A *de novo* reference genome of the golden jackal, *Canis aureus*

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Abstract

The golden jackal (*Canis aureus*) is rapidly expanding its range in Europe, driven by climate and habitat changes, human influence, and changes in competition with wolves. Its ecological flexibility enables it to thrive in various habitats, including urban areas, raising concerns about its potential role in spreading zoonotic diseases. Jackals may act as reservoirs for pathogens such as Lyme disease and babesiosis, affecting wildlife, humans, and pets. Their close genetic relationship with domestic dogs also increases the risk of hybridization and host-jumping, complicating disease dynamics.

To better understand their dispersal ability and host-pathogen dynamics, we present the first chromosome-level genome assembly of the golden jackal, generated using PacBio HiFi sequencing and reference-based scaffolding. The final assembly has a total length of 2.53 Gb in 325 scaffolds, with 98.41% of the sequence anchored to the expected 38+XY chromosomes. The assembly shows high contiguity, with scaffold and contig N50 values

of 68.03 Mb and 56.64 Mb, respectively. Annotation revealed 26,084 protein-coding genes, and repetitive elements account for 40.58% of the total assembly.

This high-quality reference genome provides an essential resource for studying the genetic basis of the golden jackal's adaptation, ecological interactions, and potential as a zoonotic reservoir. It also supports efforts to monitor population expansion and its effects on ecosystems. By advancing our understanding of golden jackal genetics, this work enables future research on evolution, host-pathogen dynamics, and the broader consequences of wildlife dispersal in a rapidly changing environment.

Keywords

Canidae, Zoonoses, Range expansion, Climate change, Pathogen transmission, Wildlife–human interaction

Introduction

Canids (*Canidae*) are a diverse group of mostly carnivorous mammals that exhibit a wide range of ecological adaptations and social behaviors (Allen, 2017). The approximately 35 species are distributed across all continents except Antarctica, highlighting their ability to thrive in vastly different environments (Krofel et al., 2022). One such species, the golden jackal (*Canis aureus* LINNAEUS, 1758), is a mid-sized canid that has been experiencing an accelerated natural dispersal, particularly within Western Asia and into Europe (Hatlauf et al., 2021). This expansion is thought to be driven by a combination of several factors, including climate change, shifts in habitat, land-use changes, and other human activities, all of which have facilitated its range expansion (Krofel et al., 2017; Spassov & Acosta-Pankov, 2019).

The golden jackal's notable adaptability allows it to occupy a wide array of habitats, ranging from forests and grasslands to urban environments (Salek et al., 2014; Torretta et al., 2020). Its opportunistic feeding habits, which include a broad diet of small mammals, birds, insects, fruits, and vegetables, make it highly resilient and capable of colonizing new areas (Lanszki et al., 2022). While the presence of golden jackals in new

ecosystems can provide benefits, such as natural pest control by regulating populations of rodents and other small vertebrates (Lanszki et al., 2016), the species' expansion also presents potential challenges (Gherman & Mihalca, 2017). As jackals move into new areas, they may compete with native species for resources and potentially disrupt local ecosystems (Krofel et al., 2017; Serva et al., 2023). Additionally, the golden jackal's capacity to survive in urban environments brings it into closer proximity with humans, which increases the likelihood of interaction with domestic animals, raising concerns about zoonotic disease transmission (Hatlauf, 2024; Lapid et al., 2023).

Figure 1. Golden jackal (*Canis aureus*) ©Jennifer Hatlauf

Recent studies have focused on the potential public health risks associated with the movement of golden jackals, especially in light of the discovery of jackals in Denmark carrying tick vectors and zoonotic pathogens (Klitgaard et al., 2017). Pathogens, such as those transmitted by ticks, can pose significant risks to both wildlife and human health, which underscores the importance of monitoring the spread of this species. The potential for golden jackals to carry and transmit diseases like Lyme disease and babesiosis demonstrates how their expanding range could influence the epidemiology of zoonoses,

78 particularly in regions where the jackal may interact with domestic animals and humans
79 (Lymbery et al., 2014). Furthermore, the close phylogenetic relationship between golden
80 jackals and domestic dogs (*Canis lupus familiaris*) raises the possibility of hybridization
81 and host jumping, which could exacerbate the spread of zoonotic diseases or introduce
82 novel pathogens into local ecosystems (Galov et al., 2015; Gherman & Mihalca, 2017;
83 Stefanovic et al., 2024).

