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Rediscovering a forgotten canid species

Suvi Viranta^{1*†}, Anagaw Atickem^{2,3,4†}, Lars Werdelin⁵ and Nils Chr. Stenseth^{2,4*}

Abstract

Background: The African wolf, for which we herein recognise *Canis lupaster* Hemprich and Ehrenberg, 1832 (*Symbolae Physicae quae ex Itinere Africam Borealem et Asoam Occidentalem Decas Secunda*. Berlin, 1833) as the valid species name (we consider the older name *Canis anthus* Cuvier, 1820 [Le Chacal de Sénégal, Femelle. In: Geoffroy St.-Hilaire E, Cuvier F, editors. *Histoire Naturelle des Mammifères* Paris, A. Belin, 1820] a *nomen dubium*), is a medium-sized canid with wolf-like characters. Because of phenotypic similarity, specimens of African wolf have long been assigned to golden jackal (*Canis aureus* Linnaeus, 1758 [Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Editio decima, reformata, 1758]).

Results: Here we provide, through rigorous morphological analysis, a species description for this taxonomically overlooked species. Through molecular sequencing we assess its distribution in Africa, which remains uncertain due to confusion regarding possible co-occurrence with the Eurasian golden jackal. *Canis lupaster* differs from all other *Canis* spp. including the golden jackal in its cranial morphology, while phylogenetically it shows close affinity to the Holarctic grey wolf (*Canis lupus* Linnaeus, 1758 [Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Editio decima, reformata, 1758]). All sequences generated during this study clustered with African wolf specimens, consistent with previous data for the species.

Conclusions: We suggest that the estimated current geographic range of golden jackal in Africa represents the African wolf range. Further research is needed in eastern Egypt, where a hybrid zone between Eurasian golden jackal and African wolf may exist. Our results highlight the need for improved studies of geographic range and population surveys for the taxon, which is classified as 'least concern' by the IUCN due to its erroneous identification as golden jackal. As a species exclusively distributed in Africa, investigations of the biology and threats to African wolf are needed.

Keywords: African wolf, Canidae, *Canis lupaster*, *Canis aureus*, Taxonomy, Conservation

Background

Most canids (Family Canidae) are easy to recognize by their characteristic long muzzle, long limbs and bushy tails. They have a conservative body plan retaining traits of early mammals, including a primitive dental formula (I 3/3, C 1/1, P 4/4, M 2/3 in the majority of Canidae) [1]. Morphological variation within the family is relatively slight [1, 2], which creates problems of species recognition and classification. Wolves are the largest members of the Canidae. They are charismatic species

with a long special relationship with people. They are also the ancestors of the first domesticate, the dog [3, 4]. During historic times and into the present wolves have been persecuted due to fear of predation on domestic animals and attacks on people. Once widespread across the Holarctic, wolves are now absent in many areas of North America and Eurasia [5]. Wolves have been thought to be absent from Africa. Instead the large and medium sized canids in Africa are the African wild dog (*Lycaon pictus* Temminck, 1820 [6]) and the two jackals: side-striped jackal (*Lupulella adusta* (Sundevall, 1847) [7]) and black-backed jackal (*Lupulella mesomelas* (Schreber, 1775) [8]). The fourth medium sized canid species, the African wolf (*Canis lupaster*), was until recently equated with the Eurasian golden jackal (*Canis aureus*). Recent papers, including this one,

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show that it is a separate species, *Canis lupaster*. In the phylogenetic tree the African wolf groups with other *Canis* species, whereas *Lupulella* and *Lycan* fall outside this clade, resulting in identification of separate genera (Additional file 1).

The presence of a wolf relative in North and West Africa was indicated in the early literature [9–12], but until recently [13–15] largely ignored in the modern literature. Here we demonstrate the presence of a species closely related to the Holarctic wolf in Africa and discuss its taxonomic status and morphology. We provide the first formal taxonomic description of the African wolf.

