies of snow leopard:

Panthera uncia baikalensisromanii (Medvedev, 2000; 29).

Type locality: Ungo River (left tributary of Khilok River) in Malkhan range, Petrovsk-Zabaikalsk District, Chita Province, Russia.

Holotype: Scientific collection of Irkutsk State Agricultural Academy, female skin.

Distribution: Southern Transbaikalia, Russia and N Khentey Mountains, Mongolia.

Comment: Originally spelt baikalensis-romanii, but scientific names containing hyphens contravene ICZN. Said to be darker and browner than Central Asian snow leopards and lacking ring-like markings except in lumbar region. Only one skin has been described in detail. It



could be an extreme individual variant; further specimens need to be examined from this region.

On the basis of the evidence so far, we recognise a monotypic species, *Panthera uncia*:

Panthera uncia (Schreber, 1775).

Distribution: C Asia, Himalayas and Tibet.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|--|------------|-----------|--------------|-----------|--|
| <i>Panthera uncia uncia</i> | ++ | ++ | ++ | | |
| <i>Panthera uncia schneideri</i> | (+) | o | ++ | | Possibly distinct; molecular study urgently required |
| <i>Panthera uncia baikalensisromanii</i> | + | o | o | | Probably not distinct, data lacking; original subspecific name does not conform to ICZN rules. |

Panthera onca

E: Jaguar; F: Jaguar; G: Jaguar; Sp: Jaguar, tigre real, yaguar, tigre americano, otorongo.

Wozencraft (2005) recognised nine subspecies of jaguar:

Panthera onca onca (Linnaeus, 1758; 42).

Locality from where the species was first described: America meridionali; fixed by Thomas (1911; 136) as Pernambuco [Brazil].

Holotype: None designated.

Distribution: E Brazil to W and N Amazon.

Panthera onca arizonensis (Goldman, 1932; 144).

Type locality: near Cibecue, Navajo County, Arizona [USA].

Holotype: USNM 244507 male skin and skull.

Distribution: Arizona, Sonora and New Mexico, USA.

Panthera onca centralis (Mearns, 1901; 139).

Type locality: Talamanca, Costa Rica.

Holotype: USNM 14177 male skull.

Distribution: From Colombia to El Salvador and Nicaragua.

Panthera onca goldmani (Mearns, 1901; 142).

Type locality: Yohatlan, Campeche, Mexico.

Holotype: USNM 105930 adult skin.

Distribution: Campeche and Guatemala in Mexico.

Panthera onca hernandesii (Gray, 1857; 278, pl. 58).

Type locality: Mazatlan in Sinaloa, Mexico.

Holotype: BMNH 1867.4.5.1 skeleton, lacking skull.

Distribution: Mexico W of Central Plateau.

Panthera onca palustris (Ameghino, 1888; 473).

Type locality: en el pampeano superior de Córdoba y en el pampeano lacustre de Luján [= from the Upper Pampean of Córdoba and on the Lake Pampean of Lujan].

Holotype: MLP 10-9 fossil mandible (Ameghino 1889). The skull is MLP 10-3 and it is not considered the type in the MLP collection.

Distribution: Matto Grosso, Paraguay and adjoining Paraná Valley, Entre Rios, NE Argentina.

Panthera onca paraguensis (Hollister, 1914; 169).

Type locality: Paraguay.

Holotype: USNM 4218 male skull.

Distribution: Paraguay, Parana Valley, Brazil and N Argentina.

Panthera onca peruviana (de Blainville, 1843; pl.8).

Type locality: Peru; fixed as probably from the coastal region by Nelson & Goldman (1933).

Holotype: MNHN-ZM-AC-1930-74 female incomplete skeleton.

Distribution: Peru and Bolivia.

Panthera onca veraecrucis (Nelson and Goldman, 1933; 236).

Type locality: San Andres Tuxtla, Vera Cruz, Mexico.

Holotype: USNM 67403 adult male skull.

Distribution: Central America E of Central Plateau to Texas, USA.

