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

Sven Winter[1,2,3,*], René Meißner[1], Stefan Prost[4,5], Carola Greve[6], Charlotte Gerheim[6], Marine Arakelyan[7], Sargis Aghayan[8], Astghik Ghazaryan[7], Jennifer Hatlauf[9], Pamela A. Burger[1,*]

[1]Research Institute of Wildlife Ecology, University of Veterinary Medicine Vienna, Vienna, Austria

[2]Faculty of Science and Technology, University of the Faroe Islands, Tórshavn, The Faroe Islands

[3]Senckenberg Biodiversity and Climate Research Centre, Frankfurt am Main, Germany

[4]Ecology and Genetics Research Unit, University of Oulu, Oulu, Finland

[5]Natural History Museum Vienna, Central Research Laboratories, Vienna, Austria

[6]Senckenberg Research Institute and Museum, Frankfurt am Main, Germany

[7]Institute of Zoology, Yerevan State University, Yerevan, Armenia

[8]Scientific Center of Zoology and Hydroecology, National Academy of Sciences of the Armenian State

[9]Institute of Wildlife Biology and Game Management, BOKU University, Vienna, Austria

Contact for correspondence*:

Sven Winter, sven.winter@vetmeduni.ac.at

Pamela Burger, pamela.burger@vetmeduni.ac.at

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

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

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

Materials and Methods

Sampling and Sequencing

107 Tissue samples from a subadult male golden jackal (sample ID: CA_001; PathoNo.:
108 SK/123/23) shot by a hunter in Villach, Carinthia, Austria, were collected during post-
109 mortem examination at the University of Veterinary Medicine Vienna, Austria, on
110 06.02.2023 and stored frozen at -80°C. High molecular weight DNA was extracted from
111 spleen tissue using the innuPrep SE HMW kit (IST Innuscreen GmbH, Germany)
112 according to the manufacturer's recommendations. The quantity and quality of the DNA
113 were evaluated using the QuantiFluor ONE dsDNA System on the Quantus Fluorometer
114 (Promega Corporation, USA) and the Genomic DNA Screen Tape on the Agilent 4150
115 TapeStation system (Agilent Technologies, Inc., USA), respectively.

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

119

120 *Assembly and QC*

121 The PacBio-generated raw data BAM file was converted into FASTQ format using
122 BAM2fastx v.1.3.0, a PacBio Secondary Analysis Tool
123 (https://github.com/PacificBiosciences/pbbioconda). The initial assemblies, including
124 two, which resemble the two potential parental haplotypes, were generated with
125 hifiasm v.0.24.0 (RRID:SCR_021069) (Cheng et al., 2021) using standard parameters. As
126 sample quality was insufficient for a proximity-ligation library, we did not aim for a
127 haplotype-resolved assembly but instead continued with the pseudohaploid assembly
128 for the next steps. As we were unable to use Hi-C data for the scaffolding, due to the
129 fact that the sample was stored in ethanol, we instead used the Mexican gray wolf

130 assembly (Accession No. GCF_048164855.1) for a reference-based scaffolding with
131 RagTag v.2.1.0 (Alonge et al., 2022). Subsequently, gaps in the scaffolded assembly
132 were breached using the original PacBio long-read data with TGS_gapcloser v.1.2.1
133 (RRID:SCR_017633)(Xu et al., 2020). The mitochondrial genome was assembled using
134 the MitoHiFi workflow (RRID:SCR_026369) in Galaxy v.3.2.3
135 (RRID:SCR_006281)(Blankenberg et al., 2014; Uliano-Silva et al., 2023).

136

137 *Assembly Quality Assessment*

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

152

153 *Annotation*

154 Repeats in the assembly were annotated with RepeatMasker v.4.1.0
155 (RRID:SCR_012954) (Smit et al., 2015) using a custom *de novo* repeat library generated
156 from the presented assembly with RepeatModeler v.2.0.1 (RRID:SCR_015027) (Flynn et
157 al., 2020) combined with the Canidae specific repeats from Dfam 3.1 and RepBase
158 (release 20181026) (Bao et al., 2015; Storer et al., 2021). Interspersed repeats were
159 hardmasked (Ns) while simple repeats were softmasked (lowercase) in preparation for
160 the gene annotation.