A medium-sized canid with a wide distribution in North, West, and East Africa has been described under various names, but is today mistakenly equated with the golden jackal, *Canis aureus* Linnaeus, 1758 [16, 17]. Recent publications [13–15] have identified this animal as a separate species, more closely related to the Holarctic grey wolf than to the golden jackal. Gaubert et al. [13] suggested the existence of both the golden jackal and African wolf in North and West Africa. Their mtDNA analysis revealed a close relationship between specimens morphologically assigned as golden jackals and those assigned as the African wolf, differentiating them from Indian golden jackal. Morphological features characteristic of the African wolf are heavy build and wider head, as well as some traits of the pelage. Koepfli et al. [15], using both mtDNA and autosomal loci, found evidence for African and Eurasian golden jackals as distinct species and found no evidence for the existence of both the golden jackal and the African wolf in Africa. They also estimated the divergence times and found an estimate of 1.9 Ma for the golden jackal and the African wolf and 1.3 Ma for the African wolf and the grey wolf. They also identified some morphological traits and provided evidence for apparent convergent evolution having resulted in the similarity of the golden jackal and African wolf. Rueness et al. [14] concluded, based on yet another sample of mtDNA, that the African wolf is a separate species, more closely related to the grey wolf than to the golden jackal.

This species, which we here call the African wolf, has, however, only cursorily been described morphologically, and a detailed investigation of its taxonomic status has not previously been undertaken. Furthermore, the putative presence of Eurasian golden jackal in Africa remains unclear and has led to confusion among researchers. With a formal taxonomic description and the demonstrated distinct evolutionary history of the African wolf, the need for a reassessment of the geographic distribution and population abundance of this species is evident.

The fact that the phylogenetic uniqueness of the African wolf has escaped the attention of science for

over a century serves as a cautionary example of reliance on outdated authority and a lack of proper taxonomic research. Biodiversity research, as well as conservation studies, is only valuable when built on solid taxonomic work [18, 19]. The erroneous merging of two distinct species (the African wolf and the golden jackal) into one as ‘golden jackal’ has resulted in confusing phylogenetic trees and false interpretations of intraspecific biological variation and evolutionary history.

Methods

We studied crania of canids labelled by earlier scholars or museum curators as *Canis aureus*, *Canis lupaster* or *Canis anthus* in the collections of Swedish Museum of Natural History, Stockholm, Sweden (NRM); Museum für Naturkunde, Berlin, Germany (ZMB); Natural History Museum of Denmark, Copenhagen, Denmark (ZMUC), and Finnish Museum of Natural History, Helsinki, Finland (FMNH). We also studied specimens of the closely related Old World canids *Lupulella mesomelas*, *L. adusta*, *C. simensis* Rüppell, 1840 [20], and *C. lupus* in the same institutes. Moreover, we studied crania collected from road kills for this project in Ethiopia. In the case of the type specimens, housed in the Museum für Naturkunde, Berlin, the skins were also studied. For skulls with a skin with the same specimen number (presumed to be from the same individual), the skin was sampled for DNA data ($n = 20$). We sampled scats ($n = 31$) and blood samples ($n = 14$) from different African countries. Eleven skin samples also were obtained from museum collections (Additional file 2: Table S1).

A total of 31 dental and 22 cranial measurements were taken on skulls using dial calipers. Additional measurements were obtained from the data files of Björn Kurtén (curated by LW). Measurement data are provided in Additional file 3. The skins were photographed and the head and body length were measured using a tape measure. By convention lower case letters are used for lower teeth and upper case letters for upper teeth.

The DNA extraction from scat samples was carried out using Dynabeads MyOne™ SILANE as given in detail in [21] and the Phenol chloroform method was used for museum and blood samples [22, 23]. Polymerase chain reaction (PCR) was carried out at two fragments of mtDNA (12S ribosomal RNA and Cytb region) for samples from blood and scat. The 12S rRNA was amplified using primers 12S3 and 12S2 [24]. The DNA extracts from museum samples were amplified using internal primers developed to sequence short sequences (Additional file 2: Table S2). Sequences were aligned using MEGA 5.2-clustal parameters [25]. The mtDNA amplification was performed in 15 µl reactions containing 2.5 µl HotStar PCR buffer (QIAGEN GmbH Hamburg, Germany), 5 nmol dNTP, 0.01 mg BSA

