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Molecular phylogeny and systematics of selected taxa of diurnal raptors and owls

Referees: Prof. Dr. Michael Wink

Prof. Dr. Thomas Braunbeck

To my mother Dr. Olga Sarantchova,
who encouraged my interest in biology since my childhood

“It can be argued that these sequences are the most delicate expression possible of the phenotype of an organism and that vast amounts of evolutionary information may be hidden away within them”

Francis Crick

*« Je cherchais une liste d'oiseaux,
Dans un petit livre jaune, la majorité
Étaient des rapaces »*

Henri Deluy

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Summary

This Doctoral thesis is focused on the phylogenetical position and evolutionary history of several groups of raptors based on mitochondrial and nuclear markers. Elaninae Kites are tropical diurnal raptors traditionally considered as an early and relatively primitive subfamily, which is phylogenetically distant from other Accipitridae. Obtained results confirm the basal position of Elaninae, apparently separated in Middle Eocene. Cytological, morphological, and ecological data together with DNA data show the singularity of Elaninae. The elevating of this group to family level as Elanidae within the order Accipitriformes is recommended. Scissor-Tailed Kite, not sequenced before, unambiguously belongs to this group as well as Pearl Kite having special features forming its own monotypic subfamily Gampsonychinae that is described as a taxon new to the science. The genetics of closely related Black and Yellow-Billed kites, that has sometimes considered as same Old World cosmopolite species, remains insufficient studied. The author and the collaborators obtained most part of sequences from these species during this project. Genetic features distinguish both species from each other. Black Kites haplogroups in general correspond well to subspecies, diverging in two main clades, European, presenting *migrans*, and Australasian which in its turn split to Northern Asian *lineatus* and Indian-Australian *govinda/affinis*. In contrast, Yellow-Billed Kite show two distant haplotype branches non-correlated with existing subspecies, further genetic research of this species is needed. Based on obtained data the general phylogeographic pattern of Black and Yellow-Billed kites and its history in Pleistocene is outlined. The taxonomy of the Little Owl, a Palearctic nocturnal raptor, is not completely clear and controversial; some of subspecies are occasionally treated as separate species. Seven currently accepted subspecies were analyzed. Most of the haplotypes are well geographically differentiated, two forms, European *vidalii* and Far Eastern *plumipes* are genetically distant from others and are recommended to be treated as proper species. Middle Eastern form *lilith* on the contrary have no significant differences with neighboring subspecies and should be not considered separately like previously suggested. The divergence of this species complex started in Pliocene. Actual Little Owl populations likely recently expanded like Black Kites which can be related with last glaciations. General phylogenetical questions are discussed in the conclusion.

Zusammenfassung

Diese Doktorarbeit enthüllt die phylogenetische Position und Evolutionsgeschichte mehrerer Gruppen von Greifvögeln basierend auf mitochondrialen und nuklearen Markern. Milane aus der Gruppe der Elaninae sind tropische Taggreifer, die traditionell als eine frühe und relativ primitive Unterfamilie angesehen werden, die phylogenetisch von anderen Accipitridae entfernt ist. Die erhaltenen Ergebnisse bestätigen die basale Position von Elaninae, die offenbar im mittleren Eozän getrennt wurden. Das Hinzufügen von zytologischen, morphologischen und ökologischen Daten zusammen mit DNA-Daten zeigt die Einzigartigkeit von Elaninae. Die Erhebung dieser Gruppe auf Familienebene als Elanidae innerhalb der Ordnung der Accipitriformes wird empfohlen. Schwalbenschwanzaar, die bisher nicht sequenziert wurden, gehören eindeutig zu dieser Gruppe, ebenso wie Perlaar mit besonderen Merkmalen, die eine eigene monotypische Unterfamilie der Gampsonychinae bilden, welche als ein für die Wissenschaft neues Taxon beschrieben wird. Die Genetik eng verwandter Schwarz- und Schmarotzermilane, die manchmal als dieselben kosmopolitischen Arten der Alten Welt angesehen wurden, ist noch unzureichend untersucht. Der größte Teil dieser Artensequenzen wurde vom Autor und den Mitarbeitern während dieses Projekts erhalten. Beide Arten unterscheiden sich durch genetische Merkmale voneinander. Haplogruppen von Schwarzmilanen stimmen im Allgemeinen gut mit Unterarten überein, die sich in zwei Hauptgruppen unterscheiden, eine europäische, die *migrans* darstellt, und eine australasiatische, die sich wiederum in nordasiatische *lineatus* und indisch-australische *govinda/affinis* aufspaltet. Im Gegensatz dazu zeigen Schmarotzermilan zwei entfernte Haplotypzweige, die nicht mit bestehenden Unterarten korrelieren, weitere genetische Forschung dieser Art ist erforderlich. Basierend auf den erhaltenen Daten wird das allgemeine phylogeographische Muster von Schwarz- und Schmarotzermilanen und seine Geschichte im Pleistozän skizziert. Die Taxonomie der Steinkauz, eine paläarktischer Nachtgreifvogel, ist nicht ganz klar und umstritten, einige der Unterarten werden gelegentlich als eigene Arten behandelt. 7 derzeit akzeptierte Unterarten wurden analysiert. Die meisten Haplotypen sind geografisch gut differenziert, zwei Formen, europäische *vidalii* und fernöstliche *plumipes*, sind genetisch von anderen entfernt und es wird empfohlen, sie als eigene Arten zu behandeln. Im Gegensatz dazu

haben *lilith*-Formen aus dem nahen Osten keine signifikanten Unterschiede zu benachbarten Unterarten und sollten nicht, wie zuvor vorgeschlagen, separat betrachtet werden. Die Divergenz dieses Artenkomplexes begann im Pliozän. Tatsächliche Steinkauzpopulationen haben sich wahrscheinlich kürzlich wie Schwarzmilan ausgebreitet, die mit den letzten Vergletscherungen in Verbindung gebracht werden können. Allgemeine phylogenetische Fragen werden abschließend diskutiert.

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Publications

Some results of this study have been published:

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2. **IVAN J. STARIKOV** & MICHAEL WINK. 2020. — Old and cosmopolite: Molecular phylogeny of tropical–subtropical kites (Aves: Elaninae) with taxonomic implications. *Diversity* 12: 327: 1–21. <https://doi.org/10.3390/d12090327>
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Conference abstracts:

4. NATALYA G. ANDREYENKOVA, OLEG V. ANDREYENKOV, IGOR V. KARYAKIN, **IVAN J. STARIKOV**, MICHAEL WINK & IGOR F. ZHIMULEV. 2018. — Phylogeography of the Black Kite based on mitochondrial cytochrome b gene polymorphism, in KARYAKIN I. & NIKOLENKO E. (eds.), Abstracts of the II International Scientific and Practical Conference “Eagles of Palearctic: Study and Conservation”, 7–10 September, 2018, Park-Hotel Lake Aya, Katun village, Altai Kray, Russia. *Raptors Conservation*, Suppl. 1: 222–223.
5. **IVAN J. STARIKOV**, HEDWIG SAUER-GÜRTH & MICHAEL WINK. 2018. — Kites represent a polyphyletic group, in Deutsche Ornithologen-Gesellschaft. 151. Jahresversammlung, 19. bis 23. September 2018 in Heidelberg. Wissenschaftliches Programm. *Vogelwarte*, 56 (4): 331.
6. **IVAN J. STARIKOV**, HEDWIG SAUER-GÜRTH & MICHAEL WINK. [2018]. — Molecular phylogeny and phylogeography of Kites *Milvus spp.* based on mitochondrial cytochrome b gene

polymorphism, in *Abstracts. 2nd European Meeting of Young Ornithologists. [26–28 October 2018, Turin]*. p. 26.

<https://drive.google.com/file/d/1CIly7FFDWVf5fAnxrhqcbqVBX5UGAxDN/view>

7. **IVAN J. STARIKOV** & MICHAEL WINK. 2018. — Phylogenetic analysis of Elaninae based on nucleotide sequences of mitochondrial and nuclear DNA, in *Raptor Research Foundation [Annual Meeting]. 12 – 16 November 2018, Skukuza Camp, Kruger National Park, South Africa*. p. 106–107.

8. **IVAN J. STARIKOV** & MICHAEL WINK. 2019. — Phylogenetic structure and phylogeography of the Little Owl *Athene noctua* group, in *VII Congress of Vavilov Society of Geneticists and Breeders (VSG&B) and Associate Symposiums. June 18-22, 2019, Saint Petersburg, Russia. Book of abstracts*. St. Petersburg. WM Publishing Ltd. p. 675.

9. **IVAN J. STARIKOV**, HEDWIG SAUER-GÜRTH & MICHAEL WINK. 2019. — Genetic diversity of the Black Kite *Milvus migrans* in Germany based on mitochondrial DNA, in *Deutsche Ornithologen-Gesellschaft. 152. Jahresversammlung, 25. bis 29. September 2019 in Marburg. Wissenschaftliches Programm. Vogelwarte 57 (4): 336*.

10. NATALYA G. ANDREYENKOVA, OLEG V. ANDREYENKOV, IGOR V. KARYAKIN, **IVAN J. STARIKOV**, IVAN LITERÁK, MICHAEL WINK & IGOR F. ZHIMULEV. 2020. — [Distribution and demographic history of the Black Kite subspecies], in BELIK V.P. & VENGEROV P.D. (eds.), *Birds of Prey in Landscapes of the Northern Eurasia: Current Challenges and Trends: Proceedings of the VIII International Conference, Voronezh Nature Biosphere Reserve, 21–27 September, 2020*. Tambov. p. 126–129. (in Russian).

1. General introduction

1.1. General characteristics and origin of raptors

The raptors or birds of prey are usually medium-sized or large carnivorous birds which primarily hunt and feed on other vertebrates, many species also feed on carrion. They have common anatomic features as robust and sharp beak, powerful legs with connected muscles, and muted colours in plumage (Brown & Amadon 1968; Ferguson-Lees & Christie 2001; König & Weick 2008). Large eyes with keen eyesight up to binocular are well developed in hawks (Brown & Amadon 1968), owls (Burton 1985) and caracaras (Potier *et al.* 2018).

Representatives of this group evolved by convergence, forming a merged group which includes orders traditionally called as diurnal raptors: Falconiformes Sharpe, 1874, Accipitriformes Vieillot, 1816 from which in some classifications New World vultures Cathartiformes Coues, 1884 are separated, and recently a small order of Cariamiformes Verheyen, 1957; and one of nocturnal, Strigiformes Wagler, 1830 are included.

According to calculations, four branches of raptors are based on multilocus sequences that appeared independently inside the major clade of Telluraves shortly after catastrophic Cretaceous-Palaeogene extinction event, completely changing life strategies and leading to independent generation of the new forms (Figure 1): accipitriforms 63 million years ago; owls 61–62 MYA; cariamas 60–62 MYA; falcons 59–60 MYA (Jarvis *et al.* 2014; Prum *et al.* 2015).

However, the earliest known fossils are more recent although are close to the times mentioned above: first diurnal raptor *Paleopsilopterus itaboraiensis* Alvarenga, 1985 questionably belonged to cariamas found in Middle Paleocene of Brazil, circa 60 MYA (Alvarenga & Höfling 2003; Tambussi & Degrange 2013); first owl *Ogygoptynx wetmorei* Rich & Bohaska, 1976 was described from the Middle Paleocene of Colorado circa 58 MYA (Rich & Bohaska 1976). Since this time diverse fossil taxa appears from all raptors orders across the entire world. Tarsometatarsus fragments of the undefined raptor, presumably first accipitriform, were found in Belgian Early Eocene, 50.5–52 MYA (Mayr & Smith 2019).

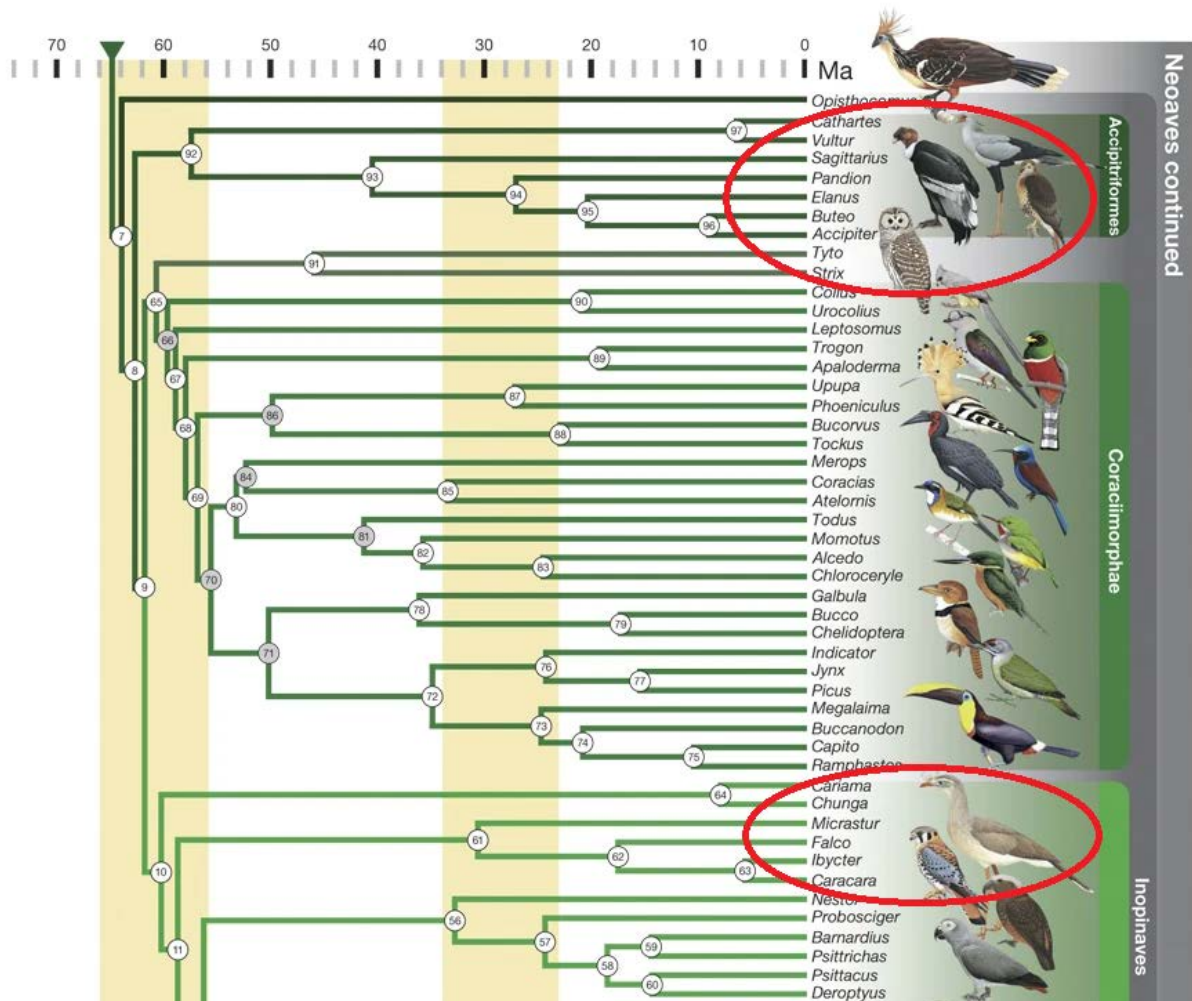


Figure 1. Different raptors (in red) on the avian tree of life issued from multilocus nuclear markers. Modified from Prum *et al.* 2015.

Milvoides kempii Harrison & Walker, 1979 from the Middle Eocene of England, 41–48 MYA are considered to be the first known accipitrid (Mayr 2009).

1.2. Classification

1.2.1. Pre-Linnean epoch

Aristotle was the first to distinguish and unify different raptors. He notified that all birds with crooked claws are carnivorous (but not vice versa) and mentioned their different kinds in his book “History of Animals” written in 4th century BC. In the Middle Ages the falconry became a popular hobby of nobility. A falconer from Umayyad Caliphate Al-Bazyar (later known under the name of Moamyn) assembled several raptors species with short

description in the “Book of falconry” in the middle of 8th century, and Holy Roman Emperor Frederick II (Figure 2), who worked with this book, divided all birds, among other dichotomies, into raptors and non-raptors in his “De arte venandi cum avibus” written in 1240s.



Figure 2. Frederick II Hohenstaufen as a falconer with Bianca Lancia. Codex Manesse, circa 1305–1315.

Development of science in early modern period led in particular to the creation of the first general book of ornithology where Pierre Belon defined raptors as one of avian groups and characterized them by detailed description of genera and species, diurnal as well as nocturnal (Belon du Mans 1555). At the same time he could not avoid curious mistakes, placing night herons and bats in the latter group. Three centuries before, Frederick II considered bats not only as non-raptors but not as birds placing it as “other animals with wings”. Jan Johnston followed Belon’s point of view describing genera and species of “*Avibus Terrestribus Carnivoris*”, where he added except mentioned above even cuckoo, parrots,

corvids and ostrich (Jonstonus 1650). More detailed classification of raptors is given by Francis Willughby and John Ray. They divide diurnal birds into majors, which are further divided respectively into Aquilae and vultures, and minors or Accipitres, which were partitioned into two-three subdivisions (Willughbei & Raius 1676). These authors are reasonably considered to be the forerunners of Linnean systematics. Nevertheless, they also made some inaccurate conclusions, focusing on external bird features and including shrike and paradise birds into diurnal group, and nightjar in owls.

1.2.2. Classic period

The first edition of Carl Linnaeus "Systema Naturæ" contained one order Accipitres with only three genera: *Psittacus* (parrots), *Falco* (diurnal raptors) and *Strix* (nocturnal raptors) (Linnæus 1735). Its famous 10th edition with diagnoses, which is regarded as the start of zoological nomenclature (Figure 3), contained four genera: *Vultur* (assembling all vultures and harpia), *Falco* (most of diurnal birds of prey), *Strix* (owls) and *Lanius* (shrikes, kingbird and waxwing), parrots were separated already (Linnæus 1758).

Mathurin Brisson removed *Lanius* from the order, divided it in two "sections", diurnal and nocturnal, and owls in two genera (Brisson 1760), count de La Cepède increased the number of raptors genera to ten (La Cepède 1799), Karl Illiger introduced three families in this order (Illiger 1811). Louis Pierre Vieillot proposed more detailed classification containing 24 genera regrouped in three families of tribe Diurni and one family of Nocturni (Vieillot 1816). However, Coenraad Jacob Temminck followed the old systematics with fewer genera (Temminck 1840). William Swainson and prince Bonaparte independently added subfamilies (Swainson 1837; Bonaparte 1840), their number and composing genera were later changed regularly by followers (Gray 1840, 1869; Brandt 1853; Reichenow 1882; Sharpe 1891, 1899; Gadow 1893).

Hermann Schlegel (1844) introduced successive trinomial nomenclature in the modern sense (not *varietas* accepted in botany) used till today. Although Linnaeus (1758) used it once for describe human forms, Schlegel was the pioneer in this not only in ornithology but among zoologists in general starting subspecies concept, however it became widely recognized only in 20th century.

CAROLI LINNÆI
EQUITIS DE STELLA POLARI,
ARCHIATRI REGII, MED. & BOTAN. PROFESS. UPSAL.;
ACAD. UPSAL. HOLMENS. PETROPOL. BEROL. IMPER.
LOND. MONSPEL. TOLOS. FLORENT. SOC.

**SYSTEMA
NATURÆ**

PER
REGNA TRIA NATURÆ,
SECUNDUM
CLASSES, ORDINES,
GENERA, SPECIES,
CUM
*CHARACTERIBUS, DIFFERENTIIS.
SYNONYMIS, LOCIS.*

TOMUS I.

EDITIO DECIMA, REFORMATA.

Cum Privilegio S:æ R:æ M:tis Sveciæ.