**Discussion**

Larson (1997) carried out a morphometric analysis of jaguar skulls from throughout their range, but was unable to discern a morphogeographical pattern. Eizirik et al. (2001) carried out a molecular study on mtDNA control region and 29 microsatellites of 44 jaguars from throughout most of the species' range. There was no major phylogeographical structure, but four incompletely isolated phylogeographical groups were found, including Mexico and Guatemala, southern Central America, and further groups north and south of the Amazon. Garcia et al. (2013) analysed 248 jaguars from most of the species' range for 12 microsatellite loci and three mitochondrial genes (NADH5, 16S rRNA and ATP8), but no phylogeographical structuring could be found.

Therefore, we conclude that the jaguar is a monotypic species:

Panthera onca (Linnaeus, 1758).

Distribution: Central and South America, from Arizona to northern Argentina.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|----------------------------------|------------|-----------|--------------|-----------|-------------------|
| <i>Panthera onca onca</i> | ++ | ++ | ++ | | Monotypic species |
| <i>Panthera onca arizonensis</i> | + | - | - | | |
| <i>Panthera onca centralis</i> | + | - | - | | |
| <i>Panthera onca goldmani</i> | + | - | - | | |
| <i>Panthera onca hernandesii</i> | + | - | - | | |
| <i>Panthera onca palustris</i> | + | - | - | | |
| <i>Panthera onca paraguensis</i> | + | - | - | | |
| <i>Panthera onca peruviana</i> | + | - | - | | |
| <i>Panthera onca veraecrucis</i> | + | - | - | | |

Panthera leo

E: Lion; F: Lion; G: Löwe; Sp: León.

Wozencraft (2005) recognised 11 subspecies of lion:

Panthera leo leo (Linnaeus, 1758; 41).

Locality from where the species was first described: Africa; restricted to the Barbary coast region of Africa, or more explicitly, Constantine, Algeria (Allen 1924).

Holotype: None designated.

Distribution: N Africa.

Panthera leo azandica (Allen, 1924; 224, pls. 37-40).

Type locality: Vankerckhovenville, northeastern Belgian Congo [= Democratic Republic of Congo].

Holotype: AMNH M-52084 adult male skull and skin.

Distribution: NE Democratic Republic of Congo and W Uganda.

Panthera leo bleyenberghi (Lönnberg, 1914; 273).

Type locality: Katanga [= Luapula and Luombwa rivers, Katanga, Democratic Republic of Congo, 10 S — 29 E].

Holotype: RMCA 1220 male skin and skull.

Distribution: Namibia, Angola, Democratic Republic of Congo, W Zambia, W Zimbabwe and N Botswana.

Panthera leo hollisteri (Allen, 1924; 229).

Type locality: Lime Springs, Sotik, British East Africa [= Kenya].

Holotype: USNM 181568 adult male skin and skull.

Distribution: Kenya.



Panthera leo kamptzi (Matschie, 1900; 92).

Type locality: Yoko am oberen Sanaga [= Yoko, Upper Sanaga River, Cameroon].

Holotype: ZMB Mam female skin and skull.

Distribution: Cameroon.

Panthera leo krugeri (Roberts, 1929; 91).

Type locality: Brixton, No. 286, Sabi Game Reserve (Kruger National Park).

Holotype: TM 4400? male skin and skull; type skull not found in June 2016, but also there are uncertainties as to which of the type series (TM 4400-4403) is the type, owing to inconsistencies in published and unpublished collecting dates (T. Kearney, pers. comm.).

Distribution: South Africa.

Panthera leo massaica (Neumann, 1900; 550).

Type locality: Kibaya Massai-Land [Tanzania].

Holotype: ZMB Mam 55352 male skin and skull.

Distribution: Tanzania.

Panthera leo melanochaita (Hamilton Smith, 1842; 177, pl. 10).

Locality from where the subspecies was first described: The Cape of Good Hope [South Africa].

Holotype: None designated.

Distribution: Cape of Good Hope, South Africa.

Panthera leo nyanzae (Heller, 1913; 4).

Type locality: Kampala, Uganda.