84 Given the important ecological role golden jackals play in their current and future
85 habitats, they serve as important models for understanding climate-mediated dispersal
86 of zoonotic diseases. Their expansion is a good example of how environmental changes
87 and human-induced factors influence the movement of wildlife and the pathogens they
88 carry. Studying jackals offers valuable insights into the broader dynamics of host-
89 pathogen coevolution and the transmission of diseases across species boundaries. To
90 support these efforts, a comprehensive genomic resource is essential.

91 In this study, we present the first chromosome-level genome assembly of the
92 golden jackal, generated using PacBio HiFi long-read sequencing, supplemented by
93 reference-based scaffolding. This high-quality reference genome provides an invaluable
94 tool for investigating the genetic basis of the species' adaptation to new environments
95 and its interactions with both its ecosystem and pathogens. It also enables more effective
96 monitoring of the species and the diseases it may carry, facilitating a better
97 understanding of how climate change and landscape fragmentation contribute to the
98 spread of zoonotic diseases. By advancing our genetic knowledge of golden jackals, we
99 provide a foundation for future studies on the evolution, population dynamics, and
100 ecological impacts of this increasingly prominent species.

101

102 **Materials and Methods**

103 *Sampling and Sequencing*

104 Tissue samples from a subadult male golden jackal (sample ID: CA_001; PathoNo.:
105 SK/123/23) shot by a hunter in Villach, Carinthia, Austria, were collected during post-
106 mortem examination at the University of Veterinary Medicine Vienna, Austria, on

107 06.02.2023 and stored frozen at -80°C. High molecular weight DNA was extracted from
108 spleen tissue using the innuPrep SE HMW kit (IST Innuscreen GmbH, Germany) according
109 to the manufacturer's recommendations. The quantity and quality of the DNA were
110 evaluated using the QuantiFluor ONE dsDNA System on the Quantus Fluorometer
111 (Promega Corporation, USA) and the Genomic DNA Screen Tape on the Agilent 4150
112 TapeStation system (Agilent Technologies, Inc., USA), respectively.

113 Library preparation for Pacific Biosciences of California, Inc (PacBio) circular consensus
114 sequencing (CCS) was prepared using the SMRTbell Express Prep Kit 3.0 (PacBio, USA)
115 and sequenced on the PacBio Revio system.

116

117 *Assembly and QC*

118 The PacBio-generated raw data BAM file was converted into FASTQ format using
119 BAM2fastx v.1.3.0, a PacBio Secondary Analysis Tool
120 (https://github.com/PacificBiosciences/pbbioconda). The initial assemblies, including
121 two, which resemble the two potential parental haplotypes, were generated with hifiasm
122 v.0.24.0 (RRID:SCR_021069) (Cheng et al., 2021) using standard parameters. As sample
123 quality was insufficient for a proximity-ligation library, we did not aim for a haplotype-
124 resolved assembly but instead continued with the pseudohaploid assembly for the next
125 steps. As we were unable to use Hi-C data for the scaffolding, due to the fact that the
126 sample was stored in ethanol, we instead used the Mexican gray wolf assembly
127 (Accession No. GCF_048164855.1) for a reference-based scaffolding with RagTag v.2.1.0
128 (Alonge et al., 2022). Subsequently, gaps in the scaffolded assembly were breached using
129 the original PacBio long-read data with TGS_gapcloser v.1.2.1 (RRID:SCR_017633)(Xu et

130 al., 2020). The mitochondrial genome was assembled using the MitoHiFi workflow
131 (RRID:SCR_026369) in Galaxy v.3.2.3 (RRID:SCR_006281)(Blankenberg et al., 2014;
132 Uliano-Silva et al., 2023).