**HOLMIÆ,
IMPENSIS DIRECT. LAURENTII SALVII,
1758.**

Figure 3. Title page of the 10th edition of Linnaeus's "Systema Naturæ".

Further raptors were even relegated to suborder in the order Ichthyornithes, together with waterbirds (Kaup 1844), to the group (including cariamas) in the enormous merged order Carinatae, contained almost all extant birds (Huxley 1867), the cohort with only two families in Ciconiiformes (Garrod 1874), the two groups in two orders, diurnals in Pelagornithes, together with seabirds and storks, and one owl family in large order Coracornithes including passerins (Fürbringer 1888). On the contrary, Fitzinger (1856) and Sundevall (1872) split the raptors order into four families for owls and 12 for diurnals.

Fitzinger (1856) was the first to divide the raptors in two orders Raptatores and Nocturni based on their different anatomic traits. This scheme was commonly accepted later with the names of the order Falconiformes and Strigiformes during the next century and half. The separation of cathartids was proposed by Seebohm (1890). Sharpe (1899) created the checklist of all birds and elevated order number to three. Also, first time fossil taxa were added in the checklist.

1.2.3. Modern times

In the widescale "Check-list of birds of the world" division of raptors families is close to the same used today, additionally, first time the accumulated information about subspecies was taken into account. Order Falconiformes with 89 genera was divided into two suborders: Falcones, containing families Sagittariidae Finsch & Hartlaub, 1870, large Accipitridae Vieillot, 1816 and Falconidae Leach, 1820, each split into subfamilies, and Cathartae for New World vultures (Peters 1931), suborders Cariamae and fossil Phororaci were distinguished among Gruiformes (Peters 1934), living Strigiformes were divided in the families Strigidae Leach, 1820, as well as Tytonidae Ridgway, 1914, extinct Protostrigidae Wetmore, 1933 were also notified (Peters 1940). This classification retains its importance to this day, particularly on subfamily and species levels.

Stresemann and Amadon (1979) made a rearrangement in Falconiformes and slightly reduced the number of genera and species. Notable alternative proposition was carried out by Voous (1973), who separated not only Cathartiformes but equally Accipitriformes as orders from Falconiformes. This was accepted by a few authors (Cramp *et al.* 1980; Wolters 1982; Ferguson-Lees & Christie 2001) before the future changes occurred, affected by genomics. Wolters even proposed orders Cariamiformes and Sagittariiformes, not accepted by other taxonomists at this time.

First use of molecular data issued by DNA-DNA hybridization in systematics led to its preliminary revision by Charles Sibley and collaborators (Sibley *et al.* 1988; Sibley & Monroe 1990). Among their propositions, not confirmed by taxonomists and latest molecular research, were placing of nightjars back to owls in one order Strigiformes, and merging of all diurnal raptors, except cariamas, with storks and sandpipers in one wide order Ciconiiformes. This classification was criticized from generally accepted points of view (Mayr

1989), using syringeal morphology (Griffiths 1994) as well as nuclear data (Fain & Houde 2004). Another unsupported curious attempt of major bird taxa classification was carried out using different types of data by Mlíkovský (2002). According to his classification, the order Accipitriformes consists not only of Accipitridae (including Sagittaridae) and Cariamidae Bonaparte, 1853 but also of rallids and cuckoos. He moved Strigidae and Falconidae to the order Columbiformes Latham, 1790 and Cathartidae to Ciconiiformes Bonaparte, 1854.

First multilocus nuclear sequence data (Hackett *et al.* 2008) reveals independent position of branches of falcons, cariamas, other diurnal raptors and owls. This fact was taken into account by systematicists. Currently all raptors are divided into five orders: Falconiformes, Cariamiformes, Cathartiformes, Accipitriformes and Strigiformes (Clements *et al.* 2019; HBW & BirdLife International 2021), or into four orders, if New World vultures are considered a family inside Accipitriformes (Gill *et al.* 2022). Having eight families, raptors include the number of taxa which exceeds one hundred genera, 500 species and one thousand subspecies. Development of systematics of raptors during classic and modern periods and increase of taxonomic forms over time is shown in Table 1.

1.3. Phylogenetics

1.3.1. Non-molecular phylogenies

Few time after introducing of the term “Phylogenie”, idea of monophyletic tree of living organisms and its implementation (Haeckel 1866), detailed phylogenetic trees of birds based on their anatomy and morphology appeared, raptors formed separate branches for diurnals and nocturnals raising either from one common branch (Reichenow 1882) or from different parts (Fürbringer 1888) of the avian tree of life. First avian tree (Figure 4) is far from current representations, all raptors (Raubvögel) here forms one branch with gamebirds (Scharrvögel) which currently with waterfowl are considered as basal to all other neognaths (Jarvis *et al.* 2014; Prum *et al.* 2015)

1.3.2. Molecular phylogeny: Start of investigations and progress

The development of the electrophoresis technique permitted to utilize egg-white protein data from birds. First protein data from raptor samples were obtained in pioneer

works in this field and the suggestion, that the group of diurnal raptors might be polyphyletic, was already proposed (Sibley 1960; Sibley & Ahlquist 1972). Rapid evolving of molecular techniques permitted to investigate DNA data directly and DNA-DNA hybridization provided the first works on bird phylogeny based on this type of data, including raptors (Sibley *et al.* 1988; Sibley & Ahlquist 1990).

The theoretical base of the future molecular phylogenetic research was created with using of mutation rates as molecular clock conception (Zuckermandl & Pauling 1965). The introducing of mathematical methods for construction and analysis of phylogenetic trees

Table 1. History of systematics of living or extinct in historical time raptors. Base taxa are in bold.

Source	Orders	Suborders	Families	Subfam.	Genera	Species	Subspecies
Linnæus 1735	1	-	-	-	3	15	-
Linnæus 1758	1	-	-	-	4	53	-
Brisson 1760	1	-	2¹	-	5	83	-
Gmelin 1788	1	-	-	-	4	231	-
Illiger 1811	1	-	3	-	6	16	-
Vieillot 1816	1	2²	4	-	23	32	-
Cuvier 1817	1	-	-	-	3	56	-
Swainson 1837	1	-	3	5	29	106	-
Temminck 1840	1	-	-	-	5	44	-
Bonaparte 1850	1	-	4	13	79	386	-
Fitzinger 1856	2	-	16	-	62	164	-
Gray 1869	2	-	5	15	172	581	-
Reichenow 1882	1	-	3	10	53	149	-
Sharpe 1899	3	2	7	11	127	833	-
Peters 1931, 1940	2	2	6	17	118	433	1080
Howard & Moore 1980	2	2	7	4	108	433	1120
Wolters 1982	6	4	8	25	125	439	nc ³
Monroe & Sibley 1993	1+⁴	3+	6+	5	109	490	nc
del Hoyo <i>et al.</i> 1994, 1999	2	4	7	7	108	510	1022
Clements <i>et al.</i> 2019	5	-	8	-	117	562	1003
HBW & BirdLife International 2021	5	-	8	10	119	568	1029
Gill <i>et al.</i> 2022	4	-	8	-	113	588	927

¹ - "sections"

² - "tribes"

³ - not concerned

⁴ - order Strigiformes with caprimulgids (not counted), infraorder Falconides and subfamily Cathartinae in Ciconiiformes

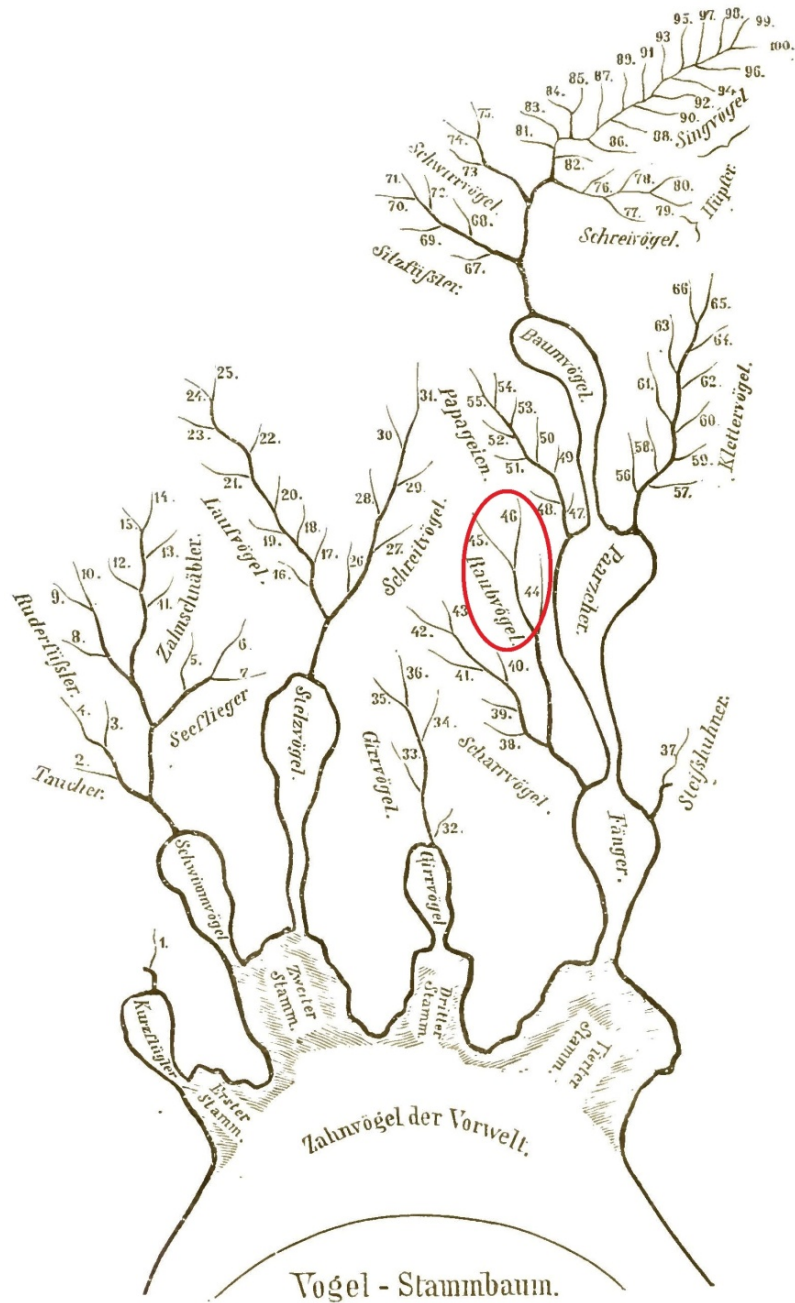


Figure 4. Raptors (in red) on the first avian phylogenetic tree. Each number corresponds to one family. From Reichenow 1882, modified.

obtained from genetic data occurred: Maximal Likelihood (Cavalli-Sforza & Edwards 1967), bootstrap approach (Felsenstein 1985), Neighbor Joining (Saitou & Nei 1987), Bayesian Inference with Markov chains (Rannala & Yang 1996).

Large taxonomic groups of raptors were phylogenetically investigated using the data obtained from mitochondrial gene of cytochrome *b* (Cyt *b*), which remains popular in zoological research: all raptors (Wink 2000), former Falconiformes (Wink & Seibold 1996;

Wink *et al.* 1998), falcons (Seibold *et al.* 1993; Griffiths 1997), vultures (Awise *et al.* 1994; Seibold & Helbig 1995; Wink 1995), Strigiformes (Heidrich & Wink 1998; Wink & Heidrich 1999, 2000a, 2000b).

Multilocus research replaced it. With Cyt *b* and nuclear LDH-B and RAG-1 markers owl (Wink *et al.* 2004, 2008) and diurnal raptors (Wink & Sauer-Gürth 2004) phylogeny was investigated. Phylogenetic relationships of several raptor species was also constructed with three clusters of short mitochondrial tRNA genes data (Wang *et al.* 2004). Phylogeny of the whole order Accipitriformes was analyzed by Kocum (2006) separately with Cyt *b* and 6 nuclear exons and introns. Taxonomically large tree of the order was produced from accessible GenBank data of several mitochondrial and nuclear loci (Nagy & Tökölyi 2014) and same with fossil calibration points (Mindell *et al.* 2018).

Analysis of mitochondrial genomes of several diurnal and nocturnal raptor species allowed to include it in general avian mitogenomic tree (Mahmood *et al.* 2014). Nuclear genomic research carried across all the class reveals always basal positions of all birds of prey to other taxa inside the relative neognath clades Australaves (falcons and cariamas) and Afroaves (accipitriforms and owls), supposedly proving predatory as ancestor lifestyle (Jarvis *et al.* 2014). Phylogenomic tree of different diurnal raptors and owls including several full genomes were carried out as well as analysis of genomes and transcriptomes looking for genes distinguishing raptors from other birds and between themselves (Cho *et al.* 2019; Zhou *et al.* 2019).

1.3.3. Phylogeny and species concepts in ornithology

An important impact on classification was brought by the idea of phylogenetic systematics based on the monophyly formulated by Willi Hennig (1950). In ornithology it was promoted mainly by Joel Cracraft, who formulated his Phylogenetic species concepts (PSC) only on the example of birds (Cracraft 1983) and applied Hennigian principles in other works (Cracraft 1972, 1981, 1989), and so did his followers (McKittrick & Zink 1988; Zink & McKittrick 1995; Zink 1996, 2006; Zink & Davis 1999; Zink & Klicka 2018). This approach comes into conflict with Ernst Mayr's Biological species concept (BSC) whose adherents take the reproductive isolation between species as a basis, ignoring monophyly with idea of polytypic species (Mayr 1974, 1993, 1996, 2000; O'Brien & Mayr 1991; Remsen 2005;

Friedmann 2012; Pfander 2012, 2018). In most of the publications cited above which is related to one of these concepts, the other is criticized. After accumulation of first molecular data used in phylogenies based on hierarchical relationships among taxa the phylogenetic concept in avian systematics was considered more useful (Zink & McKittrick 1995). Other species concepts exist but all of them may be reduced to the two mains (Rubtsov 2015)

While the subspecies problem remains relevant, we can see the approaches incompatible with accepted zoological nomenclature looking inadequate. In classic PSC there is no place for this taxonomic category, subspecies should be elevated to species being monophyletic or eliminated (Cracraft 1983; McKittrick & Zink 1988; Zink 2004). As a result of BSC being viewed too narrowly, even an artificial tetranomial nomenclature with semispecies was proposed (Pfander 2018).

At the same time, according to Avise (2000), there is no conflict between basic BSC and PSC criteria in terms of species. The confrontation of BSC and PSC proponents in avian taxonomy may be considered unnatural, as species-level taxonomy is pluralistic and eclectic. The reason behind this may be explained by the fact that many taxonomists use criteria from both concepts (Sangster 2014). PSC recognizing morphologically diagnosably distinct and geographically localized subspecies, which don't form monophyletic cluster was proposed in ornithology as a theoretic basis (Patten 2015). Another point of view is a possible creation of synthetic conceptual framework integrating better elements of PSC and BSC (Avise 2000).

1.4. Taxa of interest

1.4.1. Accipitridae

The largest family of diurnal raptors currently contains 14 subfamilies, 68–70 genera and more than 250 species (Lerner and Mindell 2005; Clements *et al.* 2019; HBW & BirdLife International 2021); Gill *et al.* 2022) and its systematics undergone several changes. Research of the phylogeny of the particular raptor taxa began after the first results on macrogroups were obtained from Cyt *b*. Large phylogenetic trees of the family were published, based on two mitochondrial and one nuclear genes (Lerner & Mindell 2005), by nuclear recombination activating protein 1 gene RAG-1 (Griffiths *et al.* 2007), and further on multilocus mitochondrial and nuclear data issued from other sources (Nagy & Tökölyi 2014;

Mindell *et al.* 2018). Combined tree reveals monophyly of subfamilies after previous taxonomic rearrangements in comparison with classic systematics (Figure 5).

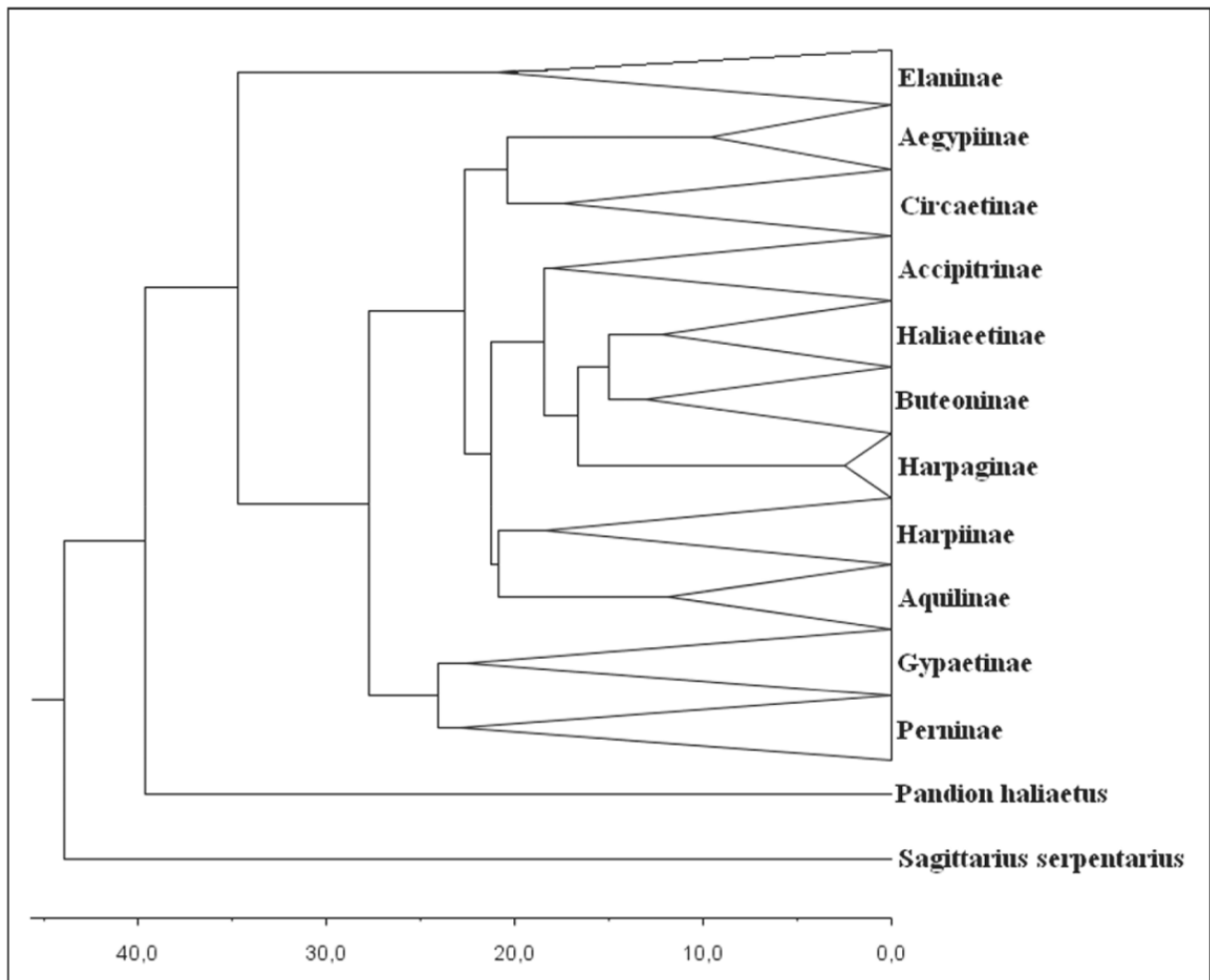


Figure 5. Simplified phylogeny of Accipitridae subfamilies based on mitochondrial and nuclear data. Timescale in MYA. From Nagy & Tökölyi 2014.

