















REVIEW

Towards resolving taxonomic uncertainties in wolf, dog and jackal lineages of Africa, Eurasia and Australasia

M. Krofel¹ , J. Hatlauf² , W. Bogdanowicz³ , L. A. D. Campbell⁴ , R. Godinho^{5,6,7} ,
Y. V. Jhala⁸ , A. C. Kitchener⁹ , K.-P. Koepfli^{10,11,12} , P. Moehlman¹³ , H. Senn¹⁴ ,
C. Sillero-Zubiri^{15,16,17} , S. Viranta¹⁸ , G. Werhahn^{16,19}  & F. Alvares^{20,21} 

¹Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia

²University of Natural Resources and Life Sciences, Vienna, Department of Integrative Biology and Biodiversity Research, Institute of Wildlife Biology and Game Management, Vienna, Austria

³Museum and Institute of Zoology, Polish Academy of Sciences, Warszawa, Poland

⁴Department of Zoology, Recanati-Kaplan Centre; Tubney, University of Oxford Wildlife Conservation Research Unit, Oxfordshire, UK

⁵InBIO Laboratório Associado, Campus de Vairão, CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Vairão, Portugal

⁶BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Vairão, Portugal

⁷Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Porto, Portugal

⁸Animal Ecology & Conservation Biology, Wildlife Institute of India, Dehradun, India

⁹Department of Natural Sciences, National Museums Scotland, Edinburgh, UK

¹⁰Smithsonian-Mason School of Conservation, George Mason University, Front Royal, VA, USA

¹¹Smithsonian Conservation Biology Institute, Center for Species Survival, National Zoological Park, Front Royal, VA, USA

¹²Computer Technologies Laboratory, ITMO University, St. Petersburg, Russia

¹³IUCN/SSC Equid Specialist Group, Tanzania Wildlife Research Institute (TAWIRI), EcoHealth Alliance and The Earth Institute, Columbia University, Arusha, Tanzania

¹⁴WildGenes Laboratory, Conservation and Science Programmes, Royal Zoological Society of Scotland, RZSS, Edinburgh, UK

¹⁵Wildlife Conservation Research Unit, Zoology, University of Oxford, Tubney, UK

¹⁶IUCN SSC Canid Specialist Group, Oxford, UK

¹⁷Born Free Foundation, Horsham, UK

¹⁸Faculty of Medicine, University of Helsinki, Helsinki, Finland

¹⁹Wildlife Conservation Research Unit, Zoology, University of Oxford, Tubney, UK

²⁰CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Universidade do Porto, Vairão, Portugal

²¹BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Vairão, Portugal

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Correspondence

Jennifer Hatlauf, University of Natural Resources and Life Sciences, Vienna, Department of Integrative Biology and Biodiversity Research, Institute of Wildlife Biology and Game Management, Gregor-Mendel Strasse 33, 1180 Vienna, Austria.
Email: jennifer.hatlauf@boku.ac.at; hatlauf@hotmail.com

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Abstract

Successful conservation depends on accurate taxonomy. Currently, the taxonomy of canids in Africa, Eurasia and Australasia is unstable as recent molecular and morphological studies have questioned earlier phenetic classifications. We review available information on several taxa of Old World and Australasian *Canis* with phylogenetic uncertainties (namely, African jackals, Asian wolves and Australasian dogs), in order to assess the validity of suggested scientific names and provide a scientific basis for reaching a taxonomic consensus primarily based on molecular data, but also including morphology, biogeography and behavioural ecology. We identify major knowledge gaps, provide recommendations for future research and discuss conservation implications of an updated taxonomic framework. Recent molecular studies indicate that the former Afro-Eurasian ‘golden jackal’ represents two distinct lineages, the golden jackal (*Canis aureus*) from Eurasia and the African wolf (*C. lupaster*) from Africa. Phylogenetic research also indicates that the side-striped and black-backed jackals form a monophyletic group that branched earlier than *Canis*, *Cuon* and *Lycaon*, which should be reassigned to the genus *Lupulella* as *L. adusta* and *L. mesomelas*, respectively. The Himalayan/Tibetan and Indian wolf lineages appear to have diverged earlier and are distinct from all other grey wolves (*C. lupus*) based on mitochondrial and nuclear genome data. However, until genome-wide data from multiple individuals across the range clarify relationships with other taxa, we suggest referring to the Himalayan/Tibetan wolf lineage

as *Canis lupus chanco*. We support the currently accepted nomenclature for the Indian wolf *Canis lupus pallipes* for the wolf populations found on the Indian sub-continent and possibly also in south-western Asia (exact geographical boundary pending). The information presented here provides a current and consistent taxonomic framework for use by conservationists and other practitioners, but it is also intended to stimulate further research to resolve current uncertainties affecting the taxonomy of Old World canids.

Background

Successful conservation depends on a stable and accurate taxonomy of species, in order to ensure that resources and actions are accurately directed for population recovery, and that national and international legislation can be implemented to prevent illegal trade and exploitation (Waples *et al.*, 2018; Zhou *et al.*, 2016). However, unresolved taxonomies and contradictory information scattered throughout the literature can create confusion and result in erroneous assessments of conservation status and prevent effective implementation of legislation, which can have serious implications for species at risk of extinction (Vogel Ely *et al.*, 2017; Zhou *et al.*, 2016). Erroneous taxonomies can also hinder ecological research, which further limits our ability to develop effective conservation schemes (Isaac *et al.*, 2004). Although taxonomic changes can have unpredictable impacts on conservation, improved understanding of evolutionary relationships is always an important addition to our knowledge about the organisms that require conservation action (Morrison *et al.*, 2009).