Holotype: USNM 164551 adult male skin and partial skull.

Distribution: Uganda.

Panthera leo persica (Meyer, 1826; 6).

Locality from where the subspecies was first described: [Persia = Iran].

Holotype: None designated.

Distribution: SW Asia.

Panthera leo senegalensis (Meyer, 1826; 6).

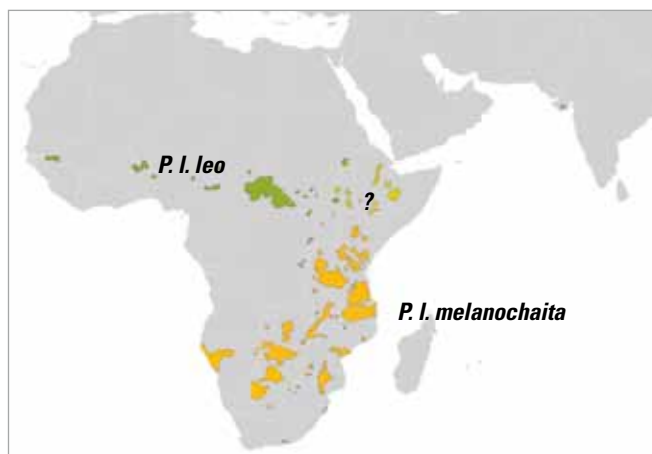
Locality from where the subspecies was first described: [Senegal].

Holotype: None designated.

Distribution: W Africa.

Discussion

There have been several recent molecular studies, which confirm that there is a clear divergence between the lions of eastern and southern Africa and those from the rest of range (e.g. Dubach et al. 2013, Barnett et al. 2014). Barnett et al. (2014) identify five phylogeographical groups, which have differentiated genetically from each other over the last c. 80,000 years. However, two of these groups are partly sympatric in southern Africa, making their recognition as separate subspecies inappropriate. The divergence of the other three groups, which range from Central and West Africa to India, has been very recent (c. 50,000 years ago or less). Asian lions, which have frequently been recognised



Distribution of subspecies of lion.

as a distinct subspecies have only colonised SW Asia within the last 20,000 years. However, this is far earlier than the suggestion by Thapar et al. (2013) that lions were introduced to India from East Africa from the 17th Century by the Mughals. Mazák (2010) analysed craniometric variation, although some populations were poorly represented, e.g. West Africa, and found a broadly similar pattern of variation with the main differentiation in skull shape being between lions in southern and eastern Africa and those in the rest of the range. Bertola et al. (2011, 2016) have confirmed this basic pattern of differentiation into two subspecies based on genetic data; one from south and east Africa and one from the rest of the range. The contact zone is somewhere in Ethiopia.

On the basis of these recent studies, we recognise two subspecies, although morphological diagnoses are currently unknown:

Panthera leo leo (Linnaeus, 1758).

Distribution: Central and West Africa and India; formerly throughout North Africa, SE Europe, the Middle East, Arabian Peninsula, SW Asia.

Panthera leo melanochaita (Hamilton Smith 1842).

Distribution: Southern and eastern Africa.

| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|----------------------------------|------------|-----------|--------------|-----------|----------|
| <i>Panthera leo leo</i> | ++ | ++ | ++ | | |
| <i>Panthera leo azandica</i> | + | - | 0 | | |
| <i>Panthera leo bleyenberghi</i> | + | - | 0 | | |
| <i>Panthera leo hollisteri</i> | + | - | 0 | | |
| <i>Panthera leo kamptzi</i> | + | - | 0 | | |
| <i>Panthera leo krugeri</i> | + | - | 0 | | |
| <i>Panthera leo massaica</i> | + | - | 0 | | |
| <i>Panthera leo melanochaita</i> | ++ | ++ | ++ | | |
| <i>Panthera leo nyanzae</i> | + | - | 0 | | |
| <i>Panthera leo persica</i> | + | + | 0 | | |
| <i>Panthera leo senegalensis</i> | + | + | 0 | | |

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Panthera pardus

E: Leopard, panther; F: Leopard, panthère; G: Leopard, Panther; Sp: Leopardo, pantera.