1.4.1.1. Elaninae kites

The small subfamily of Elaninae consists of 3 genera: *Elanus* Savigny, 1809, *Gampsonyx* Vigors, 1825 and *Chelictinia* R. Lesson, 1843 (Figure 6) and is considered to be an early branch basal to other Accipitridae (Lerner & Mindell 2005). These birds are tropical and subtropical raptors, characterized by several primitive morphological traits (Suschkin 1905; Brown & Amadon 1968; Jollie 1977c).

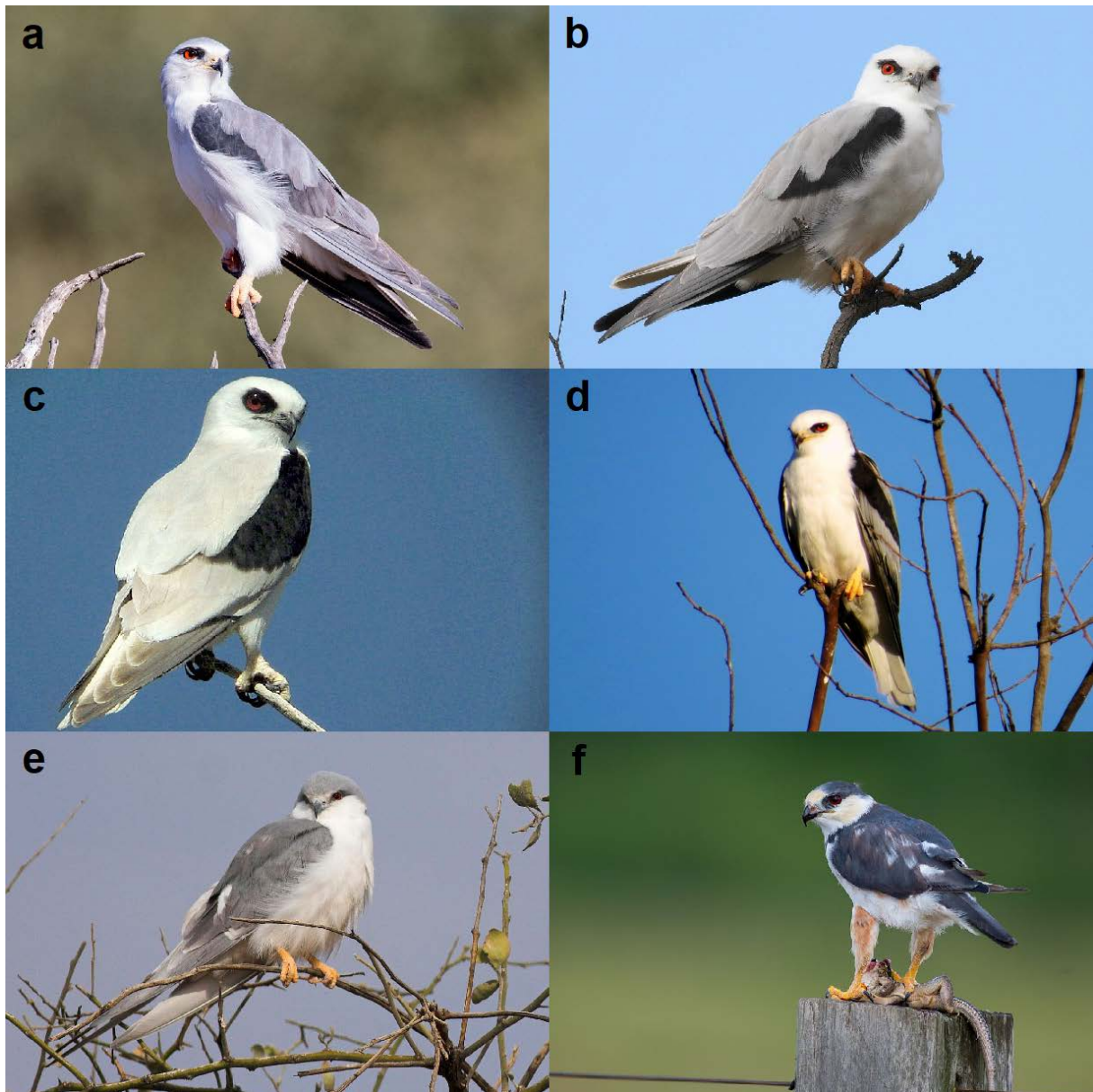


Figure 6. Elaninae kites. **a)** *Elanus caeruleus* (© S. Temple); **b)** *Elanus axillaris* (© Frankzed); **c)** *Elanus scriptus* (© F. Pierce); **d)** *Elanus leucurus* (© Intendencia de Montevideo / C. Calimares); **e)** *Chelictinia riocourii* (© A. Drewitt; modified); **f)** *Gampsonyx swainsonii* (© J. Quental). All photos are under CC BY 2.0, CC BY-SA 2.0 or CC BY-SA 4.0 licenses.

There are no special researches of phylogeny of representatives of these birds. *Elanus* species and *Gampsonyx* were analyzed among other representatives of the family Accipitridae (Lerner & Mindell 2005; Griffiths *et al.* 2007) markers and the position of *Chelictinia riocourii* (Temminck, 1821) is considered even as provisional in the absence of molecular data (Gill & Donsker 2020).

1.4.1.2. Black and Yellow-Billed kites

Black Kite *Milvus migrans* (Boddaert, 1783) and Yellow-Billed Kite *M. aegyptius* (J.F. Gmelin, 1788) (Figure 7) are closely-related and widely distributed medium-sized raptors dividing in five and two subspecies respectively (Gill *et al.* 2022). Both species are sometimes considered to be one (Clements *et al.* 2019). Genetic relationships between subspecies, as well as specific independence of the Yellow-Billed Kite, pose substantial questions. Research on the mitochondrial phylogeny of *Milvus milvus* and *M. migrans* was carried out using control region (Roques & Negro 2005), *Cyt b* and NADH dehydrogenase subunit 2, ND2 gene (Johnson *et al.* 2005), *Cyt b* and cytochromoxidase subunit I gene, COI (Dolinay 2015). Intraspecific phylogeny of Black Kite was previously investigated with *Cyt b* marker only (Scheider *et al.* 2004, 2009; Andreyenkova *et al.* 2018). The complete mitochondrial genome



Figure 7. Black (left) and Yellow-Billed kites. © A. Trepte, C.J. Sharp respectively, CC BY-SA 4.0 licenses.

of *Milvus migrans* was sequenced and integrated into the tree of raptor mitogenomes by Jeon et al. (2018).

1.4.2. Strigidae. Little Owl

Most of the owls also called typical owls belong to family Strigidae. The phylogeny of Strigidae, except the works mentioned above for the whole owl order, was also obtained with Cyt *b* marker (Ryu & Park 2003). Mitogenomes of several species also were integrated into the complete mitochondrial genome tree (Kang *et al.* 2018).

The Little Owl *Athene noctua* (Scopoli, 1769) is small relatively long-legged and short-tailed nocturnal raptor widely distributed in the Old World from the temperate zone to the tropics in open and semi-open habitats avoided dense vegetation, more terrestrial than arboreal (König & Weick 2008). This species consists of 13 subspecies differed by plumage colour, as well as by geographic range. Some races of *A. noctua* different by the plumage are present on Figure 8. Little Owl phylogeny was investigated firstly among other owls by Cyt *b* (Heidrich & Wink 1998; Wink & Heidrich 1999; Wink *et al.* 2008). Later special research on this bird was carried using Cyt *b* and Control region I loci (Pellegrino *et al.* 2014). As a resident *A. noctua* show potential genetic isolation of subspecies, and therefore status of several races may be revised (Wink & Heidrich 1999; König & Weick 2008) after obtaining sufficient genetic data.

1.5. Aims and scope

The main goal of this study is to reveal the phylogenetic structure of the selected raptors. Genetic data from molecular markers obtained by us are discussed in relation to other types of data obtained previously in these species, such as morphological, geographical and ecological data in terms of taxonomy.

In the first research project (Chapter 3) we analyzed the relationships between six species of peculiar Elaninae kites, as well as their relation to other species of the large Accipitridae family, with mitochondrial and nuclear markers. Also the question of the affiliation of the Scissor-Tailed Kite to the subfamily is considered, and systematic changes are proposed. Second research project concerns phylogenetic structure and phylogeographic

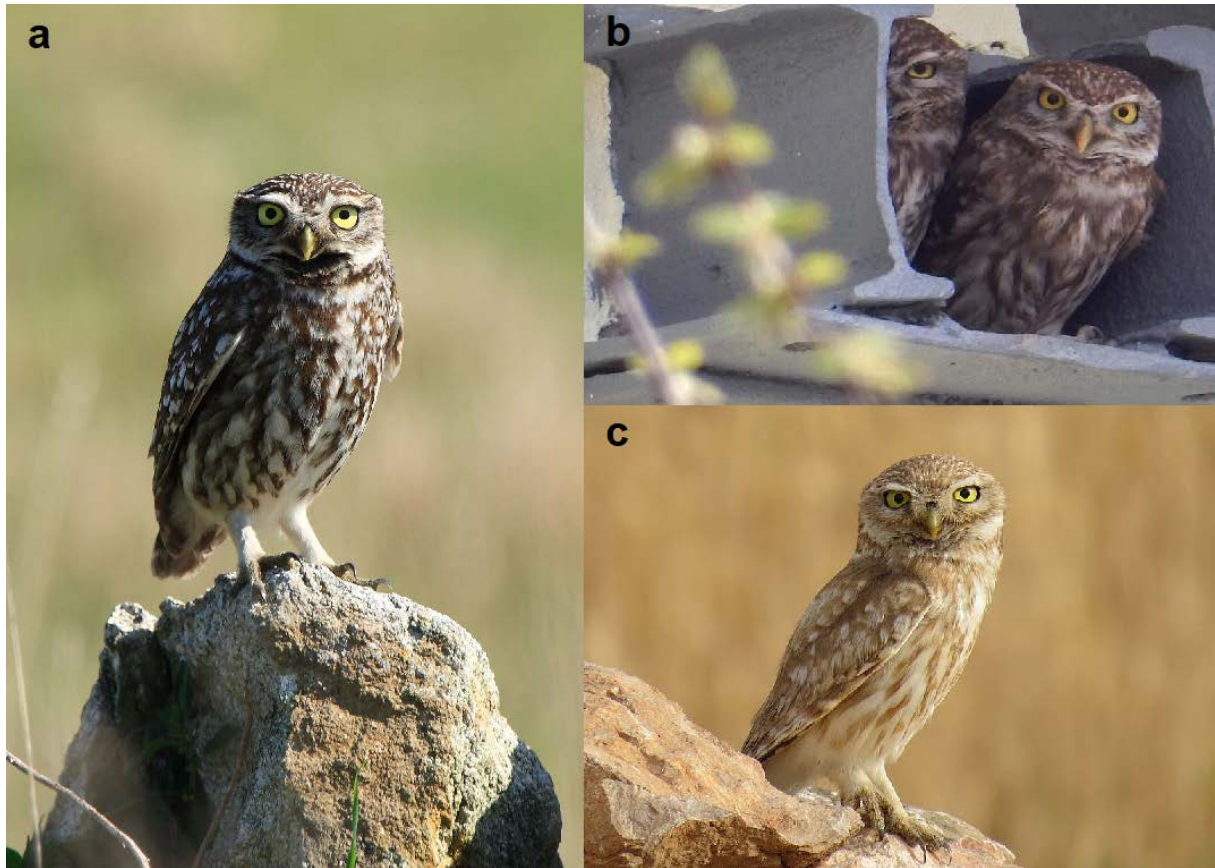


Figure 8. Examples of the Little Owl geographical races. **a)** *Athene noctua vidalii*, Spain (© A. Nikolai); **b)** *A. n. noctua*, Italy (© M.R. Gelso), **c)** *A. n. lilith*, Palestine (© Muhammad the Palestinian). Photos are under CC BY-SA 2.0, CC BY-SA 4.0 and CC BY-SA 3.0 licenses respectively.

patterns of the Black Kite and additionally Yellow-Billed Kite subspecies based on the cytochrome *b* sequences (Chapter 4). Last research project reveals phylogenetic structure of the large and polymorphic Little Owl species provided by mitochondrial and nuclear sequence data (Chapter 5). In the conclusion, obtained results are discussed in relation to the future research potentially influenced by this study.

2. Methodology

2.1. Sampling

The samples used in the PhD project consisted of skin parts, tissue parts conserved in ethanol or EDTA-buffer, blood, pin and molted feathers, and egg shells. Parts of the samples were collected by the author in Russia: Help Centre for Wild and Exotic animals of Kemerovo State University, Holzan Centre of Monitoring and Rehabilitation of Birds of Prey, Biosphera Ecopark, Simbirsk Wild Animals Rescue Centre, Limpopo Zoo, Kazan Rehabilitation Centre of Birds of Prey, Altai Falcon Birdfarm; and Hungary: Hortobágyi Bird Park – Bird Hospital Foundation (Figure 9).

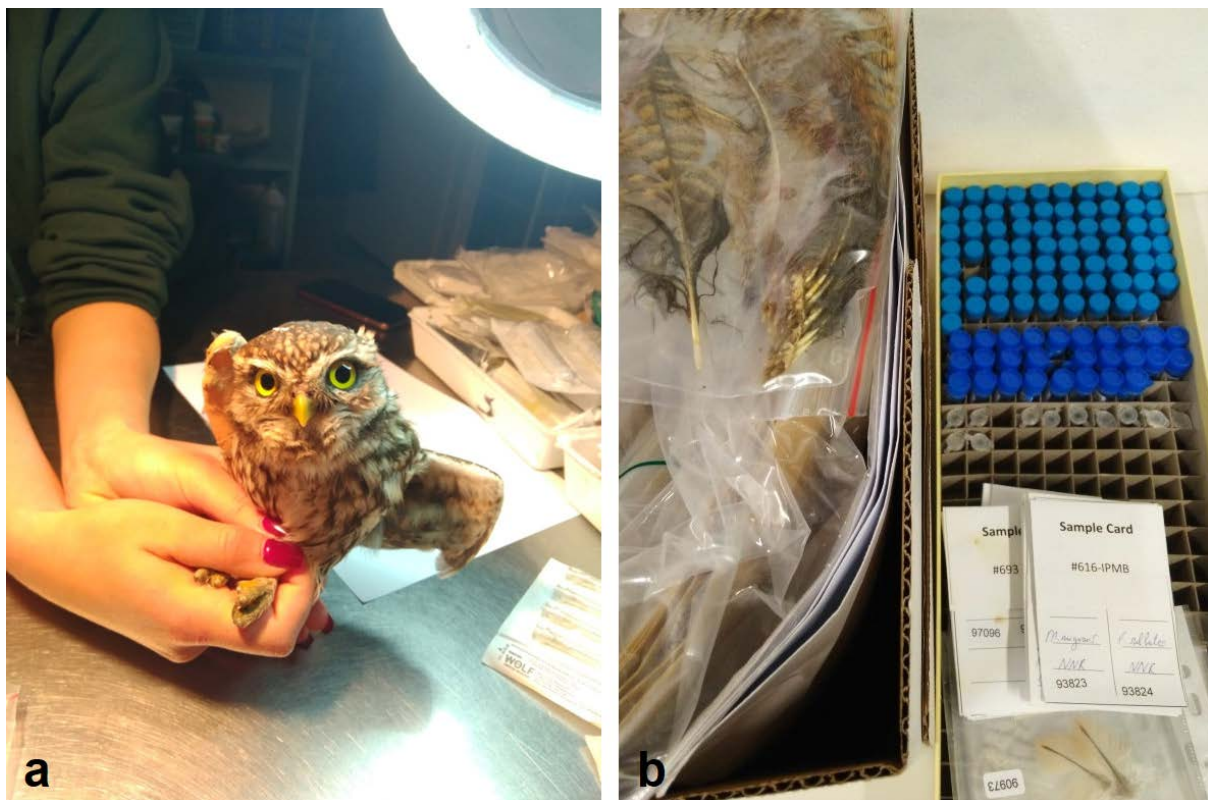


Figure 9. a) Little Owl before blood collection in the Hortobágyi Bird Hospital Foundation (Hungary). **b)** Different types of raptor samples in the IPMB collection. Photos by the author.

Other samples came from different collections except mentioned above: Institute of Pharmacy and Molecular Biotechnologies of Heidelberg University (Germany); Zoological

Museum of Moscow State University, Institute of Cytology and Genetics of Siberian Branch of the Russian Academy of Sciences; University of Veterinary and Pharmaceutical Sciences Brno (Czech Republic); Hungarian Museum of Natural History; part of these samples in its turn were obtained from individual collectors.

2.2. Chemicals and instruments

Different chemicals and solutions used in the study are documented in Tables 2 and 3, laboratory instruments in Table 4.

2.3. DNA isolation

Isolation of DNA mostly followed standard protocol (Sambrook & Russell 2001). Sample aliquots were digested for half a day at 56°C in lysis buffer B and presence of SDS and proteinase K. Cell fragments and proteins were precipitated with saturated sodium chloride solution. Precipitation of DNA from supernatant upper phase was carried with 0.8 volume ice-cold isopropanol. Extracted DNA was washed with ice-cold ethanol. The protein-precipitate was retreated with guanidine thiocyanate at 56°C for four hours followed by extraction with phenol dichloromethane (twice in case of contamination), dichloromethane isoamyl alcohol and washed as explained above. DNA from both phases was dissolved in TE buffer and kept in 4°C for further analysis. In case of low DNA concentrations the aliquot was not separated in phases, NaCl and guanidine steps were omitted and isoamyl step was repeated twice.

2 µl of each DNA solution was loaded in 1% agarose gel with ethidium bromide to determine approximate concentration of DNA by comparison of fluorescence intensities of sample bands in transilluminator. If needed exact DNA concentration were determined in a spectrophotometer at 260/280 nm.

2.4. Selection, PCR and sequencing of mitochondrial and nuclear genes

The mitochondrial DNA is widely used in animal phylogenetic and phylogeographical research because of its fast evolution rate, simple genetic structure, absence of

Table 2. Chemical reagents used in the study.