Advances in genetics and genomics are rapidly improving our understanding of the evolutionary relationships among species and have revealed numerous new cryptic species that were difficult to distinguish morphologically or are represented by inadequate sample sizes (Bickford *et al.*, 2007; Struck *et al.*, 2018). The taxonomy of species within the genus *Canis* (Canidae) is a good example of controversy caused by recent advances in molecular research. Taxonomy of this group has received little attention in the past, because there was a strong adherence to traditional phenetic classifications of what were generally regarded as mostly non-threatened species. However, in recent years canid taxonomy and evolutionary relationships have gained increasing attention from the scientific community and the general public, following that modern taxonomy should be primarily based on phylogeny (Dayrat, 2005). Recent genetic and genomic research suggests that phylogenetic relationships among taxa are often different from those traditionally accepted for this group (e.g. Gopalakrishnan *et al.*, 2018; Koepfli *et al.*, 2015; Viranta *et al.*, 2017). This is increasingly leading to controversies about canid nomenclature, with researchers, conservationists and decision-makers struggling to reach a consensus (e.g. Alvares *et al.*, 2019; Dinets, 2015; Zrzavý *et al.*, 2018). The long-running debate on the taxonomy of North American wolves (i.e. *Canis lupus*, *C. lycaon*, *C. rufus*), coyotes (*C. latrans*) and their hybrids typifies this situation (The National Academies of Sciences Engineering and Medicine, 2019). The outcome of such debates is

vitaly important to determine the allocation of limited resources for conservation and the implementation of legal protection of these species (e.g. under the US Endangered Species Act; Sacks *et al.*, 2021; Waples *et al.*, 2018).

Old World and Australasian members of the genus *Canis* (commonly known as wolves, dogs and jackals) have received less taxonomic attention than North American counterparts, but similar ambiguities and controversies persist. Recent insights from genetics raise the need to review their binomial nomenclature, in conjunction with species delimitation and assessment of distribution and conservation status. For example, in several recent publications (e.g. Bertè, 2017; Gippoliti & Lupi, 2020; Koepfli *et al.*, 2015; Machado & Teta, 2020; Moehlman & Hayssen, 2018; Temu *et al.*, 2016; Viranta *et al.*, 2017), including the *2nd Jackal Symposium* held in Greece in autumn 2018 (Giannatos *et al.*, 2018), up to four different scientific names have been used for the same taxon of an African canid known as the golden jackal or African (golden) wolf: *Canis aureus*, *C. anthus*, *C. lupaster* and *C. mensesi*. Such lack of a consensus on taxonomy has the potential to compromise research, conservation, management and legal implementation, especially where morphological variation is evident and poorly understood (Macdonald & Sillero-Zubiri, 2004).

As recommended in the revised taxonomy of the Felidae (Kitchener *et al.*, 2017), which has been adopted by the IUCN and CITES, at least three types of correlated evidence (e.g. from morphology, genetics, biogeography, behaviour, ecology or reproduction) are required to ascertain taxonomic certainty of taxa. If there are only one or two lines of correlated evidence, then further research is required to confirm the validity of a species. For many canid species, there are considerable knowledge gaps, especially where convergent evolution and hybridization have obscured the distinctiveness of evolutionary lineages (Macdonald & Sillero-Zubiri, 2004). Furthermore, there is often a tendency for accepting uncritically traditional classifications, which often date from the 19th and early 20th centuries and are usually based on phenotypic characters with little or no scientific basis for understanding phylogenetic relationships.

The advancement of molecular genetic techniques has helped to reveal numerous apparently cryptic species and identify interrelationships between species and populations (Bickford *et al.*, 2007), including the canid species reviewed here. The taxonomy of the genus *Canis* is further complicated by its conservative anatomy and plastic phenotypes, in combination with ancient and contemporary hybridization between several species of the genus, some species of which may even have a

hybrid origin (Gopalakrishnan et al., 2018; Kopaliani et al., 2014; Mallil et al., 2020; Moura et al., 2014; Pilot et al., 2019, 2021). Introgression may confuse interspecific relationships and it is recommended that multiple independent lines of evidence are used to distinguish evolutionary lineages that are recognized as distinct taxa on the basis of phylogeny (Frankham et al., 2012). Below we critically review the existing nomenclature, current evidence and research needs to resolve taxonomic uncertainties, and propose a working framework for the taxonomy of Old World and Australasian canids. We have adopted the traffic-light system proposed by Kitchener et al. (2017) to summarize evidence for distinguishing taxa at species level, which also highlights deficiencies in our current knowledge that need to be addressed in the future to improve our understanding of the relationships between and distinctiveness of the taxa discussed here (Table 1). Lastly, we discuss important implications of resolving taxonomic uncertainties for future conservation and management.

Golden jackals and African wolves

The African wolf/jackal (Fig. 1a) was first described scientifically in the early 19th century. Several distinct species with different geographical ranges were described, and their similarity to both wolves and jackals was often noted. Several authors were clear (e.g. de Winton, 1899) that despite its similar appearance, the golden or common jackal (*Canis aureus* Linnaeus, 1758) (Fig. 1b) does not occur in Africa. However, Schwarz (1926) placed many of the earlier described African wolf species as subspecies of *Canis aureus* from Eurasia. This was followed in Allen's (1939) *Checklist of African Mammals*. As a result, the African wolf and the Eurasian golden jackal were widely regarded as conspecific during the rest of the 20th century and early 21st century in both scientific literature and popular literature.