(New England Biolabs), 50 nmol MgCl₂, 1.25 units Hot-Star Taq polymerase, 8 pmol of each primer, 50–100 ng template DNA and mqH20. The program for the PCR consisted of initial denaturation at 95 °C for 15 min followed by 45 cycles of 94 °C for 1 min, 55 °C for 1 min and a final extension at 72 °C for 10 min for Cytb1 and 12S rRNA. The PCR cycle parameters for DNA extracts from museum samples were similar except for a higher annealing temperature of 58 °C and 60 °C (Additional file 2: Table S2). Additional nucleotide sequences of canids were obtained from GenBank (Additional file 2: Table S3). Phylogenetic relationships were analysed using Bayesian approach in BEAST 1.8 [26]. Site model and clock model were set as unlinked between the two partitions. A HKY + G (4 classes) + I substitution model with empirical base frequency and a strict clock-rate were set for both partitions. The Yule Process was used as a tree prior model. Three replicates were run for 10 000 000 generations and convergence of parameters was checked on Tracer 1.5 ([27, 28]. The phylogenetic tree was then drawn in FigTree 1.4 [28, 29]. Median-joining network analysis was carried out using PopART Network analysis [27]. Regional genetic variation was estimated using the DnaSP software [29].

The statistical analyses of the morphological data were carried out using the PAST software (version 2) [30].

Nomenclatural acts

This published work and the nomenclatural acts it contains have been registered in Zoobank: <http://zoobank.org/NomenclaturalActs/2D51EA46-45D3-4F31-BCC5-7AA1221F66DB>. The LSID for this publication is: [lsid:zoobank.org:act:2D51EA46-45D3-4F31-BCC5-7AA1221F66DB](http://zoobank.org/act:2D51EA46-45D3-4F31-BCC5-7AA1221F66DB).

Results

Systematics

Canis lupaster Hemprich and Ehrenberg, 1832 [9].

Synonymy (selected, for an expanded list see Additional file 4)

Canis anthus (Cretzschmar, 1826 [31] non *C. anthus* Cuvier, 1820 [10])

Dieba anthus (Gray, 1869) [32]

Canis anthus (De Winton, 1899) [12]

Canis lupaster (Hilzheimer, 1906) [33]

Canis aureus lupaster (Schwarz, 1926) [34]

Thos aureus lupaster (Allen, 1939) [17]

Original description (Hemprich and Ehrenberg, 1832) [9]

CANIS Lupaster H. et E. Dib, Sib

Vulpe maior, Lupo affiniore, inferior, longius pilosus cineracento flavidus, fusco nigroque obsolete varius, capite incrassato, ore subacuto, vertice auribus naso pedibusque flavis, cauda brevi laxius pilosa, apicibus pilorum

et macula prope basin nigricantibus aut rufis. C. Anthus Cretzschmar nec Frid. Cuvier. In Fayum vulgaris. Lupus Aegypti.

“Large fox, similar to wolf but smaller; long hair, ash-yellow to dark black pelage; head thickened, ears pointed, mouth, ears, nose and feet yellow; short tail sparsely furred, tips of hairs reddish and blackish spot near the base. *C. anthus* of Cretzschmar, not F. Cuvier; Common in Fayum; Egyptian wolf.” (our translation)

Holotype

Three specimens, all from the governate of Fayum (Fayium, Fayoum), Egypt, are marked as types in the collections of the Museum für Naturkunde, Berlin: ZMB_mam_833, a skull with worn teeth and damaged occipital region, sex unknown; ZMB_mam_834, a skull and skin of an adult female; ZMB_mam_835, a skull of a young female individual with deciduous dentition and erupting permanent teeth. Of these, ZMB_mam_834 is considered the holotype of *C. lupaster* [34]. Of the other two specimens, ZMB_mam_833 becomes a paratype as it is part of the type series [34]. Specimen, ZMB_mam_835, on the other hand, is the type specimen of *Canis sacer* Hemprich and Ehrenberg, 1832 [9], a putative synonym of *C. lupaster* [34].

Description of ZMB_Mam_834

A female individual collected by Friedrich Wilhelm Hemprich and Christian Gottfried Ehrenberg from Fayum, Egypt in the early 19th century. It consists of a complete skull and a skin (Figs. 1 and 2). Measurement data for this specimen are given in Additional file 2: Tables S4–S6.

Skull and dentition

The skull (Fig. 1) is that of a medium-sized canid. The upper and lower postcanine teeth are slightly crowded, with diastemata between the upper canine and the third incisor and between the lower canine and the first premolar.