133

134 *Assembly Quality Assessment*

135 Assembly statistics to evaluate contiguity of the assembly were generated with Quast
136 v.5.0.2 (RRID:SCR_001228)(Gurevich et al., 2013). The completeness of the assembly
137 was assessed by gene set completeness analyses using BUSCO v.5.8.3
138 (RRID:SCR_015008) (Manni et al., 2021) and compleasm v.0.2.7
139 (RRID:SCR_026370)(Huang & Li, 2023) against the carnivora_odb12 orthologs dataset, as
140 well as based on k-mers (k=21) using Merqury v.1.3 with Meryl v. 1.3
141 (RRID:SCR_022964)(Rhie et al., 2021). Minimap2 v.2.28 (RRID:SCR_018550)(Li, 2018) and
142 samtools v.1.21 (RRID:SCR_002105)(Danecek et al., 2021) were used to map the PacBio
143 reads to the final assembly and sort the mapping file to check the mapping rate with
144 Qualimap bamqc v.2.3 (RRID:SCR_001209)(Okonechnikov et al., 2016). The mapping file
145 was also used together with the results from a Diamond v.2.1.10
146 (RRID:SCR_016071)(Buchfink et al., 2021) search against Swiss-Prot (release 2025-01)
147 (The UniProt Consortium, 2019) in Blobtools v. 1.1 (RRID:SCR_017618)(Laetsch & Blaxter,
148 2017) to check for potential contamination.

149

150 *Annotation*

151 Repeats in the assembly were annotated with RepeatMasker v.4.1.0 (RRID:SCR_012954)
152 (Smit et al., 2015) using a custom *de novo* repeat library generated from the presented

153 assembly with RepeatModeler v.2.0.1 (RRID:SCR_015027) (Flynn et al., 2020) combined
154 with the Canidae specific repeats from Dfam 3.1 and RepBase (release 20181026) (Bao
155 et al., 2015; Storer et al., 2021). Interspersed repeats were hardmasked (Ns) while simple
156 repeats were softmasked (lowercase) in preparation for the gene annotation.

157 Genes were predicted using the homology-based approach implemented in the GeMoMa
158 pipeline v.1.7.1 (RRID:SCR_017646) (Keilwagen et al., 2016, 2018) using MMseqs2 v.
159 13.45111 (RRID:SCR_022962) (Steinegger & Söding, 2017) as an alignment tool. The
160 following six mammalian genomes and corresponding annotations were used as
161 references: *Homo sapiens* (GCF_000001405.40), *Mus musculus* (GCF_000001635.27),
162 *Canis lupus familiaris* (German Shepherd, GCF_011100685.1; Wang et al., 2021), *Vulpes*
163 *vulpes* (GCF_048418805.1), *Vulpes lagopus* (GCF_018345385.1;, *Canis lupus baileyi*
164 (GCF_048164855.1; Rhie et al., 2021).

165 Subsequently, the proteins predicted by GeMoMa were functionally annotated by a
166 BLASTP v.2.11.0+ (RRID:SCR_001010) (Camacho et al., 2009) search against the Swiss-
167 Prot database (RRID:SCR_002380; release 2025-01) (The UniProt Consortium, 2019) with
168 an e-value cutoff of 10^{-6}. Gene ontology (GO) terms, domains, and motifs were further
169 annotated using InterProScan v.5.59.91 (RRID:SCR_005829) (Jones et al., 2014;
170 Quevillon et al., 2005). BUSCO v.5.8.3 (RRID:SCR_015008) (Manni et al., 2021) and
171 compleasm v.0.2.7 (RRID:SCR_026370) (Huang & Li, 2023) were used to evaluate gene
172 completeness in reference to the carnivora_odb12 dataset.