Analyses of skull morphometrics show some distinction between the two taxa (Ferguson, 1981; Koepfli et al., 2015; Machado & Teta, 2020; Saleh & Basuony, 2014a; Spassov, 1989; Stoyanov, 2020; Viranta et al., 2017), but robust statistical support for species-level separation has not yet been established due to a lack of comprehensive morphological studies (Table 1). A recent study by Machado and Teta (2020), using geometric morphometrics, found overlap in the skull morphology of the African wolf with both the golden jackal and Eurasian wolves, but Saleh and Basuony (2014a) and Stoyanov (2020) were able to distinguish between the skulls of golden jackals and African wolves using morphological measurements and linear discriminant analysis, respectively. A study of the metrics of howling found differences between Arabian golden jackals and African wolves from North Africa (Kershenbaum et al., 2016), although this behavioural character may have limited taxonomic significance. Multiple independent studies on skull morphometry suggest that two sympatric taxa may occur in northern and eastern Africa, which some authors have referred to as *Canis lupaster* and *Canis anthus* (Bertè, 2017; Saleh & Basuony, 2014a; Stoyanov, 2020). Complicating matters further, potential hybridization with geographically proximate populations of grey wolves, Eurasian golden jackals and

domestic dogs should also be considered (Koepfli et al., 2015; Machado & Teta, 2020; Mallil et al., 2020; Pilot et al., 2019, 2021).

Turning to genetics, both mitochondrial and nuclear genome sequence data provide several lines of evidence suggesting that Eurasian golden jackals and African wolves represent largely distinct genetic lineages, whose evolutionary histories have been independent for a considerable length of time (Table 1). Firstly, separate phylogenetic analyses of 20 autosomal DNA sequences and whole nuclear genomes, using both coalescent-based and/or concatenated-species-tree methods, show that Eurasian golden jackals and African wolves are distinct and successive monophyletic groups relative to the clade composed of Holarctic grey wolf + coyote (Chavez et al., 2019; Gopalakrishnan et al., 2018; Koepfli et al., 2015; Viranta et al., 2017). Secondly, network or phylogenetic analyses of data derived from mitochondrial genomes show that golden jackals and African wolves largely comprise separate haplotype clades, consistent with the results obtained from nuclear genomes (Gaubert et al., 2012; Gopalakrishnan et al., 2018; Koepfli et al., 2015a; Mallil et al., 2020; Rueness et al., 2011; Viranta et al., 2017). Thirdly, golden jackals and African wolves show the highest divergence in sliding-window-based pairwise comparisons of nuclear genome data among golden jackals, African wolves and grey wolves (Koepfli et al., 2015a). Fourthly, molecular dating analyses of nuclear gene or genome data suggest that the golden jackal and African wolf lineages diverged 0.5–1.5 million years ago. And finally, population genetic analyses of microsatellite loci and sequences sampled from X and Y chromosomes also indicate that golden jackals and African wolves are largely distinct genetic clusters (Chavez et al., 2019; Koepfli et al., 2015).

Despite the strong evidence for evolutionary differentiation between golden jackals and African wolves, there is also evidence that the history of these lineages has been complicated by episodes of post-speciation gene flow. For example, Koepfli et al. (2015) found that a subset of golden jackals from Israel was more closely related to African wolves than to other golden jackals based on analyses of mitochondrial and X chromosome sequences. Furthermore, this clade was the sister group to the grey wolf clade in mitochondrial analyses. *D*-statistic analyses, which detect signatures of historical gene flow among closely related species (Durand et al., 2011), using genome-wide single nucleotide polymorphisms (SNPs) also suggested historical admixture among golden jackals, African wolves and grey wolves + domestic dogs (Koepfli et al., 2015). The latter finding was explored in greater detail with genomic analyses of historical gene flow among species within the genus *Canis*, the dhole (*Cuon alpinus*) and African wild dog (*Lycaon pictus*; Gopalakrishnan et al., 2018). Using several analytical methods to detect signals of historical admixture among species, these authors found evidence of gene flow among the ancestors and lineages of the golden jackal, African wolf, grey wolf and Ethiopian wolf (*Canis simensis*). Intriguingly, analyses found evidence of gene flow from the Ethiopian wolf and grey wolf lineages into the ancestor of the African wolf lineage, suggesting that the African wolf may have originated through hybridization between the former two species

Table 1 Overview of the current evidence for the suggested taxonomic recommendations at species level for the Old World canids in this paper based on the traffic-light system for taxonomic certainty following Kitchener *et al.* (2017)

Taxon	Evidence			Taxonomic certainty	Comments	Recommended future research topics
	Morphological	Genetic	Biogeographical			
<i>Canis aureus</i>	+	++	(+)	Yellow	Multiple lines of genetic evidence, including nuclear and mitochondrial genomes, for separation from <i>C. lupaster</i> , from which it diverged 0.5–1.5 million years ago. Morphological evidence possibly confounded by ancient-to-modern introgression within <i>Canis</i> spp., which has been shown using genetic data. Largely biogeographically separated from <i>C. lupaster</i> , but cause is currently unknown.	<ul style="list-style-type: none"> -Comprehensive morphological study using modern approaches, including geometric morphometrics, and representative specimens from across the species' range -Wider geographical sampling for genetic analysis, using ancestry-based methods that account for both incomplete lineage sorting and hybridization -Further sampling especially needed from the south-western and south-eastern Asian part of species' distribution -Investigation of possible biogeographical barriers -Better understanding of introgression from other canids, especially domestic dogs -Further studies on basic biology and ecology
<i>Canis lupaster</i>	+	++	(+)	Yellow	Multiple lines of genetic evidence, including nuclear and mitochondrial genomes, for separation from <i>C. aureus</i> , from which it diverged 0.5–1.5 million years ago. Morphological evidence possibly confounded by ancient-to-modern introgression within <i>Canis</i> spp., which was confirmed using genetic data. Largely biogeographically separated from <i>C. aureus</i> , but cause currently unknown.	<ul style="list-style-type: none"> -Comprehensive morphological study using modern approaches, including geometric morphometrics, and representative specimens from across the species' range -Wider geographical sampling for genetic analysis, using ancestry-based methods that account for both incomplete lineage sorting and hybridization -Further sampling especially needed from the north-eastern part of the species' distribution -Investigation of possible biogeographical barriers -Better understanding of introgression from other canids, especially domestic dogs -Further studies on genetic diversity and structure -Identify suggested taxon <i>C. anthus</i> and establish its relationship with currently recognized taxa -Systematic morphological assessment -Wider geographical sampling, including the range core and edges, for genome-wide analysis -Understanding influence of introgression from domestic dogs and other grey wolves -Morphological and genetic analyses of the holotypes -Further studies on basic biology, ecology, distribution and conservation status
<i>Canis (lupus) chanco</i>	(+)	+(+)	+	Red	Multiple lines of genetic evidence, including from nuclear and mitochondrial genomes, supporting evolutionary diversification and basal position relative to Holarctic <i>C. lupus</i> , with which it hybridizes. Further investigation required to understand admixture from grey wolves at the range boundaries. Morphological data are lacking. Biogeographical separation from other <i>Canis</i> spp., owing to genetic adaptation to high altitude.	<ul style="list-style-type: none"> -Further studies on basic biology, ecology, distribution and conservation status