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

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

177

178 **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

179

180

181 **Results and Discussion**

182 Sequencing of the two prepared CSS libraries on the PacBio Revio platform resulted in

183 6,520,091 HiFi reads (86.95 Gb) with a mean read length of 13.34 kb and a mean quality of

184 29.7 (Supplementary Material S1). The initial assembly with Hifiasm resulted in a draft
185 assembly of 2.54 Gb with 502 contigs and a contig N50 of 55.91 Mb (Table 2A). Due to the
186 sample quality, we were unable to generate proximity ligation libraries for scaffolding and
187 opted for a reference-based scaffolding approach. After removing some of the smallest
188 contigs, due to potential bacterial contamination (taxonomic assignments, variation in
189 sequencing depth and GC-content) identified by BlobTools (Fig. 2C; Supplementary Material
190 S2), the final highly contiguous chromosome-level assembly has a total length of 2.53 Gb
191 with 325 scaffolds and a scaffold and contig N50 of 68.03 MB and 56.64 Mb, respectively
192 (Table 2A). Of the 325 scaffolds (incl. the mitochondrial genome), the largest 40 (> 7 Mb)
193 corresponding to the expected 38 autosomes and the two allosomes (Tanomtong et al.,
194 2015) span 98.41% of the total assembly length, resulting in a L50 of 15 scaffolds. Of the
195 13,727 BUSCO genes in the carnivora_odb12 dataset, BUSCO identified 13,392 (97.6%) as
196 complete single copy and 158 (1.2%) as duplicated BUSCOs, while compleasm found 13,528
197 (98.55%) single copy and 126 (0.16%) duplicated BUSCOs (Fig. 2A). The high BUSCO and
198 compleasm scores, as well as a high mapping rate of 99.88% and a mapping quality of 39.7,
199 highlight the quality of the presented assembly. Furthermore, Merqury estimated a k-mer
200 completeness score of 96.93% with a QV score of 63.57, corresponding to an error rate of
201 4.39e-07 (see also Fig. 2 B).
202 The mitochondrial genome assembled from the HiFi reads was circular with a length of
203 16,729 bp, following the standard composition and structure of vertebrate mitochondrial
204 genome sequences with 13 protein-coding genes, 2 rRNAs, and 22 tRNAs (Fig. 2D).
205
206 **Annotation**
207 **Repeat annotation**

208 Repeat annotation identified a repeat content in the final assembly *VMU_Caureus_v1.0* of
209 40.58% or 1.02 Gb (Table 2B). With 24.19% of the assembly Long Interspersed Nuclear
210 Elements (LINEs) were the most common repeats, followed by LTR Elements (5.48%) and
211 Short Interspersed Nuclear Elements (SINEs, 4.95%). Non-Retroelements such as DNA
212 Transposons, small RNA, and simple repeats, each accounted for less than 4% of the
213 assembly.
214
215 **Gene annotation**
216 Homology-based gene prediction with GeMoMA identified 26,084 genes in
217 *VMU_Caureus_v.1.0*. The median gene length was 6,370 bp, spanning 469.26 Mb of the
218 assembly. BUSCO identified 41.2% (n = 5,653) of the 13,727 Carnivora orthologous genes
219 from the carnivora_odb12 BUSCO dataset in the assembly as single copy and 46.4% (n =
220 6,372) as duplicated, with 1,089 BUSCO genes (7.9%) missing (Fig. 2A). Compleasm identified
221 37.42% (n = 5,137) BUSCOs as single-copy and 50.11% (n = 6,879) as duplicated, with 7.71%
222 (n = 1,058) missing (Fig. 2A). InterProScan functionally annotated 61,027 of the 61,813
223 predicted proteins (98.73%) and assigned 53,147 proteins (85.98%) to the Reactome and
224 assigned at least one Gene Ontology (GO) term to 45,071 proteins (72.92%). Furthermore,
225 96.73 % (n=59,792) of the predicted proteins were matched to entries in the Swiss-Prot
226 database.
227
228 **Conclusions**
229 High-quality long-read-based genome assemblies are an essential resource for a large variety
230 of evolutionary, ecological, and phylogeographic analyses, as well as for biodiversity
231 monitoring. The presented long-read-based chromosome-level genome assembly of the