The mandible (Fig. 1) is robust with well-developed masseteric fossa and elevated coronoid. The condyloid process has a short neck. The angular process is long and convex with a pointed tip. Two mental foramina are located below p3 and just mesial to p2. The hemimandibles have been separated at the symphysis and are now glued together, so the natural angle between the two is lost. A small and round m3 is present bilaterally. The m2 is elongated and has four distinct cusps that, in accordance with other Canidae, are protoconid, metaconid, entoconid, and hypoconid. In the m1 both the trigonid and talonid are well developed. The metaconid is distinct from the protoconid and located

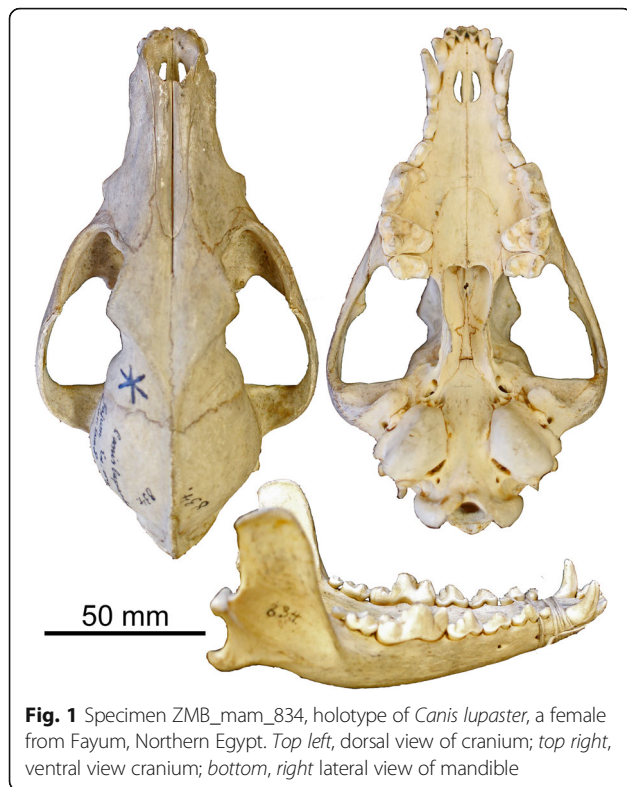


Fig. 1 Specimen ZMB_mam_834, holotype of *Canis lupaster*, a female from Fayum, Northern Egypt. *Top left*, dorsal view of cranium; *top right*, ventral view cranium; *bottom, right* lateral view of mandible

distolingually to it. The talonid has three cusps, entoconid, hypoconid and hypoconulid. The p4 is >50% of the length of the m1 and has three cusps and a lingual cingulum. The mesial cusp has a mesial crest. The p3 and p2 are of about equal length. They both have a main cusp, a distal accessory cusp, and a cingulum with a distal elevation. The p1 is round and has a sharp anterior cusp. The lower canine is mediolaterally flattened. The incisors are crowded. The i2 and i3 have two cusps.

The cranium is dome-shaped with a ca. 20° angle between the rostrum and the braincase (forehead). Sutures between bones are clearly visible and the skull has a moderate sagittal crest. The widest part of the rostrum is at the posterior end of the P4. The premolar



Fig. 2 Specimen ZMB_mam_834, holotype of *Canis lupaster*, a female from Fayum Northern Egypt. Skin; head to right, tail to left

and molar rows are angled at about 30° to each other. The incisive foramina are long, extending from the anterior end of the canines to the level of P1. There are three palatine foramina on the right side and two on the left. They are convex in shape. The infraorbital foramen is well developed and placed above the P3. The post-orbital process is large, but blunt. The auditory bullae are inflated, oval and placed at 45° to the sagittal line.

The upper incisors are crowded and have lingual cingula. The upper canines are convex. The left canine has wear that appears to be ante mortem. The reason for this is not known. The P1 is small and pointed. The P2 has two cusps and the P3 three cusps. The P4 has a protocone that is clearly separate and placed lingual to the paracone. It lies at about 100° to a line drawn through the metacone and paracone. The M1 is distally convex and has a cingulum and four cusps, paracone, protocone, metacone, and hypocone. The M2 is smaller, but displays the same cingulum and cusps.

Skin

The skin of ZMB_Mam_834 is incomplete, with the distal parts of the limbs and tail missing (Fig. 2). There is a median dorsal ruff extending from the neck to the tail, composed of hairs with black tips and ginger and white bases. The head is ginger with agouti on the forehead and ears. The hair on the limbs and ventral side is short and yellow.

Differential diagnosis

We compared the cranial and dental measurements of 69 African wolves to the measurements taken on *Canis* species and the jackals. Based on skull size *Canis lupaster* is smaller than the smallest grey wolves (*Canis lupus arabs* Pocock, 1934 [35], *C. l. pallipes* Sykes, 1831 [36], *C. l. chanco*, Gray, 1863 [37]) (Additional file 2: Table S2; Additional file 5: Figure S1).