Table 1 Continued

Taxon	Evidence			Taxonomic certainty	Comments	Recommended future research topics
	Morphological	Genetic	Biogeographical			
<i>Canis (lupus) pallipes</i>	o	++	+	Red	Multiple lines of genetic evidence, including from nuclear and mitochondrial genomes, supporting evolutionary diversification and basal position in <i>C. lupus</i> . Morphological data are lacking. Biogeographical separation from other Holarctic <i>C. lupus</i>	-Systematic morphological assessment -Understanding influence of introgression from domestic dogs and other grey wolves -Establishing exact distribution range boundaries and potential hybridization zones -Wider geographical sampling, including all potential range, for genome-wide analysis and studies on genetic diversity and structure -Further studies on basic biology and conservation status

Symbol key: '++' robust evidence within category, for example skull/pelage; mtDNA/hDNA; '+' some evidence or reasonable inference within category; '-' 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. Colour code: Yellow – two or more lines of correlated evidence as outlined above plus reasonable inferences based on data from closely related species, suggesting that taxon may be distinct although further research is required; Red – one or no lines of evidence, suggesting that status of taxon is currently unknown and further research is required.

(Gopalakrishnan et al., 2018). Moreover, the analyses suggested that the north-eastern lineage of African wolves has had continuous gene flow with modern grey wolves and Ethiopian wolves. Hybridization among species within the genus *Canis* is well known, including evidence of hybridization with domestic dogs (e.g. Mallil et al., 2020; Pilot et al., 2019, 2021), although further research, especially on past and current introgression from domestic dogs, is required.

Further analyses involving wider geographical sampling of golden jackals and African wolves and using ancestry-based methods that account for both incomplete lineage sorting and hybridization, as well as divergence in regions of high versus low recombination across the genome, will help to better elucidate the history of these two lineages (Chafin et al., 2020; Paysseur & Rieseberg, 2016; Wang et al., 2018). Nevertheless, despite the possible hybrid origins of the African wolf, there is strong support for the evolutionary differentiation of golden jackals and African wolves and hence their suggested recognition as separate species.

Regarding nomenclature, the earliest available name attributed to the African wolf is *Canis anthus* Cuvier, 1820 (Koepfli et al., 2015; Maran, 2015). However, the holotype specimen may no longer exist and the identification of the species described by Cuvier is considered by some as uncertain (Viranta et al., 2017), so that it is not possible to examine the morphology and genetics of the holotype using modern methods. Anderson and De Winton (1902), among others, noted that there are two species of *Canis* in northern Africa, one wolf-like and the other smaller and jackal-like, which they called *C. lupaster* and *C. variegatus*, respectively, but they failed to assign *C. anthus* to either taxon. Because of these doubts, we suggest the use of *C. lupaster* Hemprich & Ehrenberg, 1832 following Viranta et al. (2017). Also, *C. aureus* and *C. lupaster* were recently assessed separately for the first time in the IUCN Red List of Threatened Species (Hoffmann et al., 2018; Hoffmann & Atickem, 2019). However, a detailed taxonomic review is required to establish the likely species identification of the taxon *C. anthus* and establish with as much certainty as possible its relationship with currently recognized taxa. If this taxon remains unidentifiable, a case should be made for its suppression by the International Commission on Zoological Nomenclature. Regarding the vernacular name for *C. lupaster*, although previous studies have used 'African golden wolf' (e.g. Koepfli et al. 2015), we suggest 'African wolf' for simplicity and in accordance with recent literature (e.g. Eddine et al., 2020; Gaubert et al., 2012; Mallil et al., 2020; Rueness et al., 2011).

We recommend further research to confirm the species-level distinctions reported so far and the taxonomic recommendations we have suggested for golden jackals and African wolves. In particular, we recommend comprehensive morphological analyses using modern approaches and representative specimens from across both species' ranges (Table 1). Care should be taken to ensure that specimens are correctly assigned to taxa or unwarranted taxonomic conclusions may follow (Kitchener et al., 2020; Machado & Teta, 2020), which may further disrupt taxonomies and compromise conservation efforts. If possible, genetic samples should be taken from