232 golden jackal is the first genome assembly for this species and thus provides a solid basis for
233 in-depth genomic studies on the species' range expansion, population dynamics, adaptability
234 to new environments, and potential as zoonotic disease reservoirs.
235
236 **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%

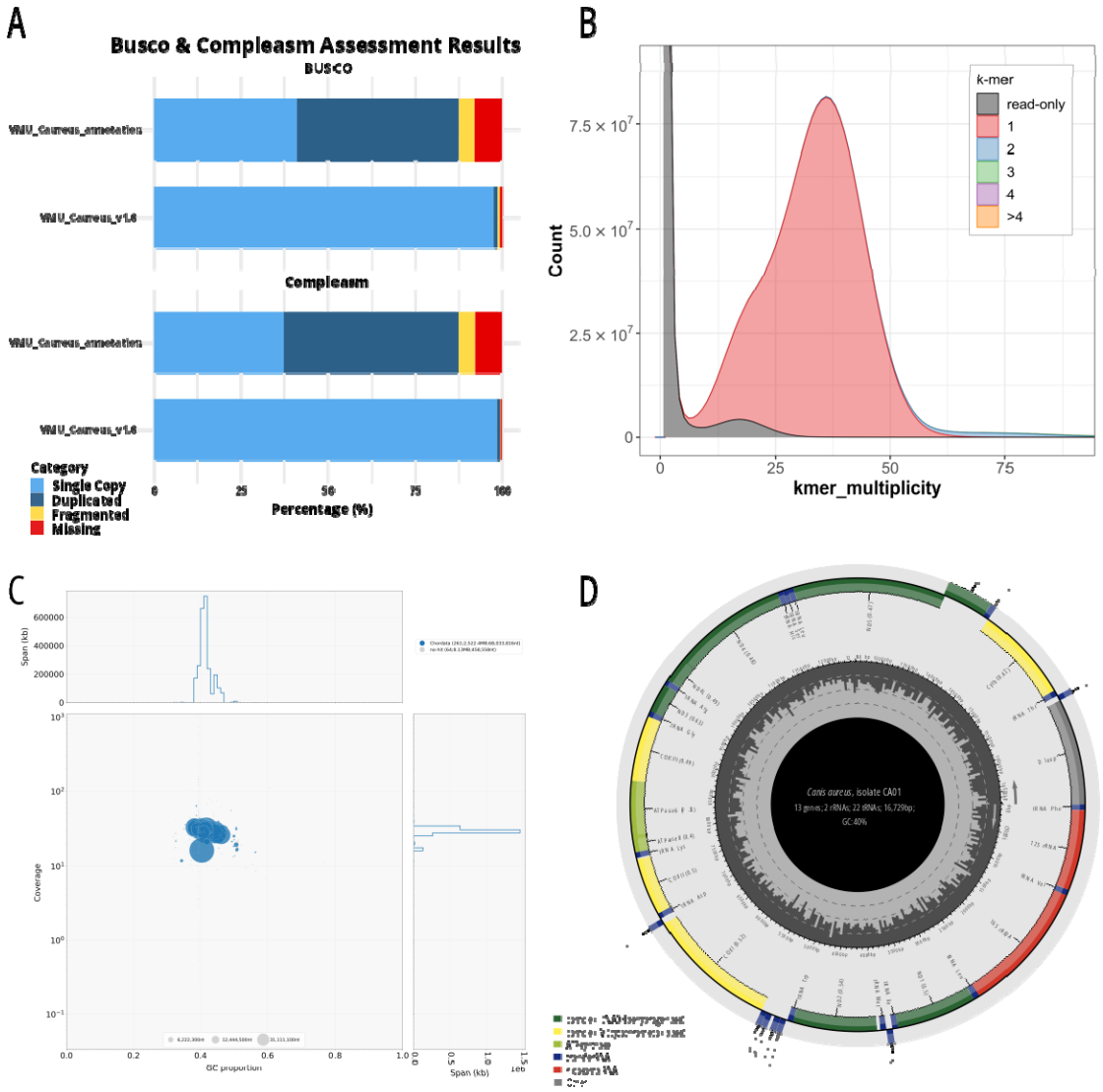

Figure 2. Assembly quality assessment and mitochondrial genome of *VMU_Caureus_v1.0*.