173

174 **Table 1. Software and versions used to generate the *Canis aureus* assembly.**

Pipeline Step	***Software***	***Version***

PacBio BAM to FASTQ	BAM2fastx	v.1.3.0
assembly & long-read polishing	hifiasm	v.0.24.0
Scaffolding	RagTag	v.2.1.0
Gap-closing	TGS-GapCloser	v.1.2.1
Mitochondrial genome assembly	MitoHiFi in Galaxy	v.3.2.3
Assembly statistics	Quast	v.5.0.2
Gene set completeness	BUSCO	v.5.8.3
	compelasm	v.0.2.7
Assembly completeness	Merqury	v.1.3
Mapping of long reads	minimap2	v.2.28
Sort & index BAM	samtools	v.1.21
Mapping statistics	QualiMap	v.2.3
Contamination analyses	Diamond	v.2.1.10
	Blobtools	v.1.1
Repeat library	RepeatModeler	v.2.0.1
Repeat masking	RepeatMasker	v.4.1.0
Homology-based gene prediction	GeMoMa pipeline	v.1.7.1
	MMseqs2	v.13.45111
Functional annotation	BLASTP	v.2.11.0+
	InterProScan	v.5.59.91

Results and Discussion

Sequencing of the two prepared CSS libraries on the PacBio Revio platform resulted in 6,520,091 HiFi reads (86.95 Gb) with a mean read length of 13.34 kb and a mean quality of 29.7 (Supplementary Material S1). The initial assembly with Hifiasm resulted in a draft assembly of 2.54 Gb with 502 contigs and a contig N50 of 55.91 Mb (Table 2A). Due to the sample quality, we were unable to generate proximity ligation libraries for scaffolding and

183 opted for a reference-based scaffolding approach. After removing some of the smallest
184 contigs, due to potential bacterial contamination (taxonomic assignments, variation in
185 sequencing depth and GC-content) identified by BlobTools (Fig. 2C; Supplementary Material
186 S2), the final highly contiguous chromosome-level assembly has a total length of 2.53 Gb with
187 325 scaffolds and a scaffold and contig N50 of 68.03 MB and 56.64 Mb, respectively (Table
188 2A). Of the 325 scaffolds (incl. the mitochondrial genome), the largest 40 (> 7 Mb)
189 corresponding to the expected 38 autosomes and the two allosomes (Tanomtong et al., 2015)
190 span 98.41% of the total assembly length, resulting in a L50 of 15 scaffolds. Of the 13,727
191 BUSCO genes in the carnivora_odb12 dataset, BUSCO identified 13,392 (97.6%) as complete
192 single copy and 158 (1.2%) as duplicated BUSCOs, while compleasm found 13,528 (98.55%)
193 single copy and 126 (0.16%) duplicated BUSCOs (Fig. 2A). The high BUSCO and compleasm
194 scores, as well as a high mapping rate of 99.88% and a mapping quality of 39.7, highlight the
195 quality of the presented assembly. Furthermore, Merqury estimated a k-mer completeness
196 score of 96.93% with a QV score of 63.57, corresponding to an error rate of 4.39e-07 (see also
197 Fig. 2 B).
198 The mitochondrial genome assembled from the HiFi reads was circular with a length of 16,729
199 bp, following the standard composition and structure of vertebrate mitochondrial genome
200 sequences with 13 protein-coding genes, 2 rRNAs, and 22 tRNAs (Fig. 2D).
201
202 **Annotation**
203 **Repeat annotation**
204 Repeat annotation identified a repeat content in the final assembly *VMU_Caureus_v1.0* of
205 40.58% or 1.02 Gb (Table 2B). With 24.19% of the assembly Long Interspersed Nuclear
206 Elements (LINEs) were the most common repeats, followed by LTR Elements (5.48%) and Short

Interspersed Nuclear Elements (SINEs, 4.95%). Non-Retroelements such as DNA Transposons, small RNA, and simple repeats, each accounted for less than 4% of the assembly.