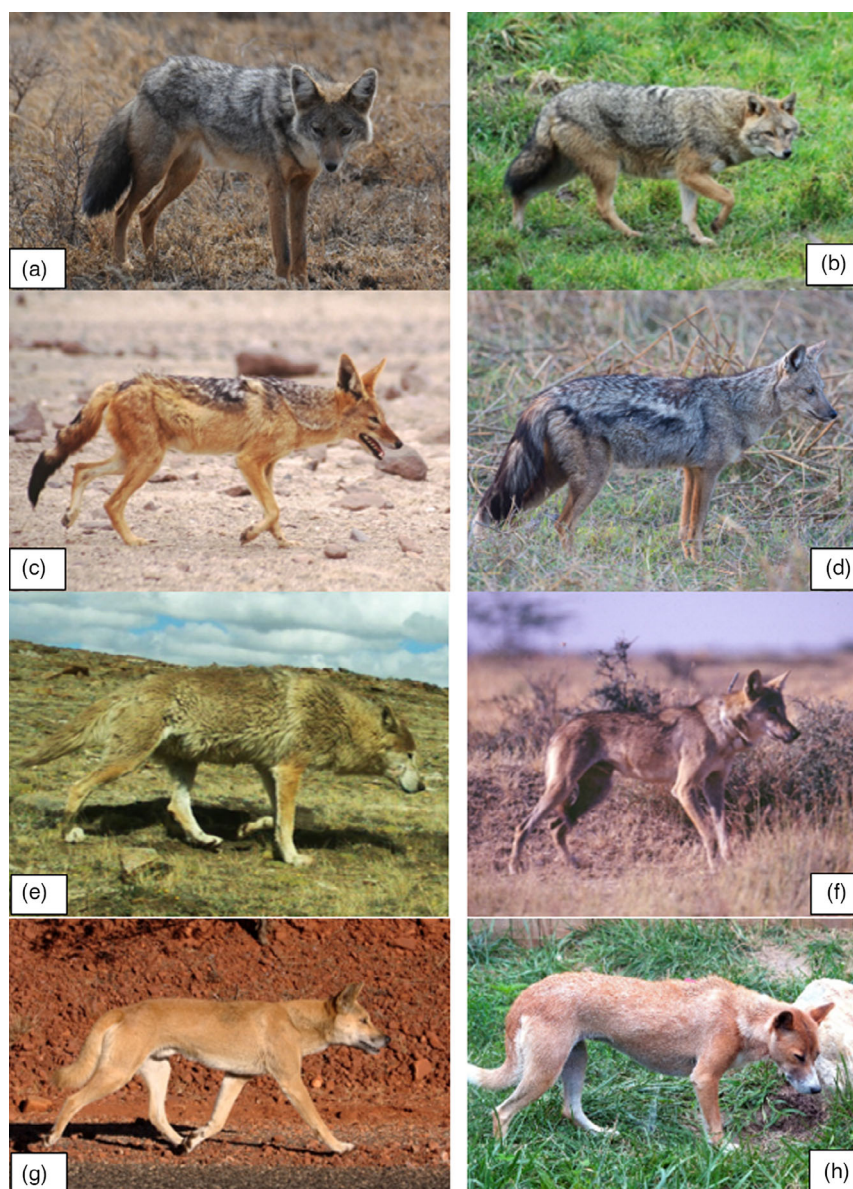


Figure 1 Pictures of the different taxa presented in this review: (a) *Canis lupaster* (also known as *Canis aureus*) in Tanzania in winter coat (Patricia Moehlman); (b) *Canis aureus* in Europe in winter coat (Jennifer Hatlauf); (c) *Lupulella mesomelas* (formerly known as *Canis mesomelas*) in Namibia (Miha Krofel); (d) *Lupulella adusta* (formerly known as *Canis adustus*) in winter coat in Botswana (Brian Sugden); (e) *Canis lupus chanco* (formerly known as *Canis laniger* and/or *Canis himalayensis*) in the Nepalese Himalayas (Geraldine Werhahn); (f) *Canis lupus pallipes* in India (Yadvendradev Jhala); (g) *Canis familiaris* in Australia (previously described by some authors as *Canis dingo*) (Jarrod Amore). (h) *Canis familiaris* in captivity, originating from New Guinea (previously described by some authors as *C. hallstromi*) (David Ellis).

observed specimens in order to establish firmly the relationship between morphology, genetics and geographical origins. In turn, these studies should be complemented with investigations of genetic diversity and structure, using either traditional markers such as microsatellites and mitochondrial DNA sequences or genomic approaches, such as restriction-site-associated DNA sequencing (RADseq) or low-coverage whole-genome sequencing. For example, recent genetic and genomic studies have

revealed significant differentiation among African wolf populations sampled from different regions of Africa, which exhibit distinct demographic histories and may reflect different ecotypes (Gopalakrishnan *et al.*, 2018; Mallil *et al.*, 2020; Sarabia *et al.*, 2020). Similar to morphological studies, we emphasize the importance of using samples collected from across the range of each species and encompassing all putative subspecies. In particular, the canids from Egypt, the Horn of

Africa, the Levant and the Arabian Peninsula require more research and sampling for genetics and morphology, since some studies suggest that up to three wild species of *Canis* may occupy these areas with possible hybridization among them (Gippoliti & Lupi, 2020; Machado & Teta, 2020; Saleh & Basuony, 2014b; Stoyanov, 2020), as well as domestic dogs.

Black-backed jackals and side-striped jackals of Africa

Based on phenetic approaches, the side-striped (*Canis adustus*) and the black-backed (also known as silver-backed) jackals (*C. mesomelas*) have long been recognized as belonging to the genus *Canis*. However, phylogenetic analyses of datasets largely comprised of nuclear DNA sequences consistently support their placement in a monophyletic lineage outside the clade that includes *Lycaon*, *Cuon* and other *Canis* species (Koepfli et al., 2015; Lindblad-Toh et al., 2005; Perini et al., 2010). Studies based on morphological and palaeontological data, as well as a combined dataset of morphological characters and genetics, support this placement (Geraads, 2011; Machado & Teta, 2020; Zrzavý et al., 2018). Inclusion of these jackals in the genus *Canis* would make this genus paraphyletic or require the inclusion of *Cuon* and *Lycaon* in *Canis*. However, some studies indicate morphometric overlap between all jackal-like species, namely golden jackal, African wolf, black-backed jackal and side-striped jackal, possibly due to eco-morphological convergence (Maran, 2015; Van Valkenburgh & Wayne, 1994). Given the phylogenetic data, the black-backed and side-striped jackals should be placed in a distinct genus, *Lupulella* Hilzheimer, 1906 (following Viranta et al., 2017), with species names *Lupulella mesomelas* (Fig. 1c) and *Lupulella adusta* (Fig. 1d), respectively.