Wozencraft (2005) recognised the following eight subspecies based mainly on the molecular study of Miththapala et al. (1996):

Panthera pardus pardus (Linnaeus, 1758; 41).

Locality from where the species was first described: "Indiis" fixed by Thomas (1911) as Egypt; see also Pocock 1930a. Conserved by Opinion 1368 (International Commission on Zoological Nomenclature 1985).
Holotype: None designated.
Distribution: Africa.

Panthera pardus delacouri Pocock, 1930b; 325, pl. XI.

Type locality: Hué in Annam [= Vietnam].
Holotype: BMNH 1928.7.1.31 female skull and skin.
Distribution: Indochina and Malay Peninsula.

Panthera pardus fusca (Meyer 1794; 394/6?).

Type locality: Bengalen [= Bengal, India].
Holotype: Specimen seen by de la Métherie in the Tower of London.
Distribution: Indian subcontinent.

Panthera pardus japonensis (Gray, 1862; 262, pl. 33).

Type locality: Japan; more likely northern China (Allen 1938; 477).



Holotype: Skin in the possession of Mr Henry Keilich.
Distribution: China.

Panthera pardus kotiya Deraniyagala 1949; 103, pl. 94a.

Type locality: Sri Lanka.
Holotype: A mounted specimen in the Colombo National Museum.
Distribution: Sri Lanka.

Panthera pardus melas (G. Cuvier, 1809; 152).

Type locality: Java.
Holotype: A living animal in the Ménagerie, Jardin des Plantes, Paris.
Distribution: Java.

Panthera pardus nimr (Hemprich and Ehrenberg 1833; gg, pl. XVII).
Type locality: Arabia; fixed by Harrison (1968) as Mountains near Qunfida, Asir, Saudi Arabia.
Syntypes: Based on a skin from Arabia and a skin from Abyssinia [= Ethiopia].
Distribution: Arabian Peninsula.

Panthera pardus orientalis (Schlegel, 1857; 23, pl. II, Fig. 13).
Type locality: Korea.
Holotype: RMNH.MAM.59135 mounted skin.
Distribution: Korea, N China, Russian Far East.

However, Wozencraft (2005) did not recognise *P. p. saxicolor* as a distinct subspecies, but Miththapala et al. (1996) and Uphyrinka et al. (2001) did recognise it as genetically distinct:

Panthera pardus saxicolor Pocock, 1927; 213.
Type locality: Asterabad in Persia [= Iran].
Holotype: BMNH 1882.11.3.4 mounted male skin and skull.
Distribution: Iran, Caucasus, Turkmenistan.

Discussion

Luo et al. (2014) published a further molecular study which included more samples from Indochina and the Malay Peninsula. The phylogeographical patterns are not clear for all putative subspecies. For example, *P. p. kotiya* is close to East Asian leopards based on mtDNA, but groups with *P. p. fusca* based on microsatellites (Uphyrinka et al. 2001). *P. p. saxicolor* also seems to group differently depending on the analysis used (Uphyrinka et al. 2001, Luo et al. 2014). Luo et al. 2014 show that *P. p. fusca* is diphyletic based on mtDNA, which was not found in previous studies. Khorozyan et al. (2006) analysed the skull morphometrics of southwest Asian leopards, and concluded that *saxicolor* and *ciscaucasica* were consubspecific, but retained *tulliana* and *millardi* as distinct. However, sample sizes were very small for some of these putative subspecies. Rozhnov et al. (2011) examined sequences of mtDNA (NADH5) and 11 microsatellites from southwest Asian leopards. They concluded that all were consubspecific from Afghanistan through Iran to the Caucasus, but no western Turkish specimens (*tulliana*) were analysed. Here *japonensis* is included in *orientalis*; there is no clear biogeographical barrier between these two forms which appear to

form a cline in northeastern Asia. As the molecular differences between continental Asian leopards are very small compared to differences in Javan leopards (*P. p. melas*; Wilting et al. 2016), there could be a case for including all Asian subspecies, excluding *melas*, in a single Asian subspecies. These conflicting results from different studies suggest that more comprehensive sampling is required from throughout the range, taking advantage of museum specimens of known provenance.