Chemicals and enzymes	Molecular formula	Company, place
2-Mercaptoethanol	C ₂ H ₆ SO	Sigma-Aldrich Chemie, Steinheim
8-Hydroxyquinoline	C ₉ H ₇ NO	Merck Schuchardt, Hohenbrunn
Acetic acid 96%	CH ₃ COOH	Merck, Darmstadt
Agarose	C ₂₄ H ₃₈ O ₁₉	Carl Roth, Karlsruhe
Ammonium acetate	C ₂ H ₇ NO ₂	Merck, Darmstadt
Bovine serum albumin (BSA)	protein	Sigma-Aldrich, St. Louis, MO, USA
Bromophenol blue, Sodium salt	C ₁₉ H ₁₀ Br ₄ O ₅ S · Na	Serva, Heidelberg
Dichloromethane	CH ₂ Cl ₂	Honeywell, Seelze
Disodium EDTA (Ethylenediaminetetraacetic acid) dihydrate	C ₁₀ H ₁₄ N ₂ Na ₂ O ₈ · 2H ₂ O	Bernd Kraft, Duisburg
Ethanol 70%	C ₂ H ₅ OH	Heidelberg University
Ethanol 96%	C ₂ H ₅ OH	Heidelberg University
Ethanol absolute 99.8%	C ₂ H ₅ OH	Sigma-Aldrich Chemie, Steinheim
Ethidium bromide	C ₂₁ H ₂₀ BrN ₃	Serva, Heidelberg
Glycerol anhydrous 99%	(HOCH ₂) ₂ CHOH	Th. Geyer, Renningen
Guanidine thiocyanate	C ₂ H ₆ N ₄ S	Carl Roth, Karlsruhe
HighTaq DNA polymerase	enzyme	Bioron Diagnostics, Römerberg
Hydrochloric acid 32%	HCl	Sigma-Aldrich Chemie, Steinheim
Isoamyl alcohol 98%	(CH ₃) ₂ CH(CH ₂) ₂ OH	Grüssing, Filsum
Isopropanol 99.9%	(CH ₃) ₂ CHOH	Heidelberg University
Magnesium chloride	MgCl ₂	Bioron Diagnostics, Römerberg
Nucleotides. Set of dNTPs (nucleoside triphosphates, dATP+dCTP+dGTP+dTTP). Tetrasodium salt	C ₁₀ H ₁₆ N ₅ O ₁₂ P ₃ ; C ₉ H ₁₆ N ₃ O ₁₃ P ₃ ; C ₁₀ H ₁₆ N ₅ O ₁₃ P ₃ ; C ₁₀ H ₁₇ N ₂ O ₁₄ P ₃ ; C ₁₀ H ₁₂ N ₂ Na ₄ O ₈	Bioron Diagnostics, Römerberg
Phenol 99-100.5%	C ₆ H ₅ OH	Grüssing, Filsum; Honeywell & Fluka, Seelze
Potassium Chloride	KCl	Bioron Diagnostics, Römerberg
Primers	DNA fragments	Eurofins Genomics Germany, Ebersberg
Proteinase K	enzyme	Qiagen, Hilden
Pst I	enzyme	Fermentas, St-Leon-Rot
Sodium chloride 0.9%	NaCl	B. Braun, Melsungen
Sodium dodecylsulphate (SDS) 99.5%	C ₁₂ H ₂₅ NaO ₄ S	AppliChem, Darmstadt
Sodium fluoride 99%	NaF	Sigma-Aldrich Chemie, Steinheim
Thymol	C ₆ H ₃ CH ₃ (OH)(C ₃ H ₇)	Sigma
Triton X-100	C ₁₄ H ₂₂ O(C ₂ H ₄ O) _n (n = 9-10)	Sigma-Aldrich Chemie, Steinheim
Tris (tris(hydroxymethyl)aminomethane)	C ₄ H ₁₁ NO ₃	Carl Roth, Karlsruhe
Water HPLC (HiPerSolv CHROMANORM) grade	H ₂ O	AppliChem, Darmstadt
λ-DNA	DNA	Thermo Fisher Scientific, Karlsruhe

recombination and easy isolation (Avisé *et al.* 1987; Rubinoff & Holland 2005). Bird mtDNA consists circa 17000 base pairs, 37 coding genes and non-coding control region (Figure 10). Two genes coding proteins, involved the mitochondrial respiratory chain, were selected: MT-

Table 3. Solutions and preparation used in the study.

Solutions and buffers	Ingredients
Agarose gel	1/1.4% of agarose, 1 µg/ml of ethidium bromide in TAE buffer 1x
Ammonium acetate	4 M ammonium acetate in water
BLM (Blue marker)	50 ml Glycerol anhydrous, 50 ml water, 0.25 g bromophenol blue, Sodium salt
Buffer B (Lysis buffer)	25 mM EDTA, 75 mM NaCl, 10 mM Tris-HCl (pH=8.5)
Dichloromethane-isoamyl alcohol	dichloromethane and Isoamyl alcohol in ratio 24:1
EDTA buffer	10% EDTA, 0.5% NaF, 0.5% thymol, 1% Tris (pH=7.5)
Guanidine thiocyanate buffer	4 M Guanidine thiocyanate, 0.1 M Tris-HCl, 1% 2-mercaptoethanol (pH=5.0)
NE Buffer 3.1 (New England Biolabs, Frankfurt am Main)	100 mM NaCl, 50 mM Tris-HCl, 10 mM MgCl ₂ , 100 g/ml BSA (pH=7.9)
Nucleotide mix	2.5 mM dATP, 2.5 mM dCTP, 2.5 mM dGTP, 2.5 mM dTTP, each contains tetrasodium salt
PCR buffer 10x	100 mM Tris, 500 mM KCl, 5% Triton X-100, 15-20 mM MgCl ₂
PCR purification kit. Binding + Wash + Elution buffers. (Thermo Fisher Scientific Baltics, Vilnius, Lithuania).	45 ml wash buffer with 225 ml ethanol. 10mM Tris-HCl in Elution buffer. Compounds of buffers are not mentioned by the company
Phenol-Dichloromethane	1000 g phenol, 960 g dichloromethane, 40 ml isoamyl alcohol, 1 g 8-hydroxyquinoline, 250 ml Tris (pH=7.6)
Proteinase K solution	500 mg Proteinase K in 25 ml water
SDS solution	20% solution in water
TAE buffer	40 mM Tris, 1 mM EDTA, Acetic acid (pH=8.0)
TE buffer	10 mM Tris, 1 mM EDTA, Hydrochloric acid (pH=7-7.5)
λ-Pst I size standard	20 µl NE buffer 3.1, 10 µl water, 167 µl λ-DNA, 3 µl Pst I

Table 4. Laboratory instruments used and their respective sources.

Instrument	Company, place
Centrifuge Biofuge Fresco 17	Kendro, Osterode
Centrifuge Pico Heraeus	Kendro, Osterode
Centrifuge Perfect spinP	Peqlab Biotechnologie, Erlangen
Centrifuge Eppendorf tubes 0.2 ml	unnamed, Mexico
Centrifuge Eppendorf tubes 0.5, 1.5, 2 ml	Eppendorf, Hamburg
Centrifuge tubes with caps 1.5 ml	Prime Chemicals Group, Mytishchi, Russia
Centrifuge tubes with caps 50 ml	Greiner Bio-One International, Frickenhausen
Digital balances Sartorius PT 600	Sartorius, Göttingen
DNA/RNA UV-cleaner UVC/T-M-AR	Biosan, Rīga, Latvia
Electronic thermostat Function Line	Heraeus Group, Hanau
Frigde Liebherr ****	Liebherr-Hausgeräte Lienz, Lienz, Austria
Fridge Liebherr Comfort	Liebherr-Hausgeräte Lienz, Lienz, Austria
Fridge Liebherr ProfiLine	Liebherr-Hausgeräte Lienz, Lienz, Austria
Gel chamber for agarose gel	Heidelberg University
Glass Pasteur pipettes 145 mm	Brand, Wertheim
Gloves latex Semperguard	Semperit, Austria, made in Malaysia
Gloves nitrile TouchNTuff	Ansell, Belgium, made in Sri Lanka
Microcomputer electrophoresis power supply	Fröbel Labor Geräte, Lindau / unnamed, Belgium
Microwave Grill hot-air	Sharp, Japan
Mini vortex Mixer	NeoLab, Germany, made in China
PCR caps, strips per 8	Kisker Biotech, Steinfurt / nerbe plus, Winsen an der Luhe
PCR microplates 96 Well	nerbe plus, Winsen an der Luhe
PCR tubes, strips per 8, 0.2 ml	Kisker Biotech, Steinfurt
Pipette tips 2 µl, 1 ml	Greiner Bio-One International, Frickenhausen
Pipette tips 200 µl	Sarstedt, Nümbrecht
Pipette single channels 2, 20, 200, 1000 µl	Gilson, Villiers-le-Bel, France
Plastic tube racks	Muhwa, China
Sequencer Applied Biosystems 3730 DNA Analyzer (outsourced by StarSeq, Mainz)	Thermo Fisher Scientific, Karlsruhe
Spectrophotometer Biowave II	Biochrom, Cambridge, United Kingdom
Syringe Sterilfilter 0.22 µm	Berrytec, Grünwald
Thermocycler LabCycler SensoQuest	SensoQuest, Göttingen
Thermocycler T-gradient Biometra	Biotron, Göttingen
UV Transilluminator Benchtop + Imaging System BioDoc-It 8.0" LCD	Ultra-Violet Products, Cambridge, United Kingdom
Vortex Genie	Bender & Hobein, Switzerland, made in Bohemia, USA

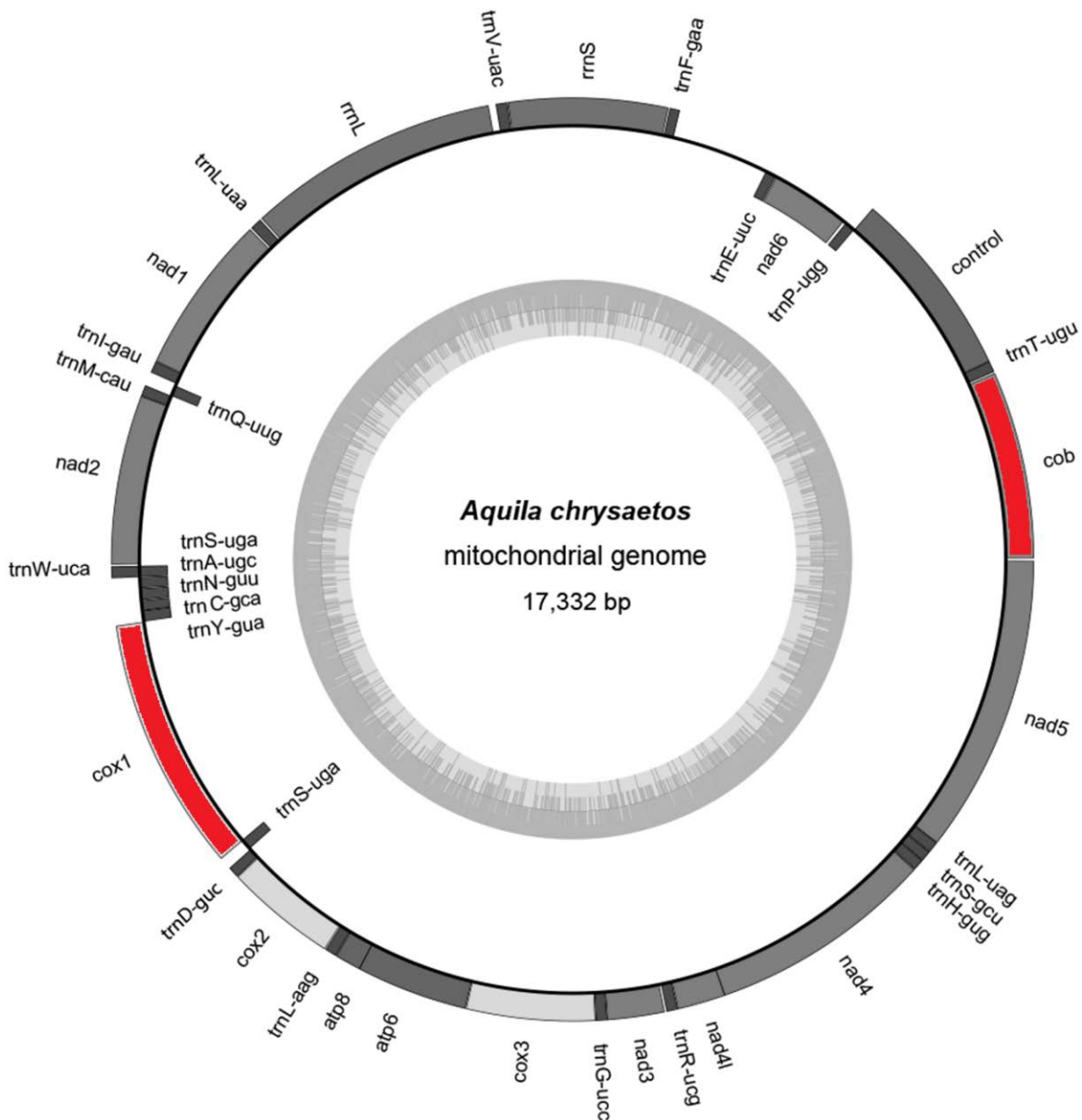


Figure 10. Mitochondrial genome of diurnal raptor (Golden Eagle), modified from Doyle *et al.* 2014. Genes investigated in this study are in red.

CYTB, mitochondrially encoded cytochrome *b*, which is popular in animal phylogenetic research and the more conservative MT-COI, mitochondrially encoded cytochrome *c* oxidase I commonly used for DNA-barcoding.

Animal nuclear genes evolve at least several times more slowly than mitochondrial (Brown *et al.* 1982; Moriyama & Powell 1997) and are utilized mostly for phylogenetic research of macrogroups. RAG-1 gene, recombination activating 1 which codes for a protein involved in antibody and T-cell receptor of V(D)J recombination was selected. It has proven as useful for the phylogeny of higher-level vertebrate taxa (Groth & Barrowclough 1999).

The PCR protocol with corresponding primers was specified for each research project characteristics of all used primers are presented in the Table 5. PCR amplifications were carried out in 50 μ L reaction volumes containing PCR buffer, 100 μ M dNTPs, 0.2 units of Taq DNA polymerase, 200 ng of DNA and 5 pmol of primers. PCR protocol was set as follow: initialization for 5 min at 95°C, denaturation for 45 s at 95°C, annealing for 1 min at 50-53/50-53/54°C and elongation for 1.5/2/2 min at 72°C for COI/Cyt b/RAG-1 genes respectively, steps from second to fourth running in 38 cycles. A final extension step was conducted for 10 min at 72°C.

Table 5. Primers used in the study.

Gene	Name	Sequence (5'-3')	Reference
COI	COI-ExtF	F-ACGGTTTAACTACTCAGCCATCTTACC	Johnsen <i>et al.</i> 2010
	Passer_F1	F-CCAACCACAAAGACATCGGAACC	Lohman <i>et al.</i> 2009
	Passer_R1	R-GTAAACTTCTGGGTGACCAAAGAATC	Lohman <i>et al.</i> 2009
	Bird1Fd	F-TCAACCAACCACAAAGAYATYGGYAC	Louette <i>et al.</i> 2011
	BirdH_351d_370d	R-CCTGCTCCWGCTTCTAYDGT	Louette <i>et al.</i> 2011
	Aves_L288_310	F-CGCATAAACAAACATAAGCTTCTG	Louette <i>et al.</i> 2011, modified
	BirdR1dt	R-ACGTGGGAGATGATTCCGAAKCKKGG	Louette <i>et al.</i> 2011, modified
Cyt b	L14764	F-TGRTACAAAAAATAGGMCCMGAAGG	Sorenson <i>et al.</i> 1999
	Mt-A1a	F-CATCTCAGCATGATGAAACTTCG	Clouet & Wink 2000, modified
	smt-A	F-CAACATCTCAGCATGATGAAACTTCG	Wink & Sauer-Gürth 2000
	Mt-c2	F-TGAGGACAAATATCATTCTGAGG	Fritz <i>et al.</i> 2006
	Mt-D	F-AAAATCCCATTCCACCCCCTACTACTCCACAAAAGA	Seibold 1994
	Mt-FSH	R-TAGTTGGCCAATGATGATGAATGGGTGTTCTACTGGTT	van der Bank <i>et al.</i> 1998
	Mt-FrS	R-CAGTTTTTGGTTTACAAGAC	Arctander <i>et al.</i> 1996
	Mt-Fr	R-CTAAGAAGGGTGGAGTCTTCAGTTTTTGGTTTACAAGAC	Seibold 1994
	Mt-E	R-GCAAATAGGAAGTATCATTCTGG	Barth <i>et al.</i> 2004
Mt-c4	R-AGTGTGGGTTGTCTACTGA	Broders <i>et al.</i> 2003	
RAG-1	R7	F-CTGTCTTTGACCAGGAGAGCTCA	Groth & Barrowclough 1999
	R17	F-CCCTCTGCTGGTATCCTTGCTT	Groth, Barrowclough, 1999
	R51	R-GACCCTCTTCTGCTATGAGGGGGC	Irestedt <i>et al.</i> 2001

The PCR product was purified by precipitation in 4 M NH_4Ac and absolute ethanol (1:1:10), centrifuged at 13000 rpm for a period of 30 min, followed by centrifugation with 70% ethanol using the same settings and later dissolved in 25 μ L of sterile H_2O . An alternative way of cleaning was carried also for the research project described in Chapter 5 with Thermo Scientific GeneJET Purification Kit (Table 3): transfer of 1:1 volume of Binding buffer and PCR product to purification columns, centrifugation for 1 min and discarding of

flow-through, repeat of the step with 700 μL of Wash buffer diluted with the ethanol (1:5), additional centrifugation of empty columns to remove Wash buffer, transfer of columns to the centrifuge tubes and adding of 50 μL of Elution buffer, centrifugation for 1 min and discarding of columns.

For sequencing, 1 μL of sequencing primer (10 pmol/ μL) was combined with a 7 μL mixture of PCR products/sterile water (where the concentration of PCR products varied from 1 to 7 μL according to the brightness of the band obtained in 1.4% agarose gel). Sanger sequencing was executed by StarSEQ GmbH in Mainz on ABI 3730 automated capillary sequencer with the ABI Prism Big Dye Terminator Cycle Sequencing Ready Reaction Kit 3.1.

2.5. Sequence alignment

Mitochondrial DNA sequences were inspected carefully in order to exclude the possibility of stop codons, indicating that these sequences did not come from nuclear copies and are not nuclear pseudogenes similar to target mitochondrial genes. Alignments were created in BioEdit 7.2.6 (Hall 1999). Nucleotide sequences were aligned using the MUSCLE algorithm (Edgar 2004) in MEGA 6.06 (Tamura *et al.* 2013). This method use distance measures for a pair of sequences, unaligned, k -mers as contiguous subsequences of length k , and aligned, Kimura's distance between sequences:

$$K = 2(\alpha + \beta + \gamma)T$$

where α are transitions, β and γ are transversions, T is divergence time. Here the evolutionary distance per site is

$$K = -\left(\frac{1}{2}\right) \ln\{(1 - 2P - Q)\sqrt{1 - 2Q}\}$$

where P is the probability of homologous sites showing a difference when both bases are either purines or pyrimidines, and Q is the same when one base is a purine and the other is a pyrimidine (Kimura 1980). In MUSCLE algorithm distance matrices are clustered with UPGMA (unweighted pair group method with arithmetic mean), an agglomerative hierarchical clustering method where all distances contribute equally to each computed average (Sokal & Michener 1958).

2.6. Phylogenetic analysis

2.6.1. Phylogeny reconstruction: Maximum likelihood and Neighbor-joining trees

Maximum likelihood and Neighbor-joining trees for each locus and average pairwise p-distances were calculated with MEGA 6.06 (Tamura *et al.* 2013). The construction of phylogenetic trees by Maximum likelihood estimation was developed by Felsenstein (1981). In general form for the point k whose immediate descendants are points i and j it can be computed for all four values corresponding to four nucleotides of the state s_k from four values of s_i and s_j respectively:

$$L_{s_k}^{(k)} = \left(\sum_{s_i} P_{s_k s_i}(\nu_i) L_{s_i}^{(i)} \right) \left(\sum_{s_j} P_{s_k s_j}(\nu_j) L_{s_j}^{(j)} \right)$$

where P is the probability and ν is the distance from k to the mentioned point. This calculation carries for the all fork points until the bottom of the tree.

Neighbor-joining method for reconstruction of phylogenetic trees was created by Saitou and Nei (1987) and corrected by Studier and Keppler (1988). This method permits construction of phylogenetic trees for sequences with common sites by measuring of distance in pairs between nearest operational taxonomic units (taxa or sequences). It starts by computing the distance between each pairs of OTU:

$$S_{ij} = (N - 2)D_{ij} - \sum_k D_{ik} - \sum_k D_{jk}$$

When the smallest S_{ij} is chosen, new node u is created and the distance to it from i is calculating:

$$D_{iu} = \frac{1}{2(N - 2)} [(N - 2)D_{ij} + \sum_k D_{ik} - \sum_k D_{jk}]$$

The distance from u to j is calculating the same way with inverse of the distance sums. From this step a distance from the node u to all remaining OTU is calculating, the smallest distance is chosen and the new distance is calculating again until all OTU will be related.

Relative branch support was evaluated with 500-1000 bootstrap replicates for the Maximum likelihood and 10000 for Neighbor-joining trees.