Canis lupaster differs from grey wolves in having a lower coronoid process of the mandible. The palatine bone is relatively longer and the distance between the upper canines smaller in *C. lupaster*. The molar row is relatively longer as compared to the premolar row (Additional file 5: Figure S1).

Canis lupaster is larger than the two African jackals (*Lupulella adusta* and *Lupulella mesomelas*) and differs from them by its relatively shorter palatine and larger skull.

The Eurasian golden jackal (*C. aureus*) has a wider and shorter palate and also relatively greater interorbital breadth than *C. lupaster*. The upper canine is mediolaterally flatter in *C. lupaster* than in *C. aureus* (Additional file 5: Figure S2).

The Ethiopian wolf (*C. simensis*) is a larger species and has a longer rostrum than *C. lupaster*. It also has a very

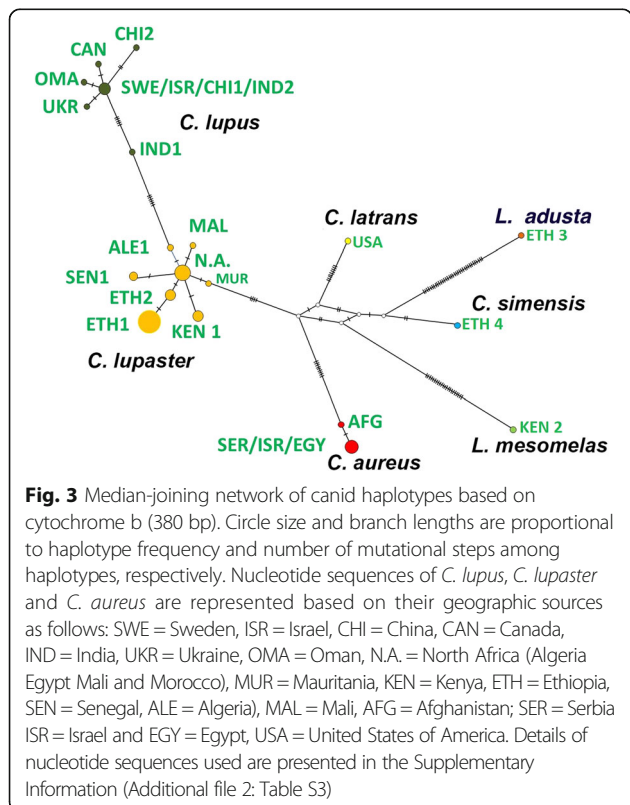
distinct pelage with white markings, while *C. lupaster* is tawny or rufous with black and grey on the dorsum.

Canis lupaster shows considerable variation in size, but sexual dimorphism has not been detected in our data (Additional file 5: Figure S3).

Separation from *Canis aureus*

We ran a discriminant analysis on the 52 morphological characters obtained for the study. Using log₁₀-transformed data for 65 individuals we obtained a correct classification of 68.3% (jackknifed) for the comparison *C. aureus* – *C. lupaster*. When only characters we considered most likely to be diagnostic were included, 89.7% correct classification was obtained (Additional file 5: Figure S4).

A total of 64 nucleotide sequences from Ethiopia, South Sudan, Egypt and Western Sahara newly generated for this study, as well as the 39 additional sequences of *C. lupaster* from GenBank (Additional file 2: Tables S3, S7), clustered to the African wolf lineage (Fig. 3; Additional file 5: Figure S5). A single *Canis aureus* haplotype has been reported from Egypt (Fig. 4) [15]. This specimen is from the Sinai Peninsula, close to the border between Egypt and Israel.



Geographic and intrapopulation variation

Several authors have noted the existence of two morphotypes of African wolf (see, e.g. [13]). Our data show that there are significant differences in size between populations of *C. lupaster*, with East African individuals being smaller than North and West African ones. This is not manifest in a bimodal distribution, however. On the other hand, our metric data do show a higher coefficient of variation (CV) in *C. lupaster* than in our *C. aureus* sample, which comes from specimens with a broad geographic distribution across Eurasia. This may be a signal of some morphotype differences within *C. lupaster* that are unmatched in *C. aureus*. Further subdividing the *C. lupaster* material into North, West and East African samples shows that all three have higher CV than the entire *C. aureus* sample. Among the three sub-samples of *C. lupaster*, the North African one has the highest CV (Additional file 2: Table S9). The *C. lupaster* population in Ethiopia has higher genetic diversity compared to the population in the northern African countries (Egypt, Algeria, Morocco; Additional file 2: Table S8).