Until such a study is carried out, we propose the following conservative arrangement of subspecies:

Panthera pardus pardus (Linnaeus, 1758).

Distribution: Africa.

Comment: Although there are two principal mtDNA clades in Africa, they both occur in southern Africa and appear to be partly sympatric. Thus it would appear that no subspecies can be distinguished within Africa. However, more comprehensive sampling is needed.

Panthera pardus tulliana (Valenciennes, 1856; 1039), including *ciscaucasica*, *saxicolor*.

Type locality: Ninfi, village situé à huit lieues est de Smyrne.

Holotype: MNHN-ZM-MO-1849-20 mounted skin (skull inside).

Distribution: Turkey, Caucasus, Turkmenistan, Uzbekistan, Iran, Iraq, Afghanistan and Pakistan.

Comment: This is the earliest name for leopards from South West Asia, and hence includes *saxicolor* and *ciscaucasica*. If *tulliana* proves to be distinct from other southwest Asian leopards, *ciscaucasica* is the earliest available name.

Panthera pardus fusca (Meyer, 1794).

Distribution: Indian subcontinent, Myanmar and China.

Panthera pardus kotiya Deraniyagala 1949.

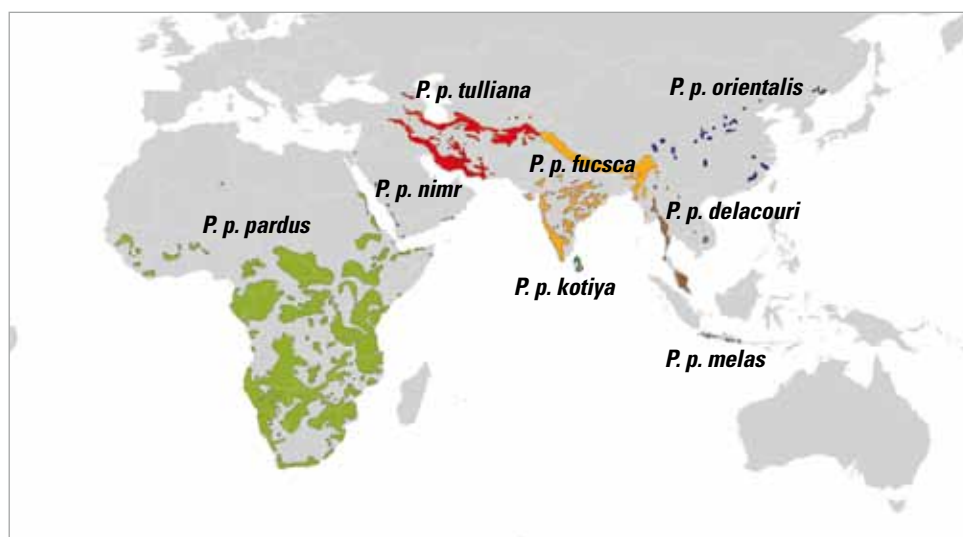
Distribution: Sri Lanka.

Panthera pardus delacouri Pocock, 1930b

Distribution: SE Asia and probably southern China

Panthera pardus orientalis (Schlegel, 1857), including *japonensis*.

Distribution: Eastern Asia from Russian Far East to China.



Distribution of tentative subspecies of leopard. Some of the borders between subspecies are speculative.

Panthera pardus melas (Cuvier, 1809; 152).

Distribution: Java.

Comment: Distinct ancient island form (Meijaard 2004, Gippoliti & Meijaard 2007, Uphyrinka et al. 2001).

Panthera pardus nimr (Hemprich and Ehrenberg, 1832).

Distribution: Arabian Peninsula.

Comment: Distinctively small form, but may prove to be consubspecific with subspecies *pardus*, although should be retained as a separate management unit if so.