2.6.2. Bayesian inference

Bayesian inference computing posterior probabilities according to Bayes theorem and being a powerful method of statistical inference is widely used in phylogenetic analysis. It is based on the posterior distribution and in general form it may be represented by the formula

$$f(\tau, \nu, \theta | X) = \frac{f(\tau, \nu, \theta) f(X | \tau, \nu, \theta)}{f(X)}$$

where X is the data matrix, τ is the topology of the tree, ν is a vector of branch lengths, ϑ is a vector of substitution model parameters. The distribution $f(\tau, \nu, \vartheta)$ is the tree prior; $f(X | \tau, \nu, \vartheta)$ is the likelihood function, describing the probability of the data under parameter values; $f(X)$ is the total probability of the summed and integrated data (Ronquist & Huelsenbeck 2003). Since it is impossible to analytically calculate the posterior probability distribution as it requires extensive numeric computations when searching for posterior maximum, Monte Carlo algorithms for Markov chains (MCMC), which permit to obtain approximative probabilities and further reduce the complexity of calculations, are also used in the Bayesian software. Mitochondrial and nuclear gene trees were prepared as XML (Extensible Markup Language) file in BEAST 1.8.0 and calculated using BEAUti 1.8.0 (Drummond *et al.* 2012).

Several Markov models of DNA evolution were proposed describing the rates at which nucleotides replace each other. For finding the best evolution model to use for a sequence dataset during Bayesian as well as Maximum likelihood analysis, jModelTest 2.1.10 or PhyML 3.0 (Guindon & Gascuel 2003; Guindon *et al.* 2010; Darriba *et al.* 2012) was applied with the Akaike information criterion

$$AIC = 2k - 2\ln(L)$$

where k is the number of system parameters and L is the maximum value of the likelihood function for the model (Akaike 1974). Since many models are not available in the BEAST/BEAUti package, they were changed to the most similar ones by delta of AIC.

Each approach for estimated phylogeny had its own advantages and disadvantages. Distance method is fast, works well with large datasets of highly similar sequences but the information is lost in compressing joining sequences into distances and the calculation becomes problematic when sequences are divergent. Likelihood and Bayesian methods are usually considered to be more powerful, especially for inferring deep phylogenies, however

they involve heavy computation. At the same time the bootstrap proportions for likelihood are hard to interpret and the topology is not a parameter in this case; Bayesian inference depends on several prior probabilities, often uninformative which may be difficult to specify (Holder & Lewis 2003; Yang & Rannala 2012). In recent research, priority is given to the Bayesian approach and therefore it is also used in this study.

2.6.3. Molecular clock

The molecular clock is the way of using mutational rates of molecules to deduce the time when two forms of life diverged. I applied modification called Relaxed Clock model which means that the rate of change inside related phylogenetical lineages is different (Drummond *et al.* 2006). To set the rates of the clock model, we used the half-value of the 2.1% sequence divergence per million years for Cyt *b*, which is accepted for birds (Weir & Schluter 2008), and 1.8% for COI (Lavinia *et al.* 2016). Tree prior was selected as speciation Birth-Death process, a continuous Markov chain stochastic process with two types of state transitions (Feller 1939; Gernhard 2008). For the MCMC method of algorithms samples from a probability distribution to measure the length of the chain were set with 10 million runs, sampling every 1000th run.

Phylogenetic trees were reconstructed in BEAST 1.8.0 and the trees with the best likelihood were summarized using TreeAnnotator 1.8.0 (Drummond *et al.* 2012), the first 10% of trees were discarded as burn-in. Completed phylogenetic trees were arranged and visualized in FigTree 1.4.3.

2.7. Haplotype analysis

Genetic diversity of haplotypes may be analyzed by using different parameters, some of them were used in this study for characterize multiple sequences for several subspecies (Chapters 4, 5). Firstly, the haplotype networks were constructed in Network 10.2 (fluxus-engineering.com 2020). The calculation of the network was carried out by Median Joining method (Bandelt *et al.* 1999).

Genetic polymorphism was analyzed in DnaSP 6.12.03 (Rozas *et al.* 2017). Following values were calculated:

- number of haplotypes H ;
- number of segregating sites S ;
- number of synonymous (silent) N_s and non-synonymous (polymorphic) N_p substitutions
- haplotype (nucleon) diversity Hd , the probability of two randomly sampled alleles being different (Nei & Tajima 1981):

$$Hd = n(1 - \sum_{i=1}^l x_i^2)/(n - 1)$$

where n is the number of sequences (nucleons), l is the number of haplotypes (nucleomorphs), and x is the frequency of i th haplotype in the sample;

- nucleotide diversity π , average number of nucleotide differences per site between any two sequences (Nei & Li 1979):

$$\pi = \sum_{ij} x_i x_j \pi_{ij}$$

where x is the frequency of i th/ j th sequence in the population and π_{ij} is the number of nucleotide differences per site between i th and j th sequences;

- nucleotide diversity k , average number of nucleotide differences per sequence between any two sequences (Tajima 1983):

$$k = \sum \sum_{i < j} k_{ij} / \binom{n}{2}$$

where k_{ij} is the number of nucleotide differences between the i th and j th sequences;

- nucleotide polymorphism ϑ per sequence – proportion of nucleotide sites that are expected to be polymorphic (Watterson 1975):

$$\theta = 4N_e u = 4N_e(1 - e^{-v}) \approx 2 \left(\frac{N_e}{N} \right) v_m = 2 \left(\frac{2N - 1}{N} \right) 2N_v$$

where N_e is effective size of population, u is mutation rate, Nv is the number of mutant sites and v_m is the mean number of mutant sites for the population per generation.

The selection mutations tests were developed according to the neutral theory of molecular evolution based on the statement that most of the variability at the molecular level within and between species occurs due to the random genetic drift of the mutant alleles which are selectively neutral (Kimura 1979). Several tests issued from haplotype parameters were performed:

- Tajima's D , number of nucleotide polymorphisms with the mean pairwise difference between sequences (Tajima 1989):

$$D = \frac{\theta_{\pi} - \theta_{\omega}}{\sqrt{\text{Var}(\theta_{\pi} - \theta_{\omega})}} = \frac{k - S/a}{\sqrt{y_1 S + y_2 S(S-1)}}$$

where ϑ_{π} is estimated ϑ based on the average number of pairwise differences, and ϑ_{ω} is estimated ϑ based on the number of segregating sites normalized by standard deviation or, described by the variables:

$$D = \frac{k - S / \sum_{i=1}^{n-1} \frac{1}{i}}{\sqrt{\left(\frac{\frac{n+1}{3(n-1)} - \frac{1}{\sum_{i=1}^{n-1} \frac{1}{i}}}{\sum_{i=1}^{n-1} \frac{1}{i}} \right) S + \left(\frac{\frac{2(n^2+n+3)}{9n(n-1)} - \frac{n+2}{(\sum_{i=1}^{n-1} \frac{1}{i})n} + \frac{\sum_{i=1}^{n-1} \frac{1}{i^2}}{(\sum_{i=1}^{n-1} \frac{1}{i})^2}}{(\sum_{i=1}^{n-1} \frac{1}{i})^2 + \sum_{i=1}^{n-1} \frac{1}{i^2}} \right) S(S-1)}}$$

- McDonald–Kreitman test, relatively simple means that compare variations of neutral and non-neutral sites within a taxon and between taxa (McDonald & Kreitman 1991). According to this we can calculate the neutrality index using the following equation (Rand & Kann 1996):

$$NI = \frac{N_{Pr}}{N_{Fr}} / \frac{N_{Ps}}{N_{Fs}}$$

where N_{Pr} is the number of polymorphic replacement (non-synonymous) sites, N_{Fr} is the number of fixed replacement sites, N_{Ps} is the number of polymorphic silent (synonymous) sites, and N_{Fs} is the number of fixed silent sites. NI value may be checked by several statistical tests. In this study Fisher's exact test was used together with calculations of McDonald–Kreitman test. This test requires outgroup for calculate polymorphic sites. Usually sister species is used for this purpose.

Two more tests without outgroup are based on the rate of unique alleles and may be described in shortened and extended form:

- Fu–Li's D^* , number of derived nucleotide variants observed only once in a sample with the total number of derived nucleotide variants (Fu & Li 1993):

$$D^* = \frac{\left(\frac{n}{n-1} \right) \eta - a_n \eta_s}{\sqrt{u_{D^*} \eta + v_{D^*} \eta^2}}$$

$$= \frac{\left(\frac{n}{n-1}\right)\eta - a_n\eta_s}{\sqrt{\left[\frac{n}{n-1}\left(a_n - \frac{n}{n-1}\right) - \frac{\left(\frac{n}{n-1}\right)^2 \sum_{k=1}^{n-1} \frac{1}{k^2} + a_n^2 d_n - 2 \frac{na_n(a_n+1)}{(n-1)^2}\right]\eta + \frac{\left(\frac{n}{n-1}\right)^2 \sum_{k=1}^{n-1} \frac{1}{k^2} + a_n^2 d_n - 2 \frac{na_n(a_n+1)}{(n-1)^2}}{a_n^2 + \left(\sum_{k=1}^{n-1} \frac{1}{k^2}\right)}\eta^2}}$$

where η is the number of mutations, η_s is the number of singletons, a_n is $\sum_{k=1}^{n-1} \frac{1}{k}$, and d_n is

$$2 \frac{n \sum_{k=1}^{n-1} \frac{1}{k} - 2(n-1)}{(n-1)(n-2)} + \frac{n-2}{(n-1)^2} + \frac{2}{n-1} + \left(\frac{3}{2} - \frac{2 \sum_{k=1}^{n-1} \frac{1}{k} - 3}{n-2} - \frac{1}{n}\right)$$

- Fu–Li's F^* – number of derived nucleotide variants observed only once in a sample with the mean pairwise difference between sequences (Fu & Li 1993):

$$F^* = \frac{\prod_n - \frac{n-1}{n} \eta_s}{\sqrt{u_{F^*} \eta + v_{F^*} \eta^2}}$$

$$= \frac{\prod_n - \frac{n-1}{n} \eta_s}{\sqrt{\left[\frac{\frac{n}{n-1} + \frac{n+1}{3n-1} - \frac{2n}{n(n-1)} + 2 \frac{n+1}{(n-1)^2} \left(a_{n+1} - \frac{2n}{n+1}\right)}{a_n - \left(d_n + 2 \frac{(n^2+n+3)}{9n(n-1)} - \frac{2}{n-1} \left(4 \sum_{k=1}^{n-1} \frac{1}{k^2} - 6 + \frac{8}{n}\right)\right)\eta + \left(d_n + 2 \frac{(n^2+n+3)}{9n(n-1)} - \frac{2}{n-1} \left(4 \sum_{k=1}^{n-1} \frac{1}{k^2} - 6 + \frac{8}{n}\right)\right)\eta^2}\right]}}$$

The more the populations were subject to selection, the more test values differed from zero (or 1 for NI in McDonald–Kreitman test). Characteristics of these neutrality tests differ. Among tests without outgroups Tajima's D is generally considered to be most powerful, particularly against the alternative hypotheses of selective sweep, population bottleneck and population subdivision (Simonsen *et al.* 1995). Nielsen (2001) concludes what interpretation of these types of tests is not always clear as null hypothesis is a complex including the demographics of the populations, such as constant population size without population structure. MK test is useful to detect selection due to its simplicity being free from so-called “nuisance parameters”. In statistics these parameters are of no interest to the researcher but cannot be ignored (Nielsen 2001). Later was shown reported, that based only on the distribution of allele frequencies, some tests are less powerful to detect both positive and negative selection. The reason for that is the transient nature of positive selection and the weak signal left by negative selection, so MK test has more power in detecting purifying selection (Zhai *et al.* 2009).

3. Molecular phylogeny and taxonomy of Elaninae kites

3.1. Introduction

Elaninae Blyth, 1850 are diurnal raptors traditionally considered as one of the subfamilies of the family Accipitridae. They are small and medium-tailed red-eyed kites usually encountered in tropical biomes in all continental habitats. Actually, there are three genera in this small group where two, *Gampsonyx* and *Chelictinia*, are monotypic. Pearl Kite *Gampsonyx swainsonii* Vigors, 1825, the small-tailed colorful species of Central and South America, consists of three subspecies. The Scissor-Tailed Kite *Chelictinia riocourii*, the small grey-white kite with long forked tail from Central Africa, is monotypic species. The genus *Elanus* includes tropical and subtropical medium-tailed white-grey-black kites having short tail. This taxon has four species: Black-Winged Kite *E. caeruleus* (Desfontaines, 1789), an Old World cosmopolite having according to current checklists either three (Dickinson & Remsen 2013; Gill *et al.* 2022) or four (Clements *et al.* 2019; Kemp *et al.* 2020) known subspecies; American White-Tailed Kite *E. leucurus* (Vieillot, 1818) and Australian monotypic kites: Black-Shouldered *E. axillaris* (Latham, 1801) and Letter-Winged *E. scriptus* Gould, 1842 (Figure 11).

Blyth (1850) was the first who distinguished elanins as a separate subfamily, including *Elanus* and *Chelictinia* genera; *Gampsonyx swainsonii* was considered by him as another species of *Elanus*. Ridgway (1873) proposed the name “group Elani” for these raptors, belonging to the subfamily Buteoninae Vigors, 1825, with genera *Elanus* and *Gampsonyx*, later he added to this group genus *Elanoides* Vieillot, 1818 (Ridgway 1876). Shufeldt (1891) examining skeletons left only the genus *Elanus* in Elaninae and placed it in the family Milvidae (Vigors, 1825); later Hartert (1914) also considered *Elanus* inside Milvidae. The subfamily was moved in Buteonidae (synonym of Accipitridae) by Pycraft (1902), together with another tropical raptor, the monotypic *Macheiramphus* Bonaparte, 1850, the placement of last genus was considered as doubtful several decades after (Brown & Amadon 1968) and much later it was moved under conditions to Perninae Blyth, 1850 (Lerner & Mindell 2005). Peters (1931) added *Chelictinia* to Elaninae and moved *Gampsonyx* into Falconidae Leach, 1820, Friedmann (1950) placed it back. Jollie (1977a, 1977b, 1977c) carried large morphological investigations of a majority of diurnal raptors. Among other

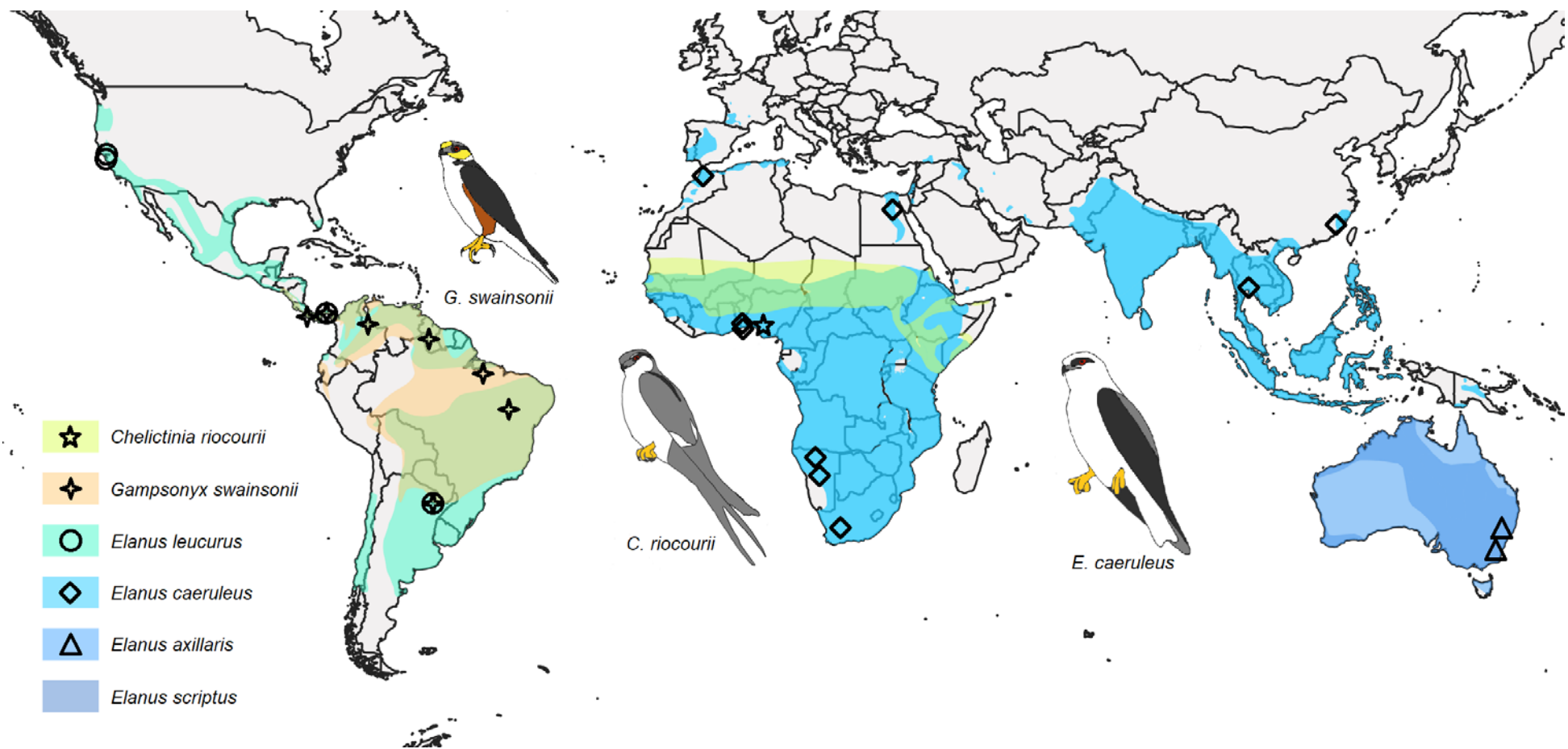


Figure 11. Sample locations (geometric symbols), range (from BirdLife International 2022) and schematic illustrations of elanin kite genera representatives.

proposals he considered “elanins” as a group consisting of *Elanus*, *Gampsonyx* and *Chelictinia* within the subfamily of Milvinae Vigors, 1825 or as a proper subfamily, possibly also with *Macheiramphus*, *Harpagus* Vigors, 1824 and *Ictinia* Vieillot, 1816 (Jollie 1977c).

Wolters (1982) proposed multiple subfamilies in the Accipitridae, among them, Elaninae with *Elanus* and *Chelictinia* and monotypic *Gampsonychinae*. Because he did not provide a diagnosis for this taxon as well as other new taxa, it should be considered as *nomina nuda* and are not valid according to the Article 13 of International Code of Zoological Nomenclature (International... 1999).

Stresemann and Amadon (1979) on the other hand, in the second edition of the first volume of Peters’s “Check-list of birds of the world” placed *Elanus*, *Gampsonyx*, and *Chelictinia* with the majority of diurnal raptors genera to the large Accipitrinae subfamily. Amadon and Bull (1988, cited by Griffiths *et al.* 2007) included in the subfamily *Elanus*, *Gampsonyx*, *Chelictinia* and *Macheiramphus*. Finally, Elaninae are considered as a subfamily of Accipitridae with three genera, *Elanus*, *Gampsonyx* and *Chelictinia* (Lerner & Mindell 2005) which corresponds to the first attempt of their classification (Blyth 1850). Latest molecular research confirmed that *Macheirhamphus* and *Elanoides* previously placed by several taxonomists in Elaninae are distant from *Elanus* and *Gampsonyx* (Lerner & Mindell 2005; Griffiths *et al.* 2007).