Taxonomy and nomenclature

Accepting the African wolf as a distinct species leads to the question of the appropriate species name. Previous authors have alternated between *Canis lupaster* (e.g., [13, 14, 38]) and *Canis anthus* [13]. Of these, *C. anthus* F. Cuvier, 1820 [10] has priority. It is based on the description of a female individual from Senegal. In a later publication, Cuvier described a male individual he ascribed to *C. anthus* [11]. However, the two specimens are markedly different and are unlikely to belong to a single species. This, and the fact that the holotype is missing (a search in the Muséum National d'Histoire Naturelle, Paris was unsuccessful; G. Veron, pers. comm. to LW) render the status of *C. anthus* very unsatisfactory. It is, in fact, possible that the holotype is a specimen of *Lupulella adusta* (side striped jackal), which was not formally described until 1847 [7]. The description and illustration in Cuvier's work are not adequate to distinguish between the two. Thus, we consider *C. anthus* a *nomen dubium* and use *C. lupaster* as the name for the African wolf. A longer discussion of the taxonomic history of these names is provided in Appendix 2 (Additional file 6). It should also be noted that the publication of the *Symbolae Physicae* of Hemprich and Ehrenberg as a whole is dated 1833, but the section on *Canis lupaster* is dated November, 1832, which is the date of publication of the name.

Phylogenetic position within the Canidae

The fact that the majority of recent phylogenetic studies have considered the African wolf and Eurasian golden jackal to be conspecific makes them useless when

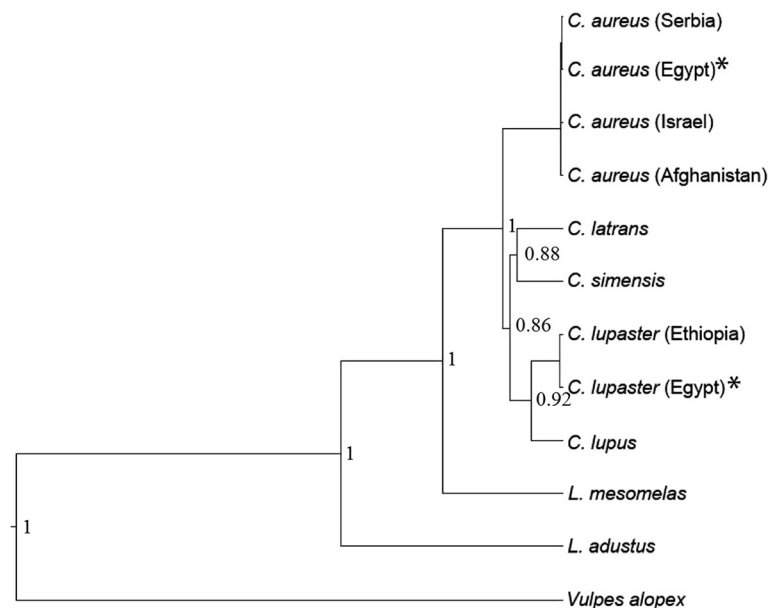


Fig. 4 Bayesian phylogenetic analysis of canids with posterior probabilities of nodal support based on cytochrome b (1140 bp). Branches marked with asterisks: *C. aureus* (Egypt) was obtained from GenBank (KT447732), while *C. lupaster* (Egypt) was generated from this study. Details of the sequences used in this analysis are given in Supplementary Information (Additional file 2: Table S3)

tracing the phylogenetic position of the African wolf. Early studies that used mitochondrial DNA sequences in phylogenetic analyses of canids, including an exclusively African '*C. aureus*', resulted in a position outside a crown clade *Canis* including Holarctic grey wolf, coyote, and Ethiopian wolf [39]. Separating '*C. aureus*' samples into a Eurasian and an African component and including a wide range of molecular markers shows the African sample to be closer phylogenetically to Holarctic grey wolf and coyote than are either Ethiopian wolf or Eurasian *C. aureus* [15].