Gene annotation

Homology-based gene prediction with GeMoMA identified 26,084 genes in *VMU_Caureus_v.1.0*. The median gene length was 6,370 bp, spanning 469.26 Mb of the assembly. BUSCO identified 41.2% (n = 5,653) of the 13,727 Carnivora orthologous genes from the carnivora_odb12 BUSCO dataset in the assembly as single copy and 46.4% (n = 6,372) as duplicated, with 1,089 BUSCO genes (7.9%) missing (Fig. 2A). Compleasm identified 37.42% (n = 5,137) BUSCOs as single-copy and 50.11% (n = 6,879) as duplicated, with 7.71% (n = 1,058) missing (Fig. 2A). InterProScan functionally annotated 61,027 of the 61,813 predicted proteins (98.73%) and assigned 53,147 proteins (85.98%) to the Reactome and assigned at least one Gene Ontology (GO) term to 45,071 proteins (72.92%). Furthermore, 96.73 % (n=59,792) of the predicted proteins were matched to entries in the Swiss-Prot database.

Conclusions

High-quality long-read-based genome assemblies are an essential resource for a large variety of evolutionary, ecological, and phylogeographic analyses, as well as for biodiversity monitoring. The presented long-read-based chromosome-level genome assembly of the golden jackal is the first genome assembly for this species and thus provides a solid basis for in-depth genomic studies on the species' range expansion, population dynamics, adaptability to new environments, and potential as zoonotic disease reservoirs.

Table 2. Assembly statistics of *VMU_Caureus_v.1.0* (A) and its repeat content (B)

A

	Scaffold-level	Contig-level	
	VMU_Caureus_v.1.0	*VMU_Caureus_v.1.0**	*VMU_Caureus_draft_asm***
No. of scaffolds/contigs	**325**	**384**	**502**
No. of scaffolds/contigs (> 10 kbp)	**325**	**384**	**502**
L50	**15**	**18**	**18**
N50 (bp)	**68,033,816**	**56,644,425**	**55,907,118**
Max. scaffold/contig length(bp)	**124,444,185**	**123,390,866**	**123,390,866**
Total length (bp)	**2,530,537,450**	**2,530,531,550**	**2,537,222,849**
GC (%)	**41.58**	**41.58**	**41.61**
No. of N's	**5,900**	**0**	**0**
No. of N's per 100 kbp	**0.23**	**0.00**	**0.00**

***broken into contigs at gaps with a length of ≥ 10 N's. Statistics for these columns are based on contigs, the remaining columns are based on scaffolds.**
****hifiasm draft assembly before reference-based scaffolding and gapclosing**

B

Type of element	Number of elements	Percentage of assembly
SINEs	**915,079**	**4.95%**
LINEs:	**1,980,627**	**24.19%**
LTR elements	**434,890**	**5.48%**
DNA transposons	**340,764**	**2.68%**
Rolling-circles	**1,562**	**0.02%**
Unclassified	**24,159**	**0.40%**
Satellites	**2**	**0.00%**
Small RNA	**632,699**	**3.31%**
Simple repeats	**835,984**	**2.25%**
Low complexity	**102,275**	**0.23%**
Total		**40.22%**