Historically all kites including Elaninae were positioned as primitive ancient representatives of accipitrids by their morphological traits (Brown & Amadon 1968). Elaninae are found as the oldest branch of Accipitridae phylogeny, basal to other subfamilies including other kite genera after trees based on mitochondrial and nuclear sequences: *Cyt b* (Wink 2000; Wink & Sauer-Gürth 2004); *Cyt b*, ND2 and BF-I7 (Lerner & Mindell 2005); RAG-1 (Griffiths *et al.* 2007). The singularity of this small group leads to the suggestion to treat it as a separate family Elanidae (Wink 2000; Wink & Sauer-Gürth 2004) or even as order Elaniformes (Debus 2004). The analysis of the molecular phylogeny of the elanin kite group obtained by several molecular markers and their position in the order Accipitriformes Vieillot, 1816 was the aim of this research.

3.2. Material and methods

3.2.1. Sampling and laboratory procedures

Samples from 17 wild individuals of Black-Winged, Black-Shouldered, White-Tailed and Scissor-Tailed kites, deposited in the specimen collection of IPMB, were investigated (Table 6, Figure 11). The DNA was extracted from tissue, feather and blood samples and isolated using standard phenol-chloroform protocol (Sambrook & Russell 2001) with proteinase K. The genes were amplified, cleaned and sequenced using standard physical, chemical and temperature conditions for each marker and specific primers: mitochondrial COI with COIExtF, Passer F1/R1, Bird1Fd, BirdH_351d, Aves_L288, BirdR1dt; Cyt *b* by L14764, Mt-A1a, Mt-c2, Mt-FrS, Mt-Fr, Mt-c4, Mt-E; nuclear RAG-1 with R17 and R51 (see Chapter 2 for details).

3.2.2. Phylogenetic analysis

I made sure that mitochondrial DNA sequences did not contain stop codons, indicating that these sequences did not come from nuclear copies. Alignments were created in BioEdit 7.2.6 (Hall 1999); nucleotide sequences were aligned using the MUSCLE algorithm (Edgar 2004).

For construction of the phylogenetic trees I added available GenBank sequences from other species as outgroups: Red Kite *Milvus milvus* (Linnaeus, 1758), Eurasian Sparrowhawk *Accipiter nisus* Linnaeus, 1758 and Bearded Vulture *Gypaetus barbatus* (Linnaeus, 1758) as representatives of “true” Accipitridae; external Accipitriformes taxa Osprey *Pandion haliaetus* (Linnaeus, 1758) (Table 6).

I choose 576 aligned base pairs (bp) of COI, 1039 bp of Cyt *b* and 650 bp of RAG-1 genes. 18 sequences from GenBank and Barcode of Life Data System (BOLD) databases were added, thus all taxa of Elaninae except *E. scriptus* were analyzed (Table 6, Figure 11).

For finding the best evolution model PhyML with Smart Model Selection (Guindon *et al.* 2010) on Montpellier Bioinformatics Platform was applied with Akaike information criterion (Akaike 1974). This showed General Time Reversible model with invariant sites (GTR+I; Tavaré 1986; Shoemaker & Fitch 1989) for COI and RAG-1 markers, and same model with gamma distributed rates among sites (GTR+ Γ ; Tavaré 1986; Yang 1994) for Cyt *b*.

Table 6. Samples of elanin kites used in the phylogenetic analysis with outgroup.

Taxon	Origin	Source	IPMB number / GenBank accession number / BOLD Process ID		
			RAG-1	COI	Cyt b
<i>Elanus caeruleus caeruleus</i>	Egypt	This study	IPMB373 / MT897851	IPMB373 / MT800534	IPMB373 / MT800519
<i>Elanus caeruleus caeruleus</i>	Morocco	This study	IPMB4251 / MT897852	IPMB4251 / MT800535	IPMB4251 / MT800520
<i>Elanus caeruleus caeruleus</i>	South Africa, Cape Province	This study	IPMB9965 / MT897853	IPMB9965 / MT800536	IPMB9965 / MT800521
<i>Elanus caeruleus caeruleus</i>	South Africa, Cape Province	This study	IPMB9966 / MT897854	IPMB9966 / MT800537	IPMB9966 / MT800522
<i>Elanus caeruleus caeruleus</i>	South Africa, Cape Province	This study	IPMB9967 / MT897855	IPMB9967	IPMB9967 / MT800523
<i>Elanus caeruleus caeruleus</i>	Namibia, Okaukuejo	This study	IPMB20593 / MT897856	IPMB20593	IPMB20593 / MT800524
<i>Elanus caeruleus caeruleus</i>	Namibia, Windhoek	This study	IPMB47115 / MT897857	IPMB47115	IPMB47115 / MT800525
<i>Elanus caeruleus caeruleus</i>	Namibia, Windhoek	This study	IPMB47116 / MT897858	IPMB47116	IPMB47116 / MT800526
<i>Elanus caeruleus caeruleus</i>	Namibia, Windhoek	This study	IPMB47117 / MT897859	IPMB47117	IPMB47117 / MT800527
<i>Elanus caeruleus caeruleus</i>	Namibia, Windhoek	This study	IPMB47118 / MT897860	IPMB47118	IPMB47118 / MT800528
<i>Elanus caeruleus caeruleus</i>	Namibia, Windhoek	This study	-	-	IPMB47119 / MT800529
<i>Elanus caeruleus caeruleus</i>	Benin, Cotonou	This study	IPMB58999 / MT897861	IPMB58999 / MT800530	IPMB58999 / MT800530
<i>Elanus caeruleus caeruleus</i>	Benin, Bohicon	This study	IPMB75231 / MT897862	IPMB75231 / MT800539	IPMB75231 / MT800531
<i>Elanus caeruleus vociferus</i>	China, Liancheng	Luo <i>et al.</i> 2022	-	OK662584	OK662584
<i>Elanus caeruleus vociferus</i>	Thailand	Boonyaparakob & Kasornrorkbua unpubl.	-	MK932886	-
<i>Elanus caeruleus ssp.</i>	unknown	Griffiths <i>et al.</i> 2007	EF078724	-	-
<i>Elanus leucurus leucurus</i>	Argentina, San Cayetano (Corrientes)	Kerr <i>et al.</i> 2009b	-	FJ027543 / KBARG184-07	-
<i>Elanus leucurus majusculus</i>	USA	Lerner & Mindell 2005	-	-	AY987233
<i>Elanus leucurus majusculus</i>	Panama, Pacora	Smithsonian Tropical Res. Inst. unpubl.	-	BSENC001-06	-
<i>Elanus leucurus majusculus</i>	Panama, Pacora	Smithsonian Tropical Res. Inst. unpubl.	-	BSPAC008-14	-
<i>Elanus leucurus majusculus</i>	USA, Rodeo (California)	Kerr <i>et al.</i> 2007	-	DQ432907 / CDMVZ014-05	-
<i>Elanus leucurus majusculus</i>	USA, Berkeley	Kerr <i>et al.</i> 2007	-	DQ432908 / CDMVZ015-05	-
<i>Elanus axillaris</i>	Australia, Birriwa	This study	IPMB8050 / MT897863	-	-
<i>Elanus axillaris</i>	Australia, Canberra?	This study	IPMB29917 / MT897864	-	-
<i>Elanus axillaris</i>	Australia, Canberra?	This study	-	IPMB29920 / MT800540	IPMB29920 / MT800532
<i>Gampsonyx swainsonii swainsonii</i>	Argentina, San Cayetano (Corrientes)	Mus. Argent. Cienc. Nat. Rivadavia unpubl.	-	FJ027613 / KBAR776-06	-
<i>Gampsonyx swainsonii swainsonii</i>	Brazil, Serra das Confusoes	Tavares <i>et al.</i> 2011	-	JN801680 / LGEMA021-07	-
<i>Gampsonyx swainsonii swainsonii</i>	Brazil, Tailândia	Tavares <i>et al.</i> 2011	-	LGEMA404-08	-
<i>Gampsonyx swainsonii leonae</i>	Guyana, Saddle Mountain	Schindel <i>et al.</i> 2011	-	JQ174910 / USNMI208-11	-
<i>Gampsonyx swainsonii leonae</i>	Guyana, Saddle Mountain	Schindel <i>et al.</i> 2011	-	JQ174911 / USNMK306-11	-
<i>Gampsonyx swainsonii leonae</i>	Panama, Pacora	Smithsonian Tropical Res. Inst. unpubl.	-	BSPBA002-07	-
<i>Gampsonyx swainsonii leonae</i>	Panama, Puerto Armuelles	Smithsonian Tropical Res. Inst. unpubl.	-	BSPBA005-07	-
<i>Gampsonyx swainsonii leonae</i>	Colombia, Caño Agua Verde (Arauca)	Inst. Invest. Recurs. Biol. von Humboldt unpubl.	-	IAVHB082-13	-
<i>Gampsonyx swainsonii leonae</i>	unknown	Griffiths <i>et al.</i> 2007	EF078725	-	-
<i>Chelictinia riocourii</i>	Nigeria, Agbor	This study	IPMB47157 / MT897865	IPMB47157 / MT800541	IPMB47157 / MT800533
<i>Milvus milvus</i>		Griffiths <i>et al.</i> 2007; Margaryan <i>et al.</i> 2021	EF078747	MN122837	MN122837
<i>Accipiter nisus</i>		Griffiths <i>et al.</i> 2007; Zhang <i>et al.</i> 2014	EF078708	KM360148	KM360148
<i>Gypaetus barbatus</i>		Helbig <i>et al.</i> 2005; Griffiths <i>et al.</i> 2007; Mwale <i>et al.</i> unpubl.	EF078728	KX012864	AJ604494
<i>Pandion haliaetus</i>		Griffiths <i>et al.</i> 2007; Feng <i>et al.</i> 2020	EF078706	MN356325	MN356325

Maximum Likelihood and Neighbor-Joining trees for each gene and average pairwise p-distances were calculated with MEGA 6.06 (Tamura *et al.* 2013). Relative branch support was evaluated with 1000 for the Maximum Likelihood (GTR model) and 10000 bootstrap replicates (p-distances) for Neighbor-Joining trees.

Bayesian concatenated mitochondrial and nuclear gene trees were calculated using BEAUti 1.8.0 (Drummond *et al.* 2012). To set the rates of clock model we used half-value of the 2.1% sequence divergence per million years for Cyt *b* which is accepted for birds (Weir & Schluter 2008) and 1.8% for COI (Lavinia *et al.* 2016), estimated default rate for nuclear alignment. Relaxed clock lognormal model (Drummond *et al.* 2006) with Birth-Death speciation process was chosen (Feller 1939; Gernhard 2008).

One fossil calibration point was added. Among the first diurnal raptors the remains of unidentified to genus level specimen lived in Lutetian stage of Eocene, 41.2–47.8 MYA were found in Crimea (Panteleyev 2011, cited by Zelenkov & Kurochkin 2014), this is practically the same age as for the first known accipitrid species *Milvoides kempi* (Mayr 2009) but more precise. This bird was firstly attributed to the subfamily Buteoninae (Panteleyev 2011, cited by Zelenkov & Kurochkin 2014), later much generally to the tribe Accipitrini Cracraft, 2013 (Zelenkov & Kurochkin 2014). Actually, its belonging to the tribe is in doubt but this specimen nevertheless is considered as accipitrid (Zelenkov pers. comm.) and was used to separate this family from ospreys. The point was modeled using a lognormal distribution (mean = 1.195, stdev = 0.75, offset = 41.2).

For Markov chain Monte Carlo method, the length of chain was set to 10 million runs with sampling every 1000 runs. Phylogenetic trees were performed in BEAST 1.8.0, the trees with the best likelihood were summarized using TreeAnnotator 1.8.0 (Drummond *et al.* 2012), the first 10% of trees were discarded as burn-in.

3.3. Results

The numbers of parsimony-informative and variable uninformative sites for elanin kites are 4 and 22 bp of 650 bp for RAG-1, 99 and 143 bp of 576 bp for COI and 91 and 209 bp of a total 1039 bp for Cyt *b* genes respectively (Tables A1–A3). Sequence divergences using pairwise distances are relatively high and consist up to 2.6% for COI between

subspecies, 8.5–9.7% for COI and 8.9–11.2% for Cyt *b* between species of the genus *Elanus*, 12.2–15.1% and for COI 11.7–13.2% for Cyt *b* between genera of the group (Table 7).

As can be seen from Figure 12, the family Pandonidae Sclater & Salvin, 1873 represents the basal branch of the order Accipitriformes. The group of all elanin kites forms a separate clade basal to other Accipitridae and its monophyly is confirmed with high support values for Bayesian Inference for nuclear RAG-1 gene (Figure A1) as well as for mitochondrial gene sequences (Figures A2, A3). As expected, the elanins and Red Kite as example, which forms clades together with other subfamily representative, show polyphyly of this artificial group “Kites”. Phylogenetic trees, which were constructed with ML and NJ provide mostly identical topologies for separate mitochondrial and nuclear datasets of elanins (Figures A4–A9).

According to the molecular clock model used in Bayesian analysis with fossil calibration point, the separation of Elaninae from other diurnal raptors may be estimated at Middle Eocene, 43.4 MYA (with 95% interval of highest posterior density 46.1–41.6 MYA; Figure 12). The divergence within the group between *Elanus* and two other genera passed

Table 7. Pairwise p-distance values for taxa of Elaninae and other Accipitridae used in the phylogenetic analysis, based on COI (below diagonal) and Cyt *b* (above diagonal).

No	Species	1	2	3	4	5	6	7	8	9	10	11	12
1	<i>Elanus caeruleus caeruleus</i>		0.21-0.23	0.11-0.112	-	0.102-0.104	0.13-0.132	-	-	0.156-0.157	0.168-0.169	0.162-0.164	0.172-0.173
2	<i>Elanus caeruleus vociferus</i>	0.024-0.026		0.110	-	0.101	0.131	-	-	0.153	0.168	0.157	0.172
3	<i>Elanus axillaris</i>	0.089-0.09	0.85		-	0.089	0.117	-	-	0.142	0.149	0.134	0.162
4	<i>Elanus leucurus leucurus</i>	0.094-0.095	0.097	0.097		-	-	-	-	-	-	-	-
5	<i>Elanus leucurus majusculus</i>	0.094-0.095	0.097	0.097	0		0.129	-	-	0.15	0.166	0.152	0.158
6	<i>Chelictinia riocourii</i>	0.135-0.137	0.132	0.123	0.142	0.142		-	-	0.137	0.149	0.14	0.156
7	<i>Gampsonyx swainsonii leonae</i>	0.141-0.142	0.139	0.151	0.122	0.122	0.13		-	-	-	-	-
8	<i>Gampsonyx swainsonii swainsonii</i>	0.141-0.142	0.139	0.151	0.122	0.122	0.13	0		-	-	-	-
9	<i>Milvus milvus</i>	0.155-0.156	0.158	0.144	0.167	0.167	0.16	0.161	0.161		0.114	0.128	0.157
10	<i>Accipiter nisus</i>	0.137-0.141	0.151	0.144	0.165	0.165	0.155	0.153	0.153	0.113		0.145	0.165
11	<i>Gypaetus barbatus</i>	0.148-0.151	0.149	0.123	0.151	0.151	0.13	0.149	0.149	0.142	0.149		0.156
12	<i>Pandion haliaetus</i>	0.148-0.149	0.146	0.153	0.156	0.156	0.123	0.148	0.148	0.144	0.148	0.144	

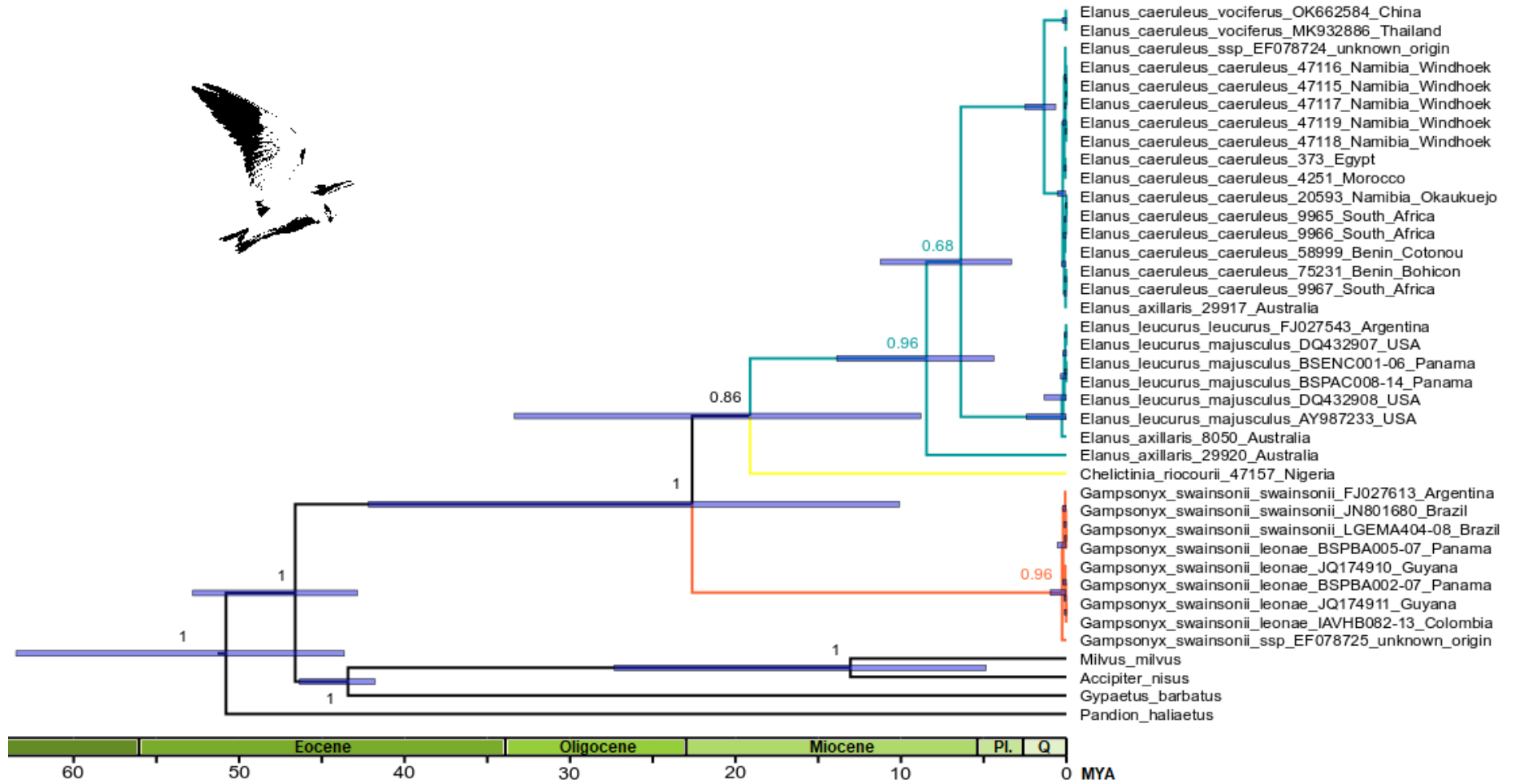


Figure 12. Bayesian phylogenetic tree of Elaninae kite sequences. Node bars show the 95% highest posterior density of nodal age estimates, node labels show posterior rates greater than 50%.

most probably 23.3–19.8 MYA, the speciation inside *Elanus* started most probably in Late Miocene from 8.3 MYA (HPD = 13.5–4.0 MYA). Exact position of *Elanus* spp. subspecies on the phylogenetic tree including currently accepted and three formerly valid subspecies of *E. caeruleus* (Parkes 1958) cannot be determined with my dataset because of lack of sufficient data. Several slightly different *Cyt b* differing for 1–3 substitutions (Figure 13) and even RAG-1 haplotypes of the African subspecies *E. c. caeruleus* (Desfontaines, 1789) were found across the entire continent.

The Scissor-Tailed Kite, never sequenced before, unequivocally belongs to the Elaninae kites clade. Several different mitochondrial as well as nuclear haplotypes exist inside *Elanus caeruleus* belonging to nominate subspecies (Table 7, Figure 12).