(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

244 coverage of the PacBio data (y-axis) after removal of potentially contaminated scaffolds,
245 see Supplementary Material S2 for BlobPlot before removal. The color of the "blobs"
246 represents taxonomic assignment of the scaffolds based on the Swiss-Prot database.
247 (D) Annotation of the circular mitochondrial genome of CA01.

248 **Data Accessibility**

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

253 **Competing Interests**

254 The authors declare no competing interests.

255 **Acknowledgements**

256 We are grateful for funding from the Austrian Partnership Program for Higher Education
257 and Research (APPEAR) project 278 by Austria's Agency for Education and
258 Internationalisation (OEAD). S.W. acknowledges funding from the Austrian Science
259 Fund (FWF) project I508-B (to P.B.).We thank Anna Kübber-Heiss and Helmut Dier from
260 the Pathology Department of the University of Veterinary Medicine Vienna for access to
261 the frozen tissue collection and the Bioscientia Institut für Medizinische Diagnostik
262 GmbH (Ingelheim, Germany) for providing the PacBio SMRT sequencing service on the
263 PacBio Revio platform.

264

265 **References**

Allen, B. (2017). Challenges and opportunities for the study and conservation of large carnivores. *Food Webs*, *12*, 1–2. https://doi.org/10.1016/j.fooweb.2017.09.001

Alonge, M., Lebeigle, L., Kirsche, M., Jenike, K., Ou, S., Aganezov, S., Wang, X., Lippman, Z. B., Schatz, M. C., & Soyk, S. (2022). Automated assembly scaffolding using RagTag elevates a new tomato system for high-throughput genome editing. *Genome Biology*, *23*(1), 258. https://doi.org/10.1186/s13059-022-02823-7

Bao, W., Kojima, K. K., & Kohany, O. (2015). Repbase Update, a database of repetitive elements in eukaryotic genomes. *Mobile DNA*, *6*(1), 11. https://doi.org/10.1186/s13100-015-0041-9

Blankenberg, D., Von Kuster, G., Bouvier, E., Baker, D., Afgan, E., Stoler, N., Taylor, J., Nekrutenko, A., & Galaxy Team. (2014). Dissemination of scientific software with Galaxy ToolShed. *Genome Biology*, *15*(2), 403. https://doi.org/10.1186/gb4161

Buchfink, B., Reuter, K., & Drost, H.-G. (2021). Sensitive protein alignments at tree-of-life scale using DIAMOND. *Nature Methods*, *18*(4), 366–368. https://doi.org/10.1038/s41592-021-01101-x

Camacho, C., Coulouris, G., Avagyan, V., Ma, N., Papadopoulos, J., Bealer, K., & Madden, T. L. (2009). BLAST+: Architecture and applications. *BMC Bioinformatics*, *10*(1), 421. https://doi.org/10.1186/1471-2105-10-421

Cheng, H., Concepcion, G. T., Feng, X., Zhang, H., & Li, H. (2021). Haplotype-resolved de novo assembly using phased assembly graphs with hifiasm. *Nature Methods*, *18*(2), 170–175. https://doi.org/10.1038/s41592-020-01056-5

Danecek, P., Bonfield, J. K., Liddle, J., Marshall, J., Ohan, V., Pollard, M. O., Whitwham, A., Keane, T., McCarthy, S. A., Davies, R. M., & Li, H. (2021). Twelve years of SAMtools and BCFtools. *GigaScience*, *10*(2), giab008. https://doi.org/10.1093/gigascience/giab008