231

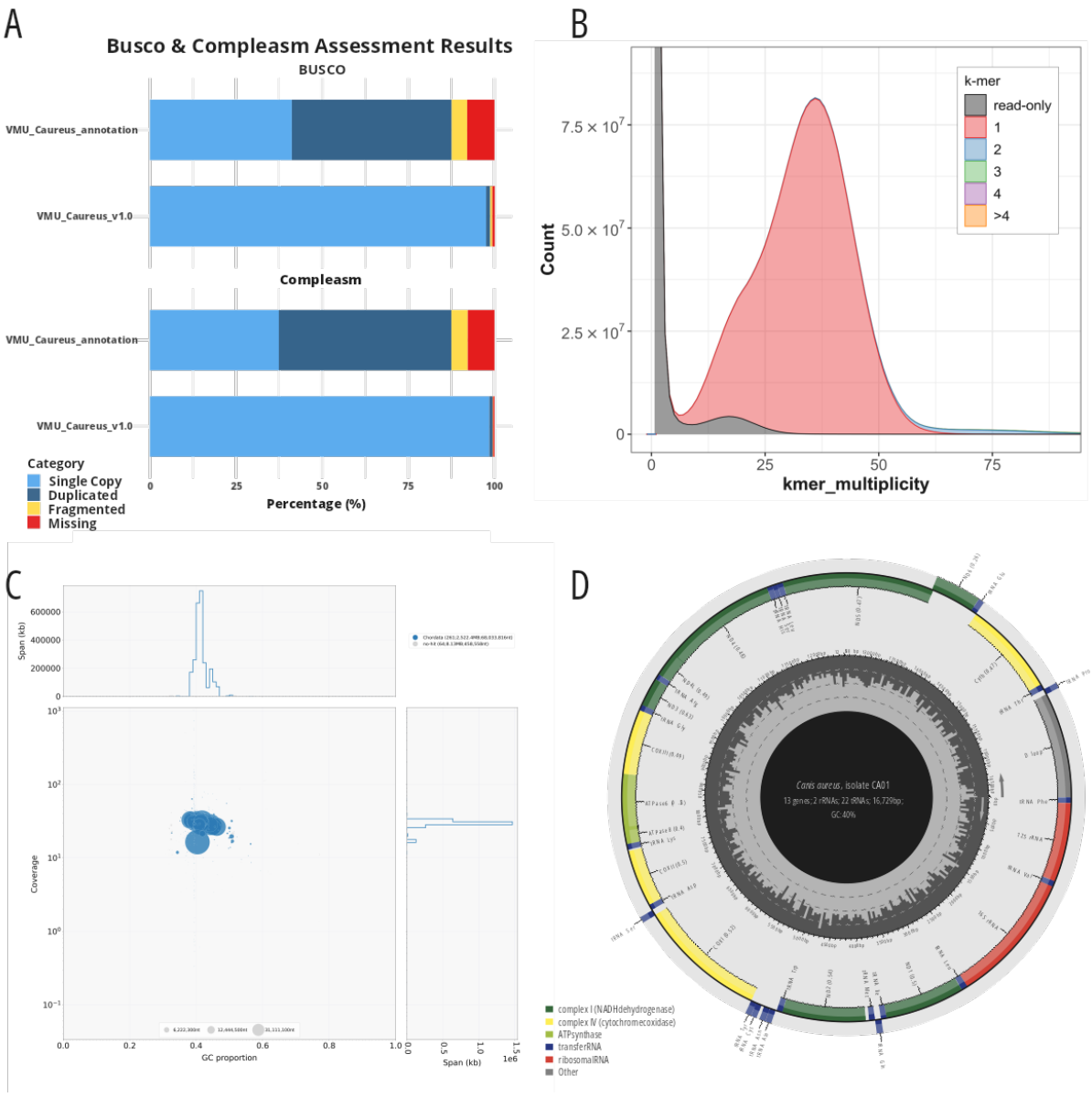

Figure 2. Assembly quality assessment and mitochondrial genome of *VMU_Caureus_v1.0*.

(A) BUSCO and compleasm assessment results for the final assembly and the annotation using the carnivora_obd12 dataset. (B) Merqury k-mer copy number spectrum plot.(C) BlobPlot analysis comparing GC content (x-axis) and sequence coverage of the PacBio data (y-axis) after removal of potentially contaminated scaffolds, see Supplementary Material S2 for BlobPlot before removal. The color of the “blobs” represents taxonomic

assignment of the scaffolds based on the Swiss-Prot database. (D) Annotation of the circular mitochondrial genome of CA01.

Data Accessibility

All underlying read data and the assembly are available under NCBI GenBank BioProject PRJNA1259920. In addition, the chromosome-level and draft assembly, as well as the annotation results, are available on Zenodo (https://doi.org/10.5281/zenodo.16779415).

Competing Interests

The authors declare no competing interests.

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