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| Subspecies | Morphology | Molecular | Biogeography | Certainty | Comments |
|-----------------------------------|------------|-----------|--------------|-----------|---|
| <i>Panthera pardus pardus</i> | ++ | ++ | ++ | | |
| <i>Panthera pardus delacouri</i> | + | - | + | | Possibly in <i>orientalis</i> |
| <i>Panthera pardus fusca</i> | + | + | + | | |
| <i>Panthera pardus japonensis</i> | + | + | 0 | | Included in <i>orientalis</i> |
| <i>Panthera pardus kotiya</i> | + | + | ++ | | Possibly in <i>fusca</i> |
| <i>Panthera pardus melas</i> | ++ | ++ | ++ | | Distinct basal subspecies |
| <i>Panthera pardus nimr</i> | ++ | + | ++ | | Possibly in <i>pardus</i> |
| <i>Panthera pardus orientalis</i> | ++ | ++ | + | | Includes <i>japonensis</i> |
| <i>Panthera pardus tulliana</i> | ++ | + | + | | Includes <i>ciscaucasica</i> , <i>saxicolor</i> |

**Revised taxonomy of the Felidae (2 subfamilies,
8 lineages, 14 genera, 41 species, 80 subspecies)**

Subfamily Pantherinae

Panthera lineage (2 genera, 7 species, 14 subspecies)

Panthera leo leo (Linnaeus, 1758)
melanochaita (Hamilton Smith,) 1842

Panthera onca (Linnaeus, 1758)

Panthera pardus pardus (Linnaeus, 1758)
nimr (Hemprich and Ehrenberg, 1832)
delacouri Pocock, 1930
fusca (Meyer, 1794)
kotiya Deraniyagala, 1949
melas (Cuvier, 1809)
orientalis (Schlegel, 1857)
tulliana (Valenciennes, 1856)

Panthera tigris tigris (Linnaeus, 1758)
sondaica (Temminck, 1844)

Panthera uncia (Schreber, 1775)

Neofelis diardi diardi (Cuvier, 1923)
borneensis Wilting, Christiansen, Kitchener,
Kemp, Ambu and Fickel 2011

Neofelis nebulosa (Griffith, 1821)

Puma lineage (3 genera, 3 species, 6 subspecies).

Puma concolor concolor (Linnaeus, 1771)
cougar (Kerr, 1792)

Acinonyx jubatus jubatus (Schreber, 1775)
hecki Hilzheimer 1913
soemmeringii (Fitzinger, 1855)
venaticus (Griffith, 1821)

Herpailurus yagouaroundi (É. Geoffroy Saint-Hilaire, 1803)

Caracal lineage (2 genera, 3 species, 8 subspecies).

Caracal aurata aurata (Temminck, 1827)
celidogaster (Temminck, 1827)

Caracal caracal caracal (Schreber, 1776)
nubicus (J. B. Fischer, 1829)
schmitzi (Matschie, 1912)

Leptailurus serval serval (Schreber, 1777)
constantina (Forster, 1780)
lipostictus (Pocock, 1907)

Bay cat lineage (2 genera, 3 species, 4 subspecies)

Catopuma badia (Gray, 1874)

Catopuma temminckii temminckii (Vigors and Horsfield, 1827)
moormensis (Hodgson, 1831)

Pardofelis marmorata marmorata (Martin, 1837)
longicaudata (Blainville, 1843)

Ocelot lineage (1 genus, 8 species, 16 subspecies).

Leopardus colocola colocola (Molina, 1782)
braccatus (Cope, 1889)
munoi (Ximénez, 1961)
budini (Pocock, 1941)
garleppi (Matschie, 1912)
pajeros (Desmarest, 1816)
wolffsohni (Garcia-Perea, 1994)

Leopardus geoffroyi (d'Orbigny and Gervais, 1844)

Leopardus guigna guigna (Molina, 1782)
tigrillo (Schinz, 1844)

Leopardus guttulus (Hensel, 1872)

Leopardus jacobita (Cornalia, 1865)

Leopardus pardalis pardalis (Linnaeus, 1758)
mitis (Cuvier, 1820)

Leopardus tigrinus tigrinus (Schreber, 1775)
oncilla (Thomas, 1903)

Leopardus wiedii wiedii Schinz, 1821
glauculus (Thomas, 1903)
vigens (Thomas, 1904)

Lynx lineage (1 genus, 4 species, 8 subspecies).