Flynn, J. M., Hubley, R., Goubert, C., Rosen, J., Clark, A. G., Feschotte, C., & Smit, A. F. (2020). RepeatModeler2 for automated genomic discovery of transposable element families. *Proceedings of the National Academy of Sciences*, *117*(17), 9451–9457. https://doi.org/10.1073/pnas.1921046117

Galov, A., Fabbri, E., Caniglia, R., Arbanasić, H., Lapalombella, S., Florijančić, T., Bošković, I., Galaverni, M., & Randi, E. (2015). First evidence of hybridization between golden jackal (Canis aureus) and domestic dog (Canis familiaris) as revealed by genetic markers. *Royal Society Open Science*, *2*(12), 150450. https://doi.org/10.1098/rsos.150450

Gherman, C. M., & Mihalca, A. D. (2017). A synoptic overview of golden jackal parasites reveals high diversity of species. *Parasites & Vectors*, *10*(1), 419. https://doi.org/10.1186/s13071-017-2329-8

Gurevich, A., Saveliev, V., Vyahhi, N., & Tesler, G. (2013). QUAST: Quality assessment tool for genome assemblies. *Bioinformatics*, *29*(8), 1072–1075. https://doi.org/10.1093/bioinformatics/btt086

Hatlauf, J. (2024). Urban encounter: First confirmed record of a golden jackal (Canis aureus) in Vienna, Austria. *Die Bodenkultur: Journal of Land Management, Food and Environment*, *75*(1), 1–7. https://doi.org/10.2478/boku-2024-0001

Hatlauf, J., Bayer, K., Trouwborst, A., & Hackländer, K. (2021). New rules or old concepts? The golden jackal (Canis aureus) and its legal status in Central Europe. *European Journal of Wildlife Research*, *67*(2), 25. https://doi.org/10.1007/s10344-020-01454-2

Huang, N., & Li, H. (2023). compleasm: A faster and more accurate reimplementation of BUSCO. *Bioinformatics*, *39*(10), btad595. https://doi.org/10.1093/bioinformatics/btad595

Jones, P., Binns, D., Chang, H.-Y., Fraser, M., Li, W., McAnulla, C., McWilliam, H., Maslen, J., Mitchell, A., Nuka, G., Pesseat, S., Quinn, A. F., Sangrador-Vegas, A., Scheremetjew, M., Yong, S.-Y., Lopez, R., & Hunter, S. (2014). InterProScan 5: Genome-scale protein function classification. *Bioinformatics*, *30*(9), 1236–1240. https://doi.org/10.1093/bioinformatics/btu031

Keilwagen, J., Hartung, F., Paulini, M., Twardziok, S. O., & Grau, J. (2018). Combining RNA-seq data and homology-based gene prediction for plants, animals and fungi. *BMC Bioinformatics*, *19*(1). https://doi.org/10.1186/s12859-018-2203-5

Keilwagen, J., Wenk, M., Erickson, J. L., Schattat, M. H., Grau, J., & Hartung, F. (2016). Using intron position conservation for homology-based gene prediction. *Nucleic Acids Research*, *44*(9), e89–e89. https://doi.org/10.1093/nar/gkw092

Klitgaard, K., Chriél, M., Isbrand, A., Jensen, T. K., & Bødker, R. (2017). Identification of Dermacentor reticulatus Ticks Carrying Rickettsia raoultii on Migrating Jackal, Denmark. *Emerging Infectious Diseases*, *23*(12), 2072–2074. https://doi.org/10.3201/eid2312.170919

Krofel, M., Giannatos, G., Cirovic, D., Stoyanov, S., & Newsome, T. (2017). *Golden jackal expansion in Europe: A case of mesopredator release triggered by continent-wide wolf persecution?* https://doi.org/10.4404/hystrix-28.1-11819'%255D

Krofel, M., Hatlauf, J., Bogdanowicz, W., Campbell, L. a. D., Godinho, R., Jhala, Y. V., Kitchener, A. C., Koepfli, K.-P., Moehlman, P., Senn, H., Sillero-Zubiri, C., Viranta, S., Werhahn, G., & Alvares, F. (2022). Towards resolving taxonomic uncertainties in wolf, dog and jackal lineages of Africa, Eurasia and Australasia. *Journal of Zoology*, *316*(3), 155–168. https://doi.org/10.1111/jzo.12946