It has been suggested that *L. mesomelas* may actually consist of two species occupying southern (*L. mesomelas*) and eastern Africa (*L. schmitzii*), respectively, as sequence data from the mitochondrial cytochrome *b* gene (Atickem et al., 2017), supported by non-overlapping morphology based on geometric morphometric analyses of skulls (Machado & Teta, 2020), suggest these two geographically separate populations are discrete lineages that diverged more than two million years ago (Atickem et al., 2017). It has also been suggested based on paleontological and mitochondrial DNA sequences that *L. adusta* and *L. mesomelas* represent independent lineages warranting a monotypic genus for each species, that is *Schaeffia adusta* and *Lupulella mesomelas*, respectively (Atickem et al., 2017; Valenciano et al., 2021; Van den Brink, 1973; Zrzavý et al., 2018) although based on current evidence that they are sister lineages and nuclear data, we do not support this distinction and recommend further research using whole-genome sequences.

Himalayan/Tibetan wolves

The taxonomy of wolves found in the Himalayas and Tibetan Plateau (hereafter, referred to as the 'Himalayan wolves', since it was used more frequently in the scientific literature compared to 'Tibetan wolves'; Fig. 1e) has long been confused,

owing to uncertainty over their geographical distribution, disparate nomenclature and morphological similarity to neighbouring populations of grey wolves. Based on current analyses of mitochondrial DNA sequences (D-loop and cytochrome *b*), whole mitogenomes, nuclear microsatellites, sex-linked markers, SNPs within regions of the genome responsible for hypoxia adaptation and comprehensive whole-genome data, the Himalayan wolf is one of the two most evolutionarily distinct lineages (the other being the Indian wolf, *C. lupus pallipes*; see below) basal to Holarctic grey wolves, spanning Europe to North America (Aggarwal et al., 2007; Ersmark et al., 2016; Hennelly et al., 2021; Joshi et al., 2020; Koepfli et al., 2015; Loog et al., 2020; Rueness et al., 2011; Sharma et al., 2004; Shrotiya et al., 2012; Wang et al., 2020; Werhahn et al., 2017b, 2018, 2020) also see phylogenies in Koepfli et al., 2015 and Rueness et al., 2011. However, genomic study using four samples by Fan et al. (2016) defined 'Highland wolves' from Tibet and Qinghai (China) as a recent clade within the grey wolf-domestic dog clade. Multiple studies have found differentiated alleles in hypoxia-pathway-related genes unique to Himalayan wolf populations and suggest that this lineage occurs in habitats above 4000 m elevation in the Himalayas and Tibetan Plateau (Fan et al., 2016; Joshi et al., 2020; Liu et al., 2019; Sharma et al., 2004; VonHoldt et al., 2017; Wang et al., 2020; Werhahn et al., 2018; Zhang et al., 2014). The results of Hennelly et al. (2021) and Wang et al. (2020) contradict the results of the study Fan et al. (2016) and support the findings above. This may be explained by the use of different phylogenomic methods and by accounting for gene flow and recombination in the former studies. Extensive sampling conducted across the Himalayas and Tibetan Plateau reveals that in several geographical regions (e.g. northern Qinghai and East Sichuan) admixture is occurring between Himalayan wolves and grey wolves (Joshi et al., 2020; Werhahn et al., 2018, 2020) and it is possible that the presence of hybrid ancestry in the samples of Fan et al. (2016) is contributing to this apparent contradiction. Ideally further studies should be based on genome-wide evidence from many animals with proven geographical provenance across the range, including both the core and edges, which also addresses the possible influence of introgression among grey wolves, domestic dogs and Himalayan wolves (Table 1).

The Himalayan wolf lacks a full morphological analysis (but see Janssens et al., 2016), and we recommend a systematic morphological assessment to inform the future discourse on the taxonomic status of this taxon. A study of the acoustics of howls of Himalayan wolves, Indian wolves and Holarctic grey wolves showed that Himalayan wolves produce significantly different vocalizations compared with other wolf lineages (Hennelly et al., 2017), although this behavioural character may have limited taxonomic significance.

The nomenclature for the Himalayan wolf has not been fully resolved to date. The earliest name *C. laniger* (Hodgson, 1847) is unavailable, owing to its earlier use by Hamilton Smith (1840) for a domestic dog. Therefore, the earliest valid name is *C. chanco* Gray, 1863, but there is some uncertainty related to the holotype's geographical origin and genetic lineage. This holotype was collected by Lieutenant W. P. Hodnett

(incorrectly spelt Hodnell in Gray, 1863) from the 54th West Norfolk Regiment, and the type locality is Chinese Tartary, which is a very broad and ill-defined area of Central Asia. However, it is most likely to have been collected in the Himalayas, because the specimen was collected by an army officer who was based in India at that time. The next available names are *C. filchneri* (Matschie, 1908) (type locality Si-ning-fu, Gansu, China), *C. karanorensis* (Matschie, 1908) (type locality Kara-nör, Gobi, Mongolia) and *C. tschiliensis* (Matschie, 1908; type locality Schan-hai-kuan, Coast of Chihli, China; Mech, 1974), but some or all of these may be grey wolves. Heptner (1998; 191) as first reviser restricted the type locality of *chanco* to Tibet and recognized the Mongolian wolf as a distinct subspecies, *C. l. tschiliensis*. We recommend further morphological and genetic analyses (including the holotypes of *chanco*, *filchneri*, *karanorensis* and *tschiliensis*) from throughout Central Asia to establish the distribution of this taxon and its taxonomic status as either a distinct species or a subspecies of grey wolf. Until further evidence becomes available, we suggest referring to this lineage as *Canis lupus chanco*.