Lynx canadensis (Kerr 1792)

Lynx lynx lynx (Linnaeus 1758)
balcanicus (Bureš 1941)
carpathicus Heptner, 1972
dinniki Satunin 1915
isabellinus (Blyth, 1847)
wrangeli Ognev, 1928

Lynx pardinus (Temminck, 1827)

Lynx rufus rufus (Schreber, 1777)
fasciatus (Rafinesque, 1817)

Leopard cat lineage (2 genera, 6 species, 14 subspecies)

- Prionailurus bengalensis bengalensis* (Kerr, 1792)
euptilurus (Elliot, 1871)
- Prionailurus javanensis javanensis* (Desmarest, 1816)
borneoensis Brongersma, 1935
heaneyi Groves, 1997
rabori Groves, 1997
sumatranus (Horsfield, 1821)
- Prionailurus planiceps* (Vigors and Horsfield 1827)
- Prionailurus rubiginosus rubiginosus* (L. Geoffroy Saint-Hilaire, 1831).
koladivius Deraniyagala, 1956
phillipsi Pocock, 1939
- Prionailurus viverrinus viverrinus* (Bennett, 1833)
rhizophoreus Sody, 1936
- Otocolobus manul manul* (Pallas, 1776)
nigripectus (Hodgson, 1842)

Domestic cat lineage (1 genus, 7 species, 10 subspecies)

- Felis bieti* Milne-Edwards, 1892
- Felis catus* Linnaeus, 1758
- Felis chaus chaus* Schreber, 1777
affinis Gray, 1830
fulvidina Thomas, 1928
- Felis lybica lybica* Forster, 1780
cafra Desmarest, 1822
ornata Gray, 1830
- Felis margarita margarita* Loche, 1858
thinobia (Ognev, 1927)
- Felis nigripes* Burchell, 1824
- Felis silvestris silvestris* Schreber, 1777
caucasica Satunin, 1905



Research priorities

Designation of neotypes or lectotypes for those taxa lacking holotypes

- *Caracal caracal nubicus* (J. B. Fischer, 1829)
- *Felis chaus* Schreber, 1777
- *Felis silvestris* Schreber, 1777
- *Leopardus colocola* (Molina, 1782)
- *Leopardus guigna* (Molina, 1782)
- *Leopardus guigna tigrillo* (Schinz, 1844)
- *Leopardus pardalis* (Linnaeus, 1758)
- *Lynx canadensis* Kerr, 1792
- *Lynx lynx* (Linnaeus, 1758)
- *Lynx rufus* (Schreber, 1777)
- *Lynx rufus fasciatus* (Rafinesque, 1817)
- *Lynx rufus floridanus* (Rafinesque, 1817)
- *Otocolobus manul* (Pallas, 1776)
- *Panthera leo* (Linnaeus, 1758)
- *Panthera leo melanochaita* (Hamilton Smith, 1842)
- *Panthera leo senegalensis* (Meyer, 1826)
- *Panthera onca* (Linnaeus, 1758)
- *Panthera pardus* (Linnaeus, 1758)
- *Panthera tigris* (Linnaeus, 1758)
- *Panthera tigris virgata* (Illiger, 1815)

Further research into taxonomic status to determine number of species or relationships with related taxa

- *Felis bieti* – relationship with *Felis silvestris* and *F. lybica*
- *Felis lybica* – does this comprise three species?
- *Pardofelis marmorata* – can more than one species be recognised cf. *Neofelis*?
- *Prionailurus bengalensis* and *P. javanensis* – where is the boundary between the two species?
- *Leopardus colocola* – can more than one species be recognised?
- *Leopardus tigrinus* – can more than one species be recognised?