Laetsch, D. R., & Blaxter, M. L. (2017). BlobTools: Interrogation of genome assemblies. *F1000Research*, *6*, 1287. https://doi.org/10.12688/f1000research.12232.1

Lanszki, J., Hayward, M. W., Ranc, N., & Zalewski, A. (2022). Dietary flexibility promotes range expansion: The case of golden jackals in Eurasia. *Journal of Biogeography*, *49*(6), 993–1005. https://doi.org/10.1111/jbi.14372

Lanszki, J., Kurys, A., Szabó, L., Nagyapáti, N., Porter, L. B., & Heltai, M. (2016). Diet composition of the golden jackal and the sympatric red fox in an agricultural area (Hungary). *Folia Zoologica*, *65*(4), 310–322. https://doi.org/10.25225/fozo.v65.i4.a3.2016

Lapid, R., Motro, Y., Craddock, H., Khalfin, B., King, R., Bar-Gal, G. K., & Moran-Gilad, J. (2023). Fecal microbiota of the synanthropic golden jackal (Canis aureus). *Animal Microbiome*, *5*(1), 37. https://doi.org/10.1186/s42523-023-00259-3

Li, H. (2018). Minimap2: Pairwise alignment for nucleotide sequences. *Bioinformatics*, *34*(18), 3094–3100. https://doi.org/10.1093/bioinformatics/bty191

Manni, M., Berkeley, M. R., Seppey, M., Simão, F. A., & Zdobnov, E. M. (2021). BUSCO Update: Novel and Streamlined Workflows along with Broader and Deeper Phylogenetic Coverage for Scoring of Eukaryotic, Prokaryotic, and Viral Genomes. *Molecular Biology and Evolution*, *38*(10), 4647–4654. https://doi.org/10.1093/molbev/msab199

Okonechnikov, K., Conesa, A., & García-Alcalde, F. (2016). Qualimap 2: Advanced multi-sample quality control for high-throughput sequencing data. *Bioinformatics*, *32*(2), 292–294. https://doi.org/10.1093/bioinformatics/btv566

Quevillon, E., Silventoinen, V., Pillai, S., Harte, N., Mulder, N., Apweiler, R., & Lopez, R. (2005). InterProScan: Protein domains identifier. *Nucleic Acids Research*, *33*(suppl_2), W116–W120. https://doi.org/10.1093/nar/gki442

Rhie, A., McCarthy, S. A., Fedrigo, O., Damas, J., Formenti, G., Koren, S., Uliano-Silva, M., Chow, W., Fungtammasan, A., Kim, J., Lee, C., Ko, B. J., Chaisson, M., Gedman, G. L., Cantin, L. J., Thibaud-Nissen, F., Haggerty, L., Bista, I., Smith, M., … Jarvis, E. D. (2021). Towards complete and error-free genome assemblies of all vertebrate species. *Nature*, *592*(7856), 737–746. https://doi.org/10.1038/s41586-021-03451-0

Salek, M., Červinka, J., Banea, O. C., Krofel, M., Ćirović, D., Selanec, I., Penezić, A., Grill, S., & Riegert, J. (2014). Population densities and habitat use of the golden jackal (Canis aureus) in farmlands across the Balkan Peninsula. *European Journal of Wildlife Research*, *60*(2), 193–200. https://doi.org/10.1007/s10344-013-0765-0

Serva, D., Iannella, M., Cittadino, V., & Biondi, M. (2023). A shifting carnivore's community: Habitat modeling suggests increased overlap between the golden jackal and the Eurasian lynx in Europe. *Frontiers in Ecology and Evolution*, *11*. https://doi.org/10.3389/fevo.2023.1165968

Smit, A., Hubley, R., & Green, P. (2015). RepeatModeler Open-1.0. 2008–2015. *Seattle, USA: Institute for Systems Biology*.