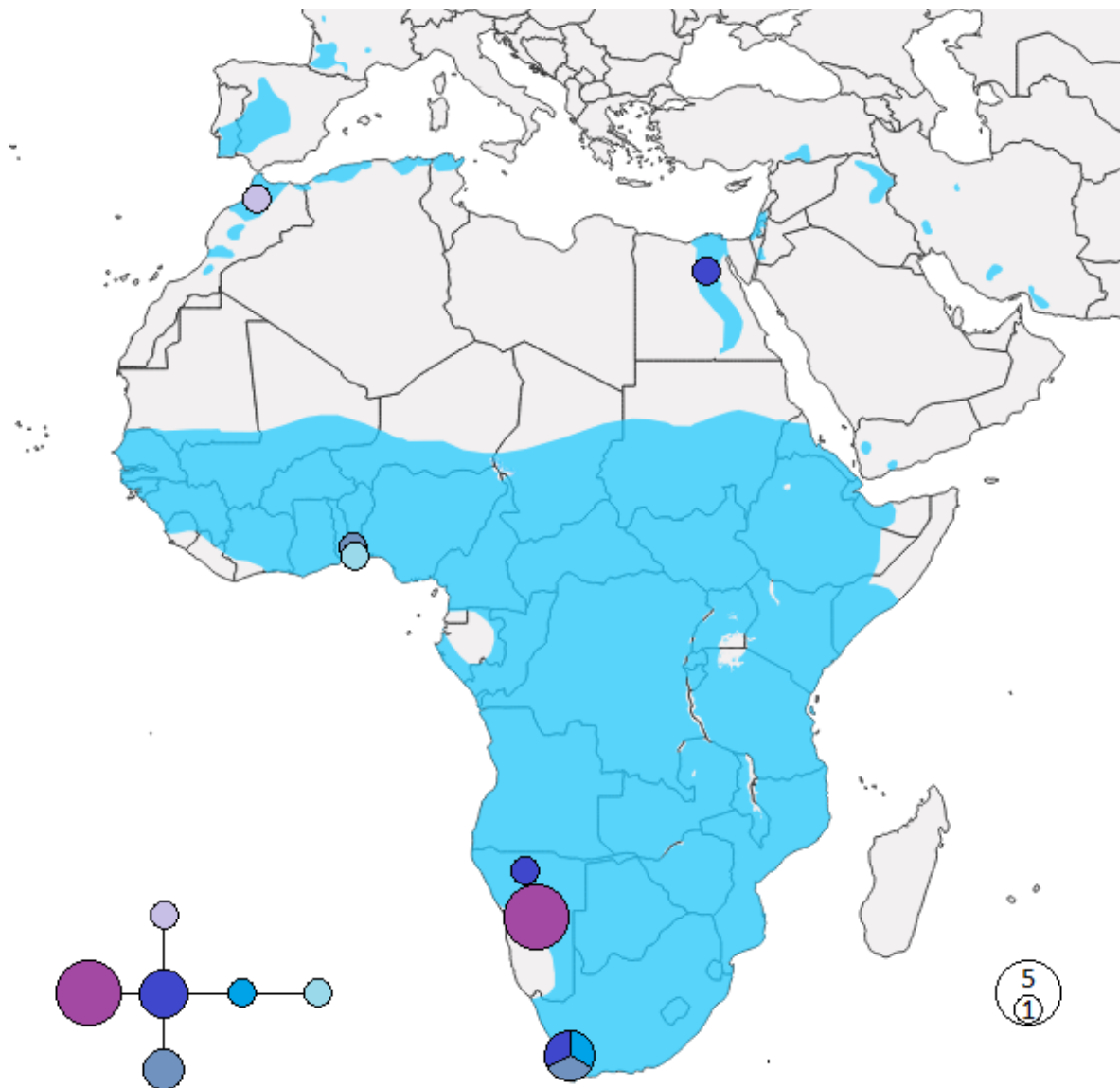


Figure 13. Distribution and structure of *Elanus c. caeruleus* *Cyt b* haplotypes.

3.4. Discussion

3.4.1. Phylogenetics of elanins

Molecular clock estimates of elanins based on our mitochondrial DNA data with fossil calibration point do not exactly correspond with previous calculations on the appearance of different Accipitridae because it was based on more recent calibration points, most of them are also phylogenetically far from elanins. Nagy and Tökölyi (2014) based their tree on two Pliocene *Buteo* hawks and the split of Pandionidae and Accipitridae which they dated on 37 MYA considering ancient Osprey *Palaeocircus cuivieri* Milne-Edwards, 1871 and accipitrid *Aquilavus* Lambrecht, 1933 in British Upper Eocene (Harrison & Walker 1976). Unfortunately, the authors did not precise which distribution and parameters of calibration point they choose. Mindell and coauthors (2018) used Snake Eagle from Late Miocene and two Miocene/Pliocene vultures. Both sources assuming a split for Elaninae circa 34 MYA.

The consistence between molecular and morphological data issued from fossils usually is not full, the median retention index between phylogenetical trees (Farris 1989) of two types of information for birds is 0.6 (Sansom & Wills 2017). At the same time my data are not so far from previous estimations of the node *Elanus/Gampsonyx* age: 23.3 MYA (HPD = 37.9–11.4 MYA) by this study and ~20.5 MYA (HPD = 29.4–14.4 MYA) by Nagy and Tökölyi (2014). No Elaninae fossils exist and the fossilization is often not usual for tropical biomes cause of warm and wet climate conditions, but their possible find eventually could bring more information on this group's origin.

The smallest Neotropical raptor Pearl Kite is ecologically distinct from other elanins being only one mostly sedentary kite of this group (Table 8), and is the most distant taxon in the phylogenetic tree (Figures 12, A1–A9). According to these facts, it is possible that the Neotropics might be the Elaninae origin and migration traits probably appeared after the first split of currently existed elanins from common ancestor. Neotropical ancestor distribution for Elaninae is also estimated by modeled with biogeographic software (Nagy & Tökölyi 2014). Three subspecies of Pearl Kite were described: *G. s. swainsonii* (Vigors, 1825), *G. s. leonae* Chubb, 1918 and *G. s. magnus* Chubb, 1918. Molecular data for two first subspecies taking into account the geographic origin of samples are available. No difference between it was observed (Table 7). The range of these forms adjoin each other, *swainsonii*

Table 8. Characteristics of elanin genera. Data from Brown & Amadon 1968; Ferguson-Lees & Christie 2001; Clark & Davies 2018; Bierregaard & Kirwan 2020; Bierregaard *et al.* 2020; Debus *et al.* 2020a, 2020b; Kemp *et al.* 2020; BirdLife International 2022.

	<i>Elanus</i>	<i>Chelictinia</i>	<i>Gampsonyx</i>
Length (cm)	29–43	33–38	20–28
Wing (mm)	249–328	225–254	141–178
Wingspan (cm)	77–102	68–76	45–55
Tail (mm)	110–186	170–216	82–108
Tarsus (mm)	32–40	28–33	28–32
Weight (g)	160–427	100–140	94–140
Egg measurements (mm)	37–46 × 29–36	34–38 × 27–31	30 × 24
Number of eggs	3–5 (2–6)	4	3–4 (2–4)
Plumage color	gray, black, and white	gray, black, and white	black, white, rufous, yellow
Eyes color	red; orange-rufous (<i>E. leucurus</i>)	red	chestnut or red
Range	tropical and subtropical biomes of the world	Subsaharan Africa	Central and South America
Habitat	open woodland, savanna, grassland, farmland, urban green areas, marsh, riverine vegetation; cultivated steppe, semi-desert, desert, rocks (<i>E. caeruleus</i>); coastal dunes (<i>E. axillaris</i>)	semi-desert, savanna, grassland	open woodland, savanna, scrub, urban green areas
Altitude (m)	0–3000 (4200)	0–500	0–1000+
Movements	migratory or nomadic; also sedentary (<i>E. axillaris</i>)	migratory, nomadic	sedentary or locally nomadic
Feeding	small mammals, also small birds, reptiles and amphibians, large insects; occasionally dead fish (<i>E. caeruleus</i>)	insects, arachnids, lizards, also small snakes, sometimes rodents	lizards, large insects, spiders, also snakes, rodents
Nest place	trees; occasionally bush (<i>E. caeruleus</i>) or artificial structures	trees or bush	trees
Height of nest place (m)	0.75–35	2–8	4–7
Nest (across, cm)	30–74	30–40	20

and *leona* vary slightly only by plumage colors (see below). Further genetic investigation of Pearl Kite subspecies is needed.

The Scissor-Tailed Kite is traditionally considered as an Elaninae genus (Peters 1931) and this position was recently notified as provisional in absence of molecular data (Gill & Donsker 2020). My study can confirm this placement.

Pairwise p-distances between genus *Elanus* and the two other genera, especially *Gampsonyx* are comparable with the distances between representatives of different subfamilies in the order Accipitridae for both investigated mitochondrial genes (Table 7).

Subspecies of White-Tailed Kite show identical haplotype from COI (Table A2). Their range is disrupted by Amazonian basin (Bierregaard *et al.* 2020), the forms are distinguished by small but significant size differences of the wing, tail and culmen (Bangs & Penard 1920; Clark & Banks 1992) thus the validity of these subspecies is not in doubt. However, there is no distinction by DNA-barcoding marker, but I can suppose that with more high-variable marker as control region it may be found.

3.4.2. Cytogenetics of Black-winged Kite

The chromosome structure of *Elanus caeruleus* differs because of specific evolution from these of other Accipitridae and by some traits even from other birds. Constitution of diurnal raptor's karyotype include less chromosomes in total, medium chromosomes with few microchromosomes instead of numerous macro- and dot-chromosomes of other birds and *E. caeruleus* have even more specific karyotype with only one pair of small chromosomes. Moreover secondary constrictions of several Black-winged Kite acrocentric chromosomes are smaller than for other Accipitridae, comparison of chromosome banding pattern demonstrate another arrangement in comparison with other diurnal raptor taxa and sex chromosomes are almost equal among them in contrast of most of other birds (Bed'Hom *et al.* 2003). Also the nucleolus organizer regions of *E. caeruleus* are not typical for Accipitridae being located on two chromosome pairs instead of one (De Boer & Sinoo 1984).

The specimens from Morocco and South Africa which should belong to nominate *E. c. caeruleus* subspecies contain 68 (Bed'Hom *et al.* 2003) and 64 (Harris & Walters 1982) chromosomes respectively. At the same time Indian specimen which should be *E. c. vociferus* (Latham, 1790) contains diploid number of 66 chromosomes (Ansari & Kaul 1986). The difference may be explained by mistake of distinguishing of microchromosomes (Bed'Hom *et al.* 2003), unlikely that in Southern Europe and Maghreb exist populations significantly distinct by cytology from main range, but possible difference with more remote birds from Asia furthermore differed genetically (Table 7, Figure 12) seems more probable. Further comparative research of Black-Winged kites subspecies should represent interest.

3.4.3. Morphology and ecology of elanin kites

Among evolutionary features that distinguish elanins from other diurnal raptors, several morphological traits are found. Some of them are absent in other Accipitridae. It may be classified in several groups. In list of osteological features stands out skull structure: schizognathous palates (Shufeldt 1891) ossifying boundary of the *foramen olfactorii* (Suschkin 1899); low basicranial angle (30° contra 40–74° for other accipitrids) for *Elanus* and curved falcon-type form of the orbital process for *Gampsonyx* (Jollie 1977b). Suschkin (1899) notified that this primitive skull structure is typical for other raptors in embryos state, was later found in several Accipitridae genera (Pycraft 1902; Jollie 1977a) but in Elaninae skull maxillopalatine processes are separated most strongly (Friedmann 1950; Jollie 1977a). Usually diurnal birds of prey have more modern desmognathous palate type where *processuum palatina* are not connected each other, unlike elanins and most part of owls (Kartashyov 1974). Features of limb bones includes *os manus* longer than *humerus*, inner spur of *hypotarsus* begins from the inner board of the shaft (Pycraft 1902), distant positions of metatarsal scars (like Osprey) with specific form of the middle trochlea, pillar-like medial process of calcaneal tuberosity and own “elanin subtype” of the tarsus in general as a result of specialization for easy flexing of the toes (Jollie 1977b). Other remarkable osteological traits: no *hypocleidium* in furcula, unusual coracoids, where high position of coracoid foramen on procoracoid process and short sternocoracoid process, large depth of the keel and constitution of the sternum like Osprey, first cervical rib fused with the vertebra for *Elanus* (Jollie 1977b, 1977c).

Elanin kites equally have several myological peculiarities. Among specific muscles related with limbs are fully developed *piriformis* serves as origin for the parts of the *flexor digitorum superficialis*, outstanding *flexor digitorum longus*, wide tendons of internal *flexor hallucis brevis*, weak *peroneus longus*, completely separated heads of the *pars perforatus digiti III*, only medial and no lateral head of the *pars perforatus digiti IV*. Other unique muscles: *ceratoglossus* arise to the medial insertion of the massive *transverses hyoideus* like cathartids, Secretarybird and in part Osprey; lack *pars mandibularis*; muscles of innominate bones reach forward beneath the anterior plates of the ilia, the *caudilio-femoralis* arising strongly forward by a tendon from the ventral point of the pygostyle. For Pearl Kite the *pars*

metapatagialis of *latissimus dorsis* is related with ribs not only three and four but also five and six by aponeurosis like falcons (Jollie 1977c).

Other unique morphological features of Elaninae are absence of grooves on the claws (Friedmann 1950); almost complete absent plumules on the crown for *Gampsonyx* (Jollie 1977a); weakly developed syringeal box; simple gut: open duodenum, non-developed ileum with absent supracecal loop (Jollie 1977c), a bony shelf above the eye (Lerner & Mindell 2005). Pearl Kite disposes most diverse color pattern of plumage among diurnal raptors and absence of the median black throat stripe. The colours are grey upper surface darker, straw-color instead of the orange-beige of forehead and sides and *magnus* race that have no rufous on flanks is also separated geographically, differing by wing and tail measurements (Chubb 1918; Jollie 1977c; Ferguson-Lees & Christie 2001; Bierregaard and Kirwan 2020). The clinal variation may exist for this species with wide range, anyway morphological (and genetic) research on Pearl Kite subspecies is required in the future.

Among some traits appearing as a result of convergence from *Elanus*, the well investigated genera of his group, is characterized unlike other diurnal raptors by owl-like features: zygodactylism (also Osprey), large frontally-placed eyes, vibrissae around the beak, velvet structure of upper parts of primary and secondary feathers structure as an adaptation for silent flight, producing of undigested bones pellets as result of low acidity of the stomach. *Elanus* representatives are more or less nocturnal, the most night-active species is Letter-Winged Kite, which disposes asymmetrical position of ear openings like several owls helping to detect their prey by sound (Negro *et al.* 2006). The eggs of elanins are intensively pigmented not like other accipitrids but falconids. And elements of their vocalization resemble to similar of Barn Owl *Tyto* Billberg, 1828: screech; and falcons: chatter, maternal croak (Debus 2004).

It is possible to explain the mixture of haplotypes (Figure 13) by the movements of subadults and adults Black-Winged Kite through their range which may be hundreds of kilometers (Mendelsohn 1983). Seems weighty the assumption of Negro *et al.* (Negro *et al.* 2006) that relatively nocturnal *Elanus* feeding rodents occupy the ecological niche of nomadic owls feel in Northern Hemisphere.

The difference in morphometric and ecological characteristics of Elaninae genera are present in the Table 8. Among other ecological features of elanins, specific parasites should be notified. Clay (1958) discovered the species group elani of *Degeeriella* (Neumann, 1906),

a genus of Mallophaga (Nitzsch, 1818), common for all genera of Elaninae, and also *Elanoides* and *Aviceda* Swainson, 1836, that each of chewing lice species correspond to its own kite genus. It seems interesting to further follow the cophylogeny of these lice together with their hosts, like it was recently shown for other ectoparasites of different groups of birds (Page *et al.* 1998; Banks *et al.* 2006; Hughes *et al.* 2007; Štefka *et al.* 2011).

3.4.4. Taxonomic implications for elanins

Systematics of only one non-monotypic in the group deserves attention. The South Asian subspecies of Black-Winged kite *Elanus caeruleus vociferus* was described from India as full species (Latham 1790), naturally the term of subspecies was not known during this time. The p-distance between African and Thai *E. caeruleus* COI sequences (Table 7) is even higher than between several species of one genus in Accipitridae (Seibold 1994; Cai *et al.* 2010; Dolinay 2015; Etherington & Mobley 2016; Retnaningtyas *et al.* 2017; Zein 2018; Kunz *et al.* 2019), their split occurred 1.9 MYA (4.9–0.6 MYA HPD, Figure 2). Indian Black-Winged Kite distinguishes by its karyotype singularity (see Section 3.4.2) and morphologically by well-defined black tips of underwing coverts (Husain 1959). Curiously this race is not recognized as subspecies by Ferguson-Lees and Christie (2001), merging it with *caeruleus*, and Mees (1982) leaves its status discussed. Actually *E. c. vociferus* is present in all main bird checklists (Dickinson & Remsen 2013; Clements *et al.* 2019; Gill *et al.* 2022). I suggest that *E. c. vociferus* may be restored as species, but currently it cannot be resolved without additional material. The rest subspecies *E. c. hypoleucus* Gould, 1859 remains unsequenced.

Simultaneously the position of Black-Shouldered Kite is contradictory, two of three sequences of this species form clade with Black-Winged Kite with low bootstrap support. The last of my three nuclear sequences of *Elanus axillaris* is apart from *caeruleus-axillaris* clade (Figure 12). It may mean that *E. axillaris* is not homogeneous or that this specimen would be confused with another Australian *E. scriptus*, which is relatively close by its exterior including plumage and shared range (Debus *et al.* 2020a, 2020b) and never was sequenced. Debus (2004) suggested that Australian *E. axillaris* is recent species, split from the Old World *E. caeruleus*. Finally, seems likely that we can observe here a case of introgression, which occurs between close bird taxa inside of nuclear as well as mitochondrial genome producing a mismatch in molecular dating (Drovetski *et al.* 2015). Black-Shouldered as well as American

White-Tailed kites formerly were merged with the “main” species of the group as subspecies (Rensch 1931; Parkes 1958; Husain 1959; Mees 1970), this taxonomic arrangement was not supported later (Brown & Amadon 1968; Mayr & Short 1970; Stresemann & Amadon 1979; Sibley & Monroe 1990). Clark and Banks (1992) proved independence of these species observing morphometric differences between it. Currently *E. axillaris* and *E. leucurus* are considered as full species (Dickinson & Remsen 2013; Clements *et al.* 2019; Gill *et al.* 2022). All three species may be treated as allospecies (Clark & Banks 1992) or forming superspecies *Elanus [caeruleus]* (Mayr & Short 1970; Stresemann & Amadon 1979). I recognize current taxonomic status of *Elanus* species with mention that the composition of this genus may change when the data from mitochondrial and nuclear markers from all species and subspecies will be available.

Describing Pearl Kite Vigors (1825) notified its remarkable appearance close to the falcons and hawks both but placed it together with lastly relaying of his bill morphology and wings size. Later this genus was placed by different authors to Falconidae (Peters 1931; Pinto 1938; Hellmayr & Conover 1949) and back to Accipitridae (Friedmann 1950; Stresemann 1959; Brodkorb 1960; Meyer de Schauensee 1971; Stresemann & Amadon 1979) families. The validity of all *Gampsonyx* subspecies may be confirmed after further genetic research (see Section 3.4.3).