Morphological and molecular studies on species of high conservation concern

- *Acinonyx jubatus* – a more comprehensive molecular study required in combination with morphological analyses
- *Caracal aurata* – determination of number of subspecies, if any, and their geographical distribution from molecular analyses
- *Catopuma temminckii* – confirmation of two subspecies through molecular analysis and their morphological differentiation and geographical distribution
- *Felis silvestris* – determination of number of subspecies, especially in Europe through molecular and morphological analyses
- *Leopardus colocola* – determination of number of subspecies through comprehensive molecular, morphological and biogeographical analyses
- *Leopardus jacobita* – determination as to whether this monotypic species is in fact four or more subspecies through more comprehensive molecular and morphological analyses
- *Neofelis nebulosa* – confirmation as to whether this



Black serval, Aberdares, Kenya (Photo L. Bahaa-el-Din).

is a monotypic species or not through molecular and morphological analyses

- *Panthera leo* – further molecular analyses combined with morphology
- *Panthera pardus* – more comprehensive molecular analyses, especially using historical samples, to determine numbers of subspecies throughout range
- *Panthera uncia* – confirmation of whether this species is monotypic or not, based on comprehensive molecular and morphological analyses
- *Pardofelis marmorata* – confirmation of two or more subspecies based on combined molecular and morphological analyses
- *Prionailurus planiceps* – investigation if inter-island variation using molecular and morphological analyses
- *Prionailurus viverrinus* – determination of geographical variation, especially disjunct Javan population, using molecular and morphological variation

Morphological and molecular studies on species of low conservation concern

- *Caracal caracal* – basic phylogeographical study required to examine geographical variation
- *Felis chaus* – basic phylogeographical study required to examine geographical variation
- *Felis lybica* – more comprehensive phylogeographical study required combined with morphological analyses
- *Felis margarita* – basic phylogeographical study required to examine geographical variation
- *Felis nigripes* – basic phylogeographical study required to examine geographical variation
- *Leopardus pardalis* – more comprehensive phylogeographical study required to examine geographical variation throughout range
- *Leopardus wiedii* – more comprehensive phylogeographical study required to examine geographical variation throughout range
- *Leopardus tigrinus* – more comprehensive phylogeographical study required to examine geographical variation throughout range

- *Leptailurus serval* – basic phylogeographical study required to examine geographical variation
- *Lynx lynx* – more comprehensive phylogeographical study required to examine geographical variation throughout range combined with morphological analyses
- *Otocolobus manul* – basic phylogeographical study required to examine geographical variation
- *Prionailurus bengalensis* – more comprehensive phylogeographical study required to examine geographical variation throughout range combined with morphological analyses
- *Prionailurus javanensis* – comprehensive phylogeographical study required to examine geographical variation throughout range combined with morphological analyses
- *Prionailurus rubiginosus* – basic phylogeographical study required to examine geographical variation, especially in Sri Lanka

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Glossary

Holotype – The single specimen or other element used or designated as the type specimen of a species or subspecies in the original published description of the taxon.

Lectotype – A biological specimen or other element that is selected as the type specimen when a holotype was not originally designated.

Neotype – A biological specimen or other element that is selected as the type specimen when the holotype, lectotype, and any syntypes or paratypes have been lost or destroyed.

Syntype – One of two or more biological specimens or other elements simultaneously designated as type specimens in the original published description of a species or subspecies.

Nomen nudum – The term is used to indicate a designation which looks exactly like a scientific name of an organism, and may well have originally been intended to be a scientific name, but fails to be one because it has not (or has not yet) been published with an adequate description (or a reference to such a description), and thus is a “bare” or “naked” name, one which cannot be accepted as it currently stands.

Because a nomen nudum fails to qualify as a formal scientific name, a later author can publish a real scientific name that is identical in spelling. If one and the same author puts a name in print, first as a nomen nudum and later on publishes it for real, accompanied by a description that does meet the formal requirements, then the date of publication of the latter, formally correct publication becomes the name’s date of establishment.



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