Discussion

History of the African wolf

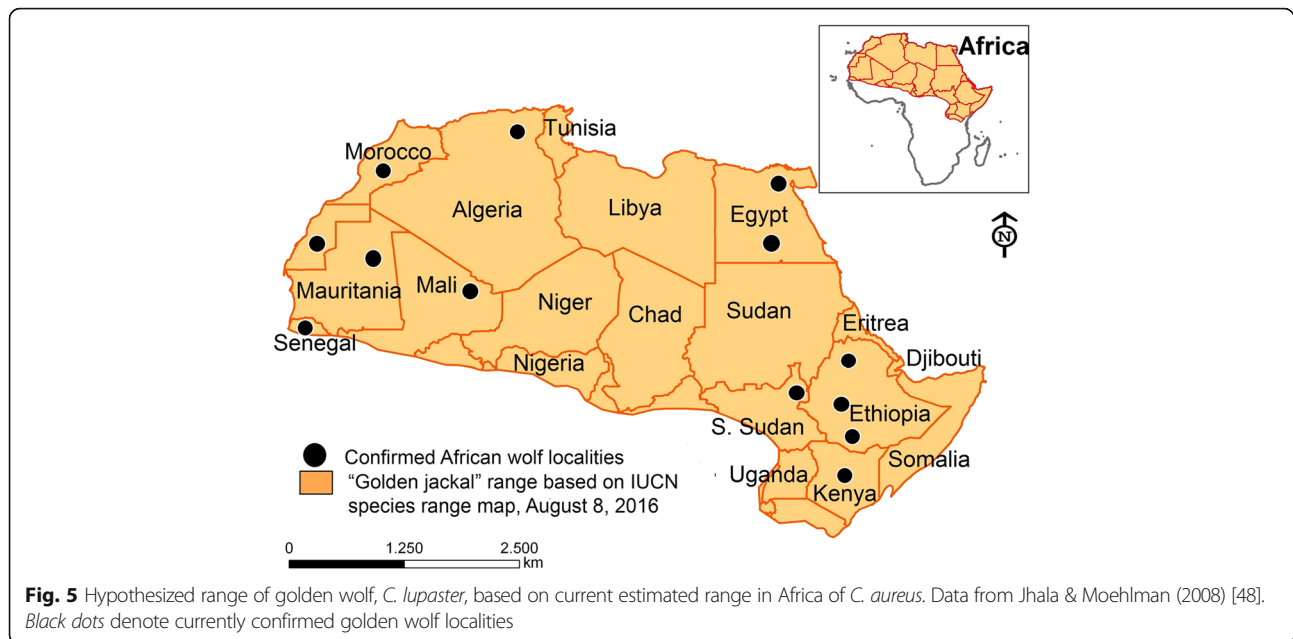
We have provided evidence for and described the African wolf as a distinct taxonomic entity clearly separate from the Eurasian golden jackal and as a species closely related to the Holarctic grey wolf. It should be noted, however, that the Holarctic grey wolf might not be a single species. Some wolf lineages, e.g., in India and North America may deserve species status as well [40–42].

From the first descriptions of African wolf [9–11, 31] until the 1920s the majority of authors maintained a distinction between the African wolf and the Eurasian golden jackal. Some also maintained a distinction between *C. anthus* and *C. lupaster* based on the original descriptions [43, 44].

The African wolf and golden jackal were synonymized by Schwarz [34] for reasons that are not clear in that

publication, and Allen accepted this synonymy in his highly influential checklist of African mammals [17]. Allen's viewpoint was rapidly accepted in both the ecological and evolutionary research communities and since that time few authors have considered the African wolf a distinct species, despite there being a few notable exceptions: Keimer mentions *C. lupaster* in his faunal work on Egypt [45]; Kurtén lists the wolf jackal (*C. lupaster*) for a fossil collection from the Levant and suggests the presence of extant *C. lupaster* in North Africa [46]; Ferguson studied *C. lupaster* crania from Israel and concluded that *C. aureus lupaster* differs from *C. aureus* and represents a small desert race of *C. lupus* [38]. Most recently an m1 from Middle Pleistocene deposits in the Nefud Desert, Saudi Arabia, has been identified as *C. anthus* [47].

It is only recently that new data from molecular genetic studies have resurrected the African wolf [13–15]. Thus far, presence of African wolf has been confirmed from southern Ethiopia to Egypt and West African countries, covering the former range of golden jackal delineated by IUCN [48] (Fig. 5). The golden jackal haplotype from Egypt alluded to above needs further study to determine whether it is from an isolated golden jackal in Egypt or from golden jackal-African wolf hybrids in the region. In Egypt, in particular in the Sinai Peninsula, which serves as a land bridge between Asia and Africa, hybrid canids could be a possibility. Eurasian golden jackals from Israel are reported to show signals of hybridization with grey wolves, dogs, and the African wolf [15].