Spassov, N., & Acosta-Pankov, I. (2019). Dispersal history of the golden jackal (Canis aureus moreoticus Geoffroy, 1835) in Europe and possible causes of its recent population explosion. *Biodiversity Data Journal*, *7*, e34825. https://doi.org/10.3897/BDJ.7.e34825

Stefanovic, M., Bogdanowicz, W., Adavoudi, R., Martínez-Sosa, F., Doan, K., Flores-Manzanero, A., Srinivas, Y., Banea, O. C., Ćirović, D., D'Amico, G., Djan, M., Giannatos, G., Hatlauf, J., Hayrapetyan, V., Heltai, M., Homel, K., Hulva, P., Ionică, A. M., Jhala, Y. V., … Pilot, M. (2024). Range-wide phylogeography of the golden jackals (*Canis aureus*) reveals multiple sources of recent spatial expansion and admixture with dogs at the expansion front. *Biological Conservation*, *290*, 110448. https://doi.org/10.1016/j.biocon.2024.110448

Steinegger, M., & Soeding, J. (2017). MMseqs2 enables sensitive protein sequence searching for the analysis of massive data sets. *Nature Biotechnology*, *35*(11), 1026–1028. https://doi.org/10.1038/nbt.3988

Storer, J., Hubley, R., Rosen, J., Wheeler, T. J., & Smit, A. F. (2021). The Dfam community resource of transposable element families, sequence models, and genome annotations. *Mobile DNA*, *12*(1), 2. https://doi.org/10.1186/s13100-020-00230-y

Tanomtong, A., Chaiyaphan, P., Supanuam, P., Puramongkol, T., Maneechot, N., & Jangsuwan, N. (2015). The Standard Karyotype of the Asiatic Jackal, Canis aureus (Carnivora, Canidae) from Thailand. *Cytologia*, *80*(1), 3–13. https://doi.org/10.1508/cytologia.80.3

The UniProt Consortium. (2019). UniProt: A worldwide hub of protein knowledge. *Nucleic Acids Research*, *47*(D1), D506–D515. https://doi.org/10.1093/nar/gky1049

Torretta, E., Dondina, O., Delfoco, C., Riboldi, L., Orioli, V., Lapini, L., & Meriggi, A. (2020). First assessment of habitat suitability and connectivity for the golden jackal in north-eastern Italy. *Mammalian Biology*, *100*(6), 631–643. https://doi.org/10.1007/s42991-020-00069-z

Uliano-Silva, M., Ferreira, J. G. R. N., Krasheninnikova, K., Blaxter, M., Mieszkowska, N., Hall, N., Holland, P., Durbin, R., Richards, T., Kersey, P., Hollingsworth, P., Wilson, W., Twyford, A., Gaya, E., Lawniczak, M., Lewis, O., Broad, G., Martin, F., Hart, M., … Darwin Tree of Life Consortium. (2023). MitoHiFi: A python pipeline for mitochondrial genome assembly from PacBio high fidelity reads. *BMC Bioinformatics*, *24*(1), 288. https://doi.org/10.1186/s12859-023-05385-y

Wang, C., Wallerman, O., Arendt, M.-L., Sundström, E., Karlsson, Å., Nordin, J., Mäkeläinen, S., Pielberg, G. R., Hanson, J., Ohlsson, Å., Saellström, S., Rönnberg, H.,

413 Ljungvall, I., Häggström, J., Bergström, T. F., Hedhammar, Å., Meadows, J. R. S., &
414 Lindblad-Toh, K. (2021). A novel canine reference genome resolves genomic
415 architecture and uncovers transcript complexity. *Communications Biology*, *4*(1), 185.
416 https://doi.org/10.1038/s42003-021-01698-x

417 Xu, M., Guo, L., Gu, S., Wang, O., Zhang, R., Peters, B. A., Fan, G., Liu, X., Xu, X., Deng,
418 L., & Zhang, Y. (2020). TGS-GapCloser: A fast and accurate gap closer for large genomes
419 with low coverage of error-prone long reads. *GigaScience*, *9*(giaa094).
420 https://doi.org/10.1093/gigascience/giaa094

421