Indian wolf

The Indian wolf (*Canis lupus pallipes*) (Fig. 1f) is recognized as a grey wolf subspecies by the IUCN (Boitani *et al.*, 2018). It is adapted to the arid and semi-arid lowland of southern Asia, although the exact range has yet to be established. The Indian wolf exhibits divergent mitochondrial haplotypes, mitogenomes, low-recombining regions of the X chromosome and parts of the nuclear genome that support a distinct taxon that appears largely restricted to the Indian subcontinent (Aggarwal *et al.*, 2007; Bray *et al.*, 2014; Ersmark *et al.*, 2016; Fan *et al.*, 2016; Hamid *et al.*, 2019; Hennelly *et al.*, 2021; Loog *et al.*, 2020; Pilot *et al.*, 2010; Sharma *et al.*, 2004; Werhahn *et al.*, 2017b). Mitochondrial haplotypes for wolves over the vast majority of this range, including Iran and north-western Pakistan, cluster with those of Holarctic grey wolves, whereas those of the Indian subcontinent (including lowland Pakistan) form the distinct Indian wolf lineage (Hennelly *et al.*, 2021). Nuclear genomic analyses from Indian and West Asian wolves showed that the nuclear genome of West Asian wolves largely reflects ancestry with the Holarctic grey wolf lineage (Hennelly *et al.*, 2021). On the other hand, the autosomal phylogeny groups the wolves from the Indian subcontinent together with the West Asian wolves in a monophyletic clade. This pattern suggests that there is Indian ancestry beyond the Indian subcontinent possibly due to gene flow between Indian and West Asian wolves, and/or that Indian and West Asian wolves derive from a common ancestor (Hennelly *et al.*, 2021).

Additional geographical sampling for genomic analyses at contact zones and morphological analysis for wolves of the Indian subcontinent and south-west Asia would facilitate resolving both the taxonomic designation and correct range limits for these wolves. A systematic morphological analysis is still required for the Indian wolf in comparison with other *C. lupus* and related lineages, in order to help resolve its taxonomic status (Table 1). The Indian wolf produces distinct vocalizations compared with Holarctic grey wolves, although

the distinction was found to be less compared to differences between Himalayan wolves and Holarctic wolves (Hennelly *et al.*, 2017).

The currently accepted nomenclature for the Indian wolf is *C. l. pallipes* (Sykes, 1831) with the type locality being Decan, India. Aggarwal *et al.* (2007) proposed species status as *Canis indica* based on mtDNA analysis of a limited number of museum and zoo specimens, but *C. indica* is a *nomen nudum* and *C. pallipes* remains the first available name for this taxon. Taxonomic re-evaluation of this taxon may be warranted in light of emerging whole-genome data and future morphological analyses from specimens throughout southern Asia.

Dingoes and New Guinea singing dogs

The taxonomy and conservation status of dingoes (Fig. 1g) and New Guinea singing dogs (Fig. 1h) is controversial and unresolved. Some authors argue for species status for dingoes, *Canis dingo*, and New Guinea singing dogs, *C. hallstromi*, which has led to revised species' descriptions (Crowther *et al.*, 2014; Koler-Matznick *et al.*, 2003; Smith *et al.*, 2019). Among the evidence presented for their species status is that they comprise an ancient distinct lineage, compared with most domestic dogs, as well as displaying distinctive morphological and behavioural traits (Crowther *et al.*, 2014; Smith *et al.*, 2019). Other authors regard them as ancient feral domestic dogs, *C. familiaris* (Jackson *et al.*, 2017, 2019). Genetic studies suggest that dingoes diverged from ancestral domestic dogs in South-East Asia 15 000–5000 years ago with strong admixture with grey wolves and prior to their arrival in Australia from about 5000–3500 years ago (Savolainen *et al.*, 2004; Wang *et al.*, 2016). A recent genomic study dated the divergence between Indonesian village dogs and dingoes/New Guinea singing dogs as *c.* 8300 years ago (95% CI: 5400–11 200 years) and confirmed that dingo ancestors may have been introduced to Australia more than once (Zhang *et al.*, 2020). These data are consistent with archaeological evidence that dingoes were widespread by *c.* 3500 years ago (Fillios & Taçon, 2016). This ancestry is very recent for a speciation event and would in theory make the domestic dog a paraphyletic species, although this should not be strictly inferred based on these data. These studies also place dingoes and New Guinea singing dogs on a single branch within the Asian domestic dog clade that includes mainly East Asian breeds such as chow chow, Alaskan malamute and Siberian husky (Skoglund *et al.*, 2015; Surbakti *et al.*, 2020; VonHoldt *et al.*, 2010; Wang *et al.*, 2016). Recent re-descriptions of both canids failed to elucidate diagnostic characters to distinguish them from domestic dogs (Crowther *et al.*, 2014; Koler-Matznick *et al.*, 2003). Therefore, we suggest that dingoes and New Guinea singing dogs should be both treated as ancient dogs, *C. familiaris*.