Population status of the African wolf

The basic biology and population status of the African wolf are insufficiently known. Our biological knowledge of the African wolf is further complicated by the fact that many ecological and behavioural conclusions are made based on observations of golden jackals and assuming taxonomic identity between the two. The African wolf is likely to face threats from the growing human population, although it seems to habituate to human propinquity relatively well [49].

There are no data on distribution patterns for the African wolf in recent times and African wolf is still cited as golden jackal in recent publications [50]. However, the geographic range of golden jackal in Africa given by IUCN [48] may be considered as the potential range of the African wolf (Fig. 5). This shows African wolf documented from the Ethiopian highlands to the Rift Valley, across North Africa and the Sahara desert, to the west coast of the continent (but not to the coast of the Bay of Benin). It is thus distributed across a wide range of ecological zones.

Persecution by pastoral communities as a result of livestock predation is probably the greatest challenge for the African wolf populations. Several studies document African wolf as one of the most important livestock predators [51–55].

All wolves living near human occupation risk interbreeding with domestic dogs. All *Canis* spp. share the same chromosome number ($2n = 78$) [56] and occasionally interbreed in the wild [57, 58]. The domestic dog, as a descendant of the wolf, mates with wild canids [59, 60], including the Ethiopian wolf [61]. To our

knowledge no record of hybridization with the African wolf exists, although Rueness et al. [14] found evidence of introgression in one of their samples.

There are five species of large and medium sized canids in Africa (side-striped and black-backed jackals, (*Lupulella* spp.) African wolf (*Canis lupaster*), Ethiopian wolf (*Canis simensis*) and African wild dog [*Lycaon pictus*]). The jackal and African wild dog lineages have long fossil records in Africa [62, 63] and can be considered endemic taxa following initial entry of Canidae into Africa in the latest Miocene. The two species of *Canis* are likely to be relatively recent immigrants from lineages originating in Eurasia. Neither lineage has a definitive fossil record in Africa or elsewhere, so their evolutionary history remains to be discovered, including why they were able to successfully colonize Africa in the face of the presence of the endemic lineages already there.

Conclusions

The erroneous inclusion of the African wolf (*Canis lupaster*) in the taxonomic envelope of Eurasian golden jackal (*Canis aureus*) has obscured the unique evolutionary history of the species. For a century, the African wolf was considered as a part of a widely distributed species with a recent history of immigration into Africa [13]. New research is now needed to assess the evolutionary history and population status of *C. lupaster* and to understand the biology of this species. While there is little evidence for the presence of Eurasian golden jackal in Africa, further study is needed to confirm whether it may be present in eastern Egypt.

Additional files

- Additional file 1:** Comment on use of *Lupulella*. (DOCX 115 kb)
- Additional file 2:** Additional information: tables. The file contains tables from S1 to S9. (DOC 358 kb)
- Additional file 3:** Metric data. Contains all the morphometric measurements taken for the study. (XLS 127 kb)
- Additional file 4:** Expanded synonymy of *Canis lupaster*. (DOCX 85 kb)
- Additional file 5:** Additional information: figures. The file contains figures from S1 S5. (PDF 5588 kb)
- Additional file 6:** Taxonomy and nomenclatural history of the African wolf. (DOCX 3905 kb)

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Availability of data and materials

This work has been registered in Zoobank: <http://zoobank.org/NomenclaturalActs/2D51EA46-45D3-4F31-BCC5-7AA1221F66DB>. The LSID for this publication is: [lsid:zoobank.org/act:2D51EA46-45D3-4F31-BCC5-7AA1221F66DB](http://zoobank.org/act:2D51EA46-45D3-4F31-BCC5-7AA1221F66DB). Data are accessible in the electronic supplementary material. All genetic data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.63rb4>.

Authors' contributions

SV and AA did most of the research and writing; LW assembled the historic literature used, helped acquire data and assisted in the writing; NCS supervised the study and helped interpret the data as well as assisted in the writing. All authors gave final approval for publication.

Competing interests

The authors declare that they have no competing interests.

Consent to publication

Not applicable.

Ethics approval

Ethiopian Wildlife Conservation Authority approved permits for capture and immobilization of the African wolf.

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