Implications and conclusions

Inaccurate, uncertain or confusing taxonomies and nomenclature can create several challenges for scientific practice, conservation and management, which fundamentally rely on the pre-

defined entities of species or subspecies (Vogel Ely et al., 2017; Waples et al., 2018). A clarified taxonomy has several implications, since it can benefit assessments of species distribution and conservation status, improve establishment of protected areas and guide conservation activities, including prioritization of funding (Mace, 2004). Taxonomy is also strongly linked to listing species under national or international agreements (e.g. IUCN Red lists, CITES, Convention on Migratory Species, fishery and trade agreements), which include essential legal instruments that guide conservation decisions and implement legal protection locally and internationally (Vogel Ely et al., 2017). Therefore, taxonomic uncertainties and ambiguities can harm species at high risk of extinction and hinder international policing and prosecution of wildlife crime (Zhou et al., 2016). Since species are fundamental units in macroecology, poor taxonomy can also jeopardize our understanding of ecological patterns (Isaac et al., 2004). It is thus crucial to promote collaboration and agreement among conservation biologists, taxonomists and legislators for reaching a consensus on taxonomic and legal ambiguities (Mace, 2004; Zhou et al., 2016). Old World and Australasian canids represent a typical case of unresolved taxonomy with contradictory information scattered throughout the literature. To advance the debate and clarify current knowledge for conservationists and other practitioners, we provide a working framework for canid taxonomy. However, further research is needed to resolve remaining uncertainties (Table 1).

A revised taxonomy of the taxa discussed here has several implications, for both conservation and research. For example, if available literature on ecology and behaviour of the golden jackal and African wolf (for reviews, see Jhala & Moehlman, 2004; Moehlman & Hayssen, 2018; Moehlman & Jhala, 2013) is viewed according to the suggested taxonomy presented above, large knowledge gaps become evident. This is primarily connected with the fact that important parts of our basic knowledge about these canids, including most of behavioural ecology and reproduction, come from a relatively small part of the distribution range in East Africa and are limited to only one of the taxa, *C. lupaster*. It is therefore a research priority to document important aspects of the basic biology of *C. aureus* throughout Eurasia, where we would expect potentially wide ecological and behavioural variation. This is especially important given increasing concerns and management challenges connected with the rapidly expanding population of this mesocarnivore in Europe (Ćirović et al., 2016; Hatlauf et al., 2021; Rutkowski et al., 2015; Trouwborst et al., 2015).

There is a similar lack of knowledge about the Himalayan and Indian wolves, which have only recently been recognized as distinct lineages that branched off earlier compared with other grey wolf populations and consequently have received little research and conservation attention. However, populations of both Himalayan and Indian wolves face severe threats, underscoring the importance of further research for their conservation (Hennelly et al., 2021; Jhala, 2003; Singh & Kumara, 2006; Werhahn et al., 2017a, 2020). In particular, population estimates and trends are unknown for *C. l. chanco*, despite persecution for depredation on livestock and illegal trade (Werhahn et al., 2017a, 2017b, 2018). Therefore, detailed research

on population status, distribution range, ecology, behaviour, diseases and human–wildlife conflict of the Himalayan wolf, as well as the Indian wolf, are required to establish its conservation status and develop appropriate conservation measures. We also recommend continuing research on the evolutionary dynamics at the edges of the Himalayan and Indian wolf's range. The individuals in these boundary regions should be considered in taxonomic and conservation decisions in order to preserve dynamic evolutionary processes through gene flow to enable adaptation to changing environments, including the impact of climate change.

The assignment of black-backed and side-striped jackals to the genus *Lupulella* enhances their importance as an evolutionary lineage distinct from *Canis* with possible broader implications related to the genus re-classifications (Zhou et al., 2016). Although these African jackals are not currently endangered, we cannot be certain that their current status will be maintained into the future as habitats and wildlife communities in Africa are changing rapidly owing to human impacts, including climate change (Thuiller et al., 2006). Although we regard dingoes and New Guinea singing dogs as ancient dogs, we also recognize the ecological role of these dogs as top predators in their fragile insular environments, as well as their socio-cultural value (Claridge & Hunt, 2008; Glen et al., 2007; Koler-Matznick et al., 2003; Letnic et al., 2012; Newsome et al., 2017).

For the taxonomic suggestions presented in Table 1, using the traffic-light system adopted from Kitchener et al. (2017), to indicate taxonomic certainty for taxa at species level, we gave a yellow score to *C. aureus* and *C. lupaster*, owing primarily to deficiencies in our knowledge of morphological differences between and within them, and biogeographical evidence for their separation. In contrast, *C. (lupus) chanco* and *C. (lupus) pallipes* were evaluated as red because we have no clear morphological or biogeographical evidence so far, while the available genetic evidence analysed to date consistently shows these as the earliest diverging lineages relative to other populations of *C. lupus*, but it is unclear whether they should be treated as distinct species or subspecies of the grey wolf.

Although a combination of modern molecular and morphological studies has brought greater clarity to the relationships between taxa within and outside the genus *Canis*, several areas of the taxonomy of Old World canid species remain unresolved (Table 1). Nevertheless, we hope that this review will be useful for further elucidating canid taxonomy and nomenclature, while providing a working framework in future years. Taxonomies are always evolving as new evidence becomes available and some taxonomic problems are unlikely ever to be solved completely (Isaac et al., 2004). The recent upsurge in molecular studies on Old World canids, in particular, has resulted in a proliferation of suggested scientific names that have created uncertainty for conservationists and researchers. This could compromise conservation efforts and implementation of legal protections to the detriment of the species involved (Vogel Ely et al., 2017). We believe that our suggestions will facilitate continuing research and stimulate further studies to answer unresolved questions as well as highlight the need to collect additional opportunistic samples and specimens for research. It

will also help practitioners and legislators to gain a clearer picture about the current taxonomic status of these taxa, which can help in identifying conservation priorities and support effective management actions when needed. Similar efforts would be welcome also for several other groups of canids, leading to a taxonomic revision of the Canidae in general, similar to the recently revised classification of the Felidae (Kitchener et al., 2017).

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Conflict of interests

The authors confirm no conflict of interest.

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