Based on the synthesis of different type of data discussed above I made following taxonomic implications. We recommend elevating the subfamily of Elaninae to the family Elanidae (Blyth, 1850) **stat. nov.**, LSID urn:lsid:zoobank.org: act:4E7580BA-7338-48F4-9100-B3A85F760B3C (Starikov & Wink 2020); conserving internal subfamily Elaninae and distinguishing inside a monotypic subfamily Gampsonychinae previously proposed by Wolters (1982) as invalid taxon. The description of the new subfamily is provided below (Starikov & Wink 2020):

“Gampsonychinae Starikov & Wink, subfam. nov.

Type genus: *Gampsonyx* Vigors, 1825

Type species: *Gampsonyx swainsonii* Vigors, 1825

LSID: urn:lsid:zoobank.org:act:D25DE61A-7AE6-46BC-919A-44071B7AB9EA

Diagnosis: The new subfamily is distinguished by combination of molecular phylogenetic, morphological and ecological data. Small falcon-like predators. Males and females have black upperparts, crown on the head, patch on breast side, bill, white underparts, chin and throat, yellow to orange forehead and cheeks. Plumules on the crown are practically absent. Orbital processes in the skull are rounded. *Pars metapatagialis* of *latissimus dorsis* muscle is related with ribs three to six. Mild sexual dimorphism, females are 10–20% larger than males. Feeds on small lizards and large insects. Inhabits dry and arid regions, savannas, shrubs, snags, pastures, open woodlands, also edges of tropical evergreen forest. Non-migratory, nomads and juvenile dispersal. Distributed in Neotropics from El Salvador to North Argentina. Monotypic, one genus and species, three subspecies”.

4. Phylogeny and phylogeography of Black and Yellow-Billed kites based on cytochrome *b*

4.1. Introduction

The Black Kite *Milvus migrans* and Yellow-Billed Kite *Milvus aegyptius* are two allopatric species of diurnal polyphagous raptors distributed in the Old World. The Black Kite is ubiquitous mostly migrant species with a wide range that covers Eurasia, Africa and Australia and occupies many different biomes, boreal, deciduous and tropical forests, steppes, as well as anthropogenically transformed landscapes. The Yellow-Billed Kite is a partial migrant located on the African continent and in some areas in Western Asia (Ferguson-Lees & Christie 2001; Johnson *et al.* 2005; Gill *et al.* 2022).

As a taxon, *Milvus migrans* is divided into five subspecies (Figure 14). Nominate European Black Kite *M. m. migrans* (Boddaert, 1783) is widely distributed in Europe, North Africa, Turkey, Iran and Central Asia. This form is a winter migrant up to tropical Africa, has a brown to dark-brown with a whiteness throat and often rufous ventral side, paler brown-greier head. European Black Kite is tree-breeding, frequently colonial and less synanthropic than other subspecies (Swann 1922; Dementiev 1951b; Stepanyan 2003; Karyakin 2017).

In Western Siberia, Kazakhstan and mountain parts of Central Asia it intergradates with Black-Eared or Siberian Kite *Milvus migrans lineatus* (J. E. Gray, 1831), here we can find birds with intermediate traits (Dementiev 1951b; Mitropol'skiy *et al.* 1987; Stepanyan 2003; Karyakin 2017). Black-Eared Kite inhabits Siberia, China, Korea, Japan and partially Russian Far East, equally migrant, except birds from Eastern and Southern China, Korea and Japan (BirdLife International 2022). This kite is associated with trees as others but well adapted to the steppe and rocky landscapes, more tailed in comparison with European Kite, characterized by dark chocolate above, deep rufous-brown below, paler brown-rufous tail and white spots under the wings (Swann 1922; Dementiev 1951b; Stepanyan 2003; Karyakin 2017).

Indian Small or Pariah Kite *Milvus migrans govinda* Sykes, 1832 lives in Asia from Pakistan to Indochina, is non-migrant but exercising movements; it is smaller than nominate

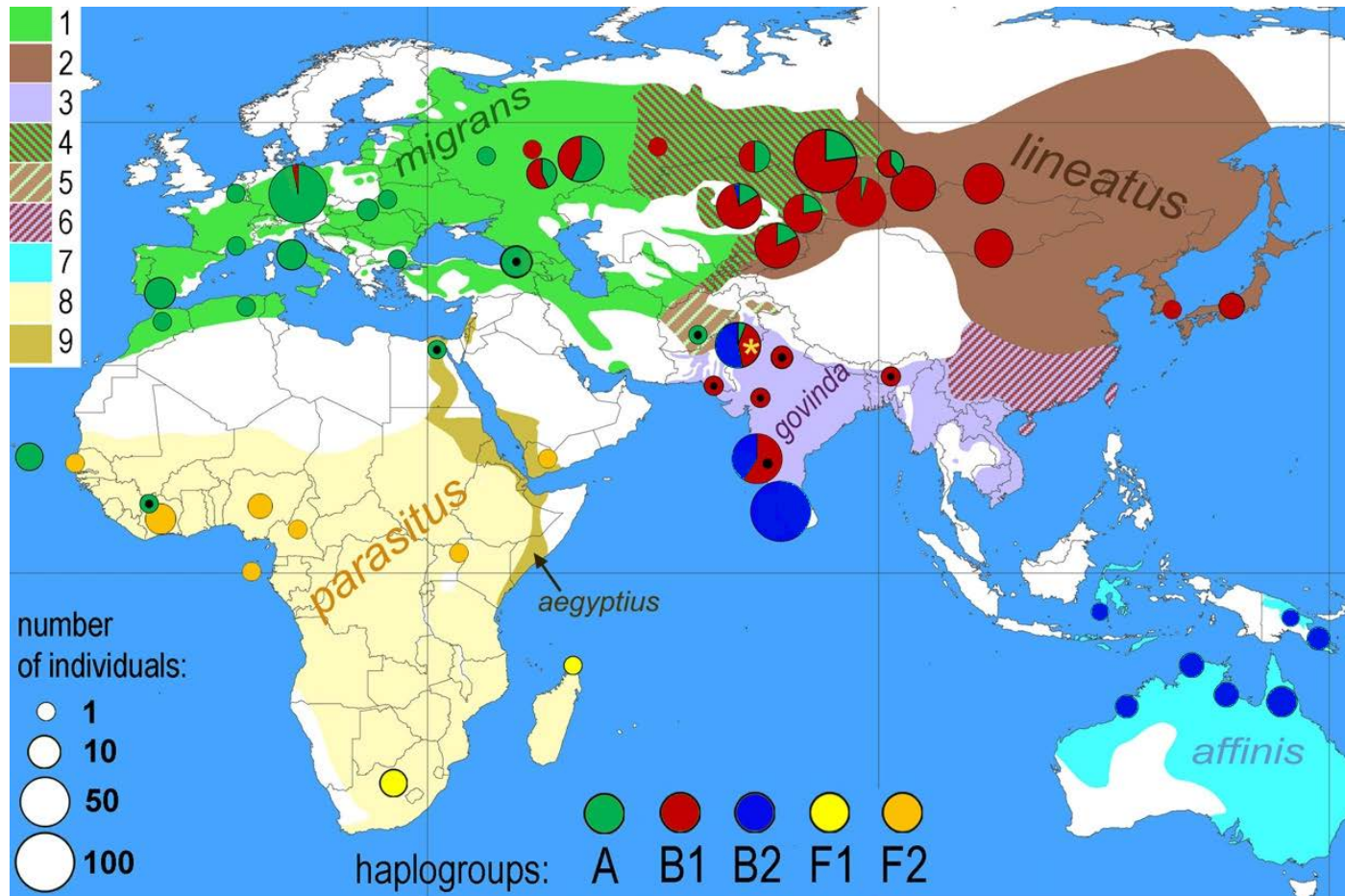


Figure 14. Range of Black and Yellow-Billed kite subspecies with locations of sampled individuals. Legend: *Milvus migrans*: 1 – *migrans*, 2 – *lineatus*, 3 – *govinda*, 4 – *migrans/lineatus* IZ, 5 – *migrans/lineatus/govinda* IZ, 6 – *govinda/lineatus (formosanus)* IZ, 7 – *affinis*; *M. aegyptius*: 8 – *parasitus*, 9 – *aegyptius*. Black dot indicates that migrating individuals were sampled, yellow star indicates specimens that could be either sedentary or migratory. Original drawn by I. Karyakin and N. Andreyenkova, modified by I. Starikov, haplogroup data obtained jointly by N. Andreyenkova and I. Starikov.

types, grey-brown with reddish-brown head plumage, tending to the human habitats (Ali & Ripley 1968; Galushin 1971; Orta 1994; Mazumdar 2013; Karyakin 2017).

A resident Taiwan Kite *Milvus migrans formosanus* Kuroda, 1920 occupies South-Eastern China, Hainan and Taiwan islands; it has Indian and Siberian black kites traits and is poorly known, the validity of this form sometimes is questioned (Karyakin 2017) or even not recognized (Ferguson-Lees & Christie 2001).

Fork-Tailed or Allied Kite *Milvus migrans affinis* Gould, 1838 inhabits Australasia and is the smallest kite, colored above dark chocolate brown with red-brown ventral side and head, resident with seasonal movements, occasionally vagrant (Swann 1922; Orta 1994; Ferguson-Lees & Christie 2001).

Several other races had formerly been described, currently they are considered as invalid and were included in existing subspecies: *glaucopus* from Orenburg Region in nominate form (Zarudny 1881), as well as *reichenowi* from Tunisia, *rufiventris* from Turkmenistan later was treated as red form also of *migrans*, *ferganensis* from Kyrgyzstan and *major* from India as part of *lineatus* (Hartert 1914), equally *tianshanicus* which probably represent hybrids of nominate and Black-Eared kites (Dementiev 1936), Indian *palustris* was included in *govinda* (Hartert 1914), Australian *napieri* is considered as part of *affinis* (Peters 1931).

The Yellow-Billed Kite *Milvus aegyptius* (Gmelin, 1788) consists of two subspecies (Figure 14), they are characterized as the name suggests by yellow bill instead of grey for the Black Kite. They inhabit semi-deserts, savannas, cultivated landscapes and towns, both are intracontinental partial migrants. The nominate Yellow-Billed Kite *M. a. aegyptius* (Gmelin, 1788) lives in Eastern Africa, Nile valley, Israel-Palestine Mediterranean coast and West of Arabian peninsula, migrates south to the East African coast after breeding season. This form resembles *M. migrans migrans* but is darker, less rufous and cinnamon-brown below (Swann 1922; Orta 1994; Ferguson-Lees & Christie 2001; Clark & Davies 2018).

Secondly, the Parasite Kite *Milvus aegyptius parasitus* (Daudin, 1800) is smaller, distributed in sub-Saharan Africa except Congo basin, Comoros, Seychelles and Madagascar. South African birds migrate north, related with rain season. The color is rufous-brown to blackish, with fulvous stripes on the breast (Swann 1922; Orta 1994; Ferguson-Lees & Christie 2001; Clark & Davies 2018).

Former subspecies also were included in the current *Milvus aegyptius: tenebrosus* from Ghana in *parasitus* and *arabicus* from Saudi Arabia in nominate (Stresemann & Amadon 1979). The last may represent certain interest being geographically partially isolated from other Yellow-Billed kites. Swann (1922) described *arabicus* as smaller and slightly different in color, however Mundy (2011) examined its skins and concluded that these are not distinguishable from *M. a. aegyptius*. Anyway, obtaining genetic material from Arabian kites would be desirable to resolve the question of validity of this form.

Morphologically, *Milvus aegyptius* is close to the Black Kite and previously was treated by several checklists as its subspecies (Swann 1920; Peters 1931; Brown & Amadon 1968; Stresemann & Amadon 1979; Orta 1994; Ferguson-Lees & Christie 2001; Dickinson & Remsen 2013; Clements *et al.* 2019). Recently other general lists consider Yellow-Billed Kite as a separate species (Sibley & Monroe 1990; Ferguson-Lees & Christie 2001; HBW & BirdLife International 2021; BirdLife International 2022; Gill *et al.* 2022) and I follow this decision in my research.

Both species like other diurnal raptors suffered from a decrease of population numbers during the second half of the last century, mostly related with poisoning by pesticides used in agriculture, chemical pollution of water, destruction of habitats or direct shooting (Ferguson-Lees & Christie 2001). The decline was notified for most of Europe, former USSR, Turkey, Israel, North Africa (Orta 1994; BirdLife International 2004), Cape Verde (Hille & Thiollay 2000), India (Kaushik & Gupta 2014) and Japan (Kuhlman 1987). In 21st century appears a new threat, mass death of Black kites on the wind power plants (Lekuona & Ursúa 2009). These factors may influence the population structure and lead to decreasing of genetic diversity.

Genetic investigations of these kite species had been carried before but were limited by number of samples (Schreiber *et al.* 2000; Wink & Sauer-Gürth 2000, 2004; Scheider *et al.* 2004, 2009; Johnson *et al.* 2005; Andreyenkova *et al.* 2018; Simakov *et al.* 2021) or location (Heneberg *et al.* 2016). The aim of this study was to investigate phylogenetic structure of Black and Yellow-Billed kites on the large number of specimens covering most parts of species ranges.

4.2. Material and methods

4.2.1. Sampling, laboratory procedures and sequence alignment

123 Black Kite and 10 Yellow-Billed Kite specimens were sampled by the author from the IPMB collection. 532 specimens were sampled in Institute of Molecular and Cell Biology in Novosibirsk, Russia by N. Andreyenkova and O. Andreyenkov. For the DNA isolation tissue, molted and fresh contour feathers, blood and egg shell, conserved in dry conditions, ethanol or EDTA buffer were used. Subspecies were identified by geographical location and phenotype traits (Karyakin 2017). The specimens from India and Pakistan coming from *govinda* race range but were collected during migration time and may represent local birds, migrant *migrans*, *lineatus* or their hybrids. Only the specimens collected in Kerala State in the south of India may be considered as true *govinda* and were included in the subspecies analysis according to the field observations and the photographs available in GBIF, we can suggest that winter migrants coming from the northern areas never reach that part of India, and that all the birds in the area are typical of *govinda* range (Andreyenkova *et al.* 2021).

DNA was extracted using standard phenol/chloroform (dichloromethane) protocol (Sambrook & Russell 2001), in few cases already isolated DNA from IPMB was used. A 699 base pairs fragment of Cyt *b* gene was sequenced. I used Mt-c2 (Fritz *et al.* 2006) as forward primer for amplification, Mt-Fr (Seibold 1994) and Mt-FSH (van der Bank *et al.* 1998) as reverse. Same fragment from IMCB samples was sequenced with F3, R8, In1 and In2 primers by N. Andreyenkova and O. Andreyenkov (Andreyenkova *et al.* 2021). The part of alignments obtained by the author were created in BioEdit 7.2.6 (Hall 1999), nucleotide sequences were aligned using the MUSCLE algorithm (Edgar 2004). 45 new haplotypes were added to GenBank (MT024189–MT024234). For the phylogenetic analysis sequences of sufficient length from GenBank without undefined nucleotides were added: 24 Black Kite sequences (Johnson *et al.* 2005; Heneberg *et al.* 2016; Jeon *et al.* 2018; Nagai & Tokita in press) and 11 Yellow-Billed Kite sequences (Johnson *et al.* 2005; Heneberg *et al.* unpubl.). Also 53 Black Kite sequences shorter than studied fragment (Heneberg *et al.* 2016) were used only for the haplotype analysis, 5 Red Kite *Milvus milvus* (Linnaeus, 1758) sequences (Johnson *et al.* 2005) and one Brahminy Kite *Haliastur indus* (Boddaert, 1783) sequence also belonging to *Milvinae* Vigors, 1825 subfamily (Lerner & Mindell 2005) were analyzed as outgroup. All investigated samples are presented in Table A4.

4.2.2. Phylogenetic analysis

Bayesian tree was performed using BEAUti/BEAST 1.8.0 package (Drummond *et al.* 2012). PhyML 3.0 (Guindon & Gascuel 2003; Darriba *et al.* 2012) with Smart Model Selection (Lefort *et al.* 2017) on Montpellier Bioinformatics Platform was applied for choice of the best evolution model, the Akaike information criterion (Akaike 1974) was used. The Hasegawa-Kishino-Yano model with invariant sites (Hasegawa *et al.* 1985; Shoemaker & Fitch 1989) was chosen for the analysis. For the rate of molecular clock, I used half-value of 2.1% sequence divergence per million years (Weir & Schluter 2008), lognormal relaxed clock model and Birth-Death speciation process (Feller 1939; Gernhard 2008), Markov chain Monte Carlo method with 10 million runs, sampling every 1000th run. The trees with the best likelihood were summarized using TreeAnnotator 1.8.0 (Drummond *et al.* 2012), first 1000 of trees were discarded as burn-in.

In MEGA 6.06 (Tamura *et al.* 2013), Maximum Likelihood (1000 bootstrap replicates, HKY+I model) and Neighbor-Joining (10000 replicates, Kimura 2-parameter distances) trees were constructed for all sequences and K2P distances were calculated between taxa haplotypes.

4.2.3. Analysis of haplotypes and genetic structure

The minimum-spanning haplotype network was drawn in Network 10.2.0.0 (fluxus-engineering.com 2020). The calculation of the network was carried by Median Joining calculations (Bandelt *et al.* 1999).

Genetic polymorphism was analyzed in DnaSP 6.12.03 (Rozas *et al.* 2017). Following haplotype indices were calculated for each taxon: number of haplotypes (H), segregating sites (S), synonymous (N_s) and non-synonymous (N_p) substitutions, haplotype (Hd) and nucleotide diversity per site (π) and per sequence (k), nucleotide polymorphism per sequence (ϑ). Selection neutrality tests were performed: McDonald–Kreitman (MK), index of neutrality (NI), *Milvus milvus* as outgroup for comparison; Tajima's D (TD); Fu–Li's D^* and F^* (see Section 2.6. for details).

4.2.4. Morphometric measurements

Insofar as a large intergradation zone in Siberia and Central Asia between *M. m. migrans* and *lineatus* was localized (Karyakin 2017), I obtained morphology data of both subspecies and intermediate forms from collections of Zoological Museums of Russian Academy of Sciences and Moscow University for compare it with genetic data. The length of wing, tail, tarsometatarsus from tibiotarsus joint until the beginning of first digit and bill from the cere center to the end were measured. Only adult birds were taken into account, the males and females were analyzed separately because both races have size dimorphism (Dementiev 1951b; Cramp *et al.* 1980). The differences between subspecies morphometric values were statistically checked with Student's T-test.

4.3. Results

The alignment reveals 89 variable and 36 parsimony-informative sites, 58 haplotypes in total (Table A5). 54 haplotypes were identified for Black and 4 for Yellow-Billed kites.

Time-calibrated Bayesian tree is able to resolve the divergence of the Black Kite main clades A and B of Eurasia, the Yellow-billed Kite clades F1 and F2 of Africa, and the Red Kite clade (Figure 15), as well as corresponding Maximum Likelihood (Figure A10) and Neighbor-joining (Figure A11) trees with relatively more weak support of the branches. Due to low *Cyt b* variability, we could not divide Asian and Indian haplotype reliably. The divergence between the African and Eurasian branches approximately 0.7 MYA relates to the Chibanian stage of Pleistocene. The A–B and F1–Red Kite branches diverged 0.8 MYA on the Calabrian-Chibanian boundary. The separation of existing kite's species started circa 1.1 MYA. All these branches were supported at the significance edge.

The genetic distances between the Black, Red Kite subspecies and Yellow-Billed Kite are shown in Table 9. These values are substantial between races for Black and Yellow-Billed kite but not for the Red Kite. Between subspecies of Yellow-Billed and Black kites consist 0.6–1% of K2Pdistances, except the distance between *govinda* and *affinis*, which are two time more close to each other. Interspecific distances amounted in the range of 1.4–2.5%.

Clade A comprises major and 18 minor haplotypes of European predominance (Figure 16). Several affined haplotypes formed subbranch A15–15.2 which is remote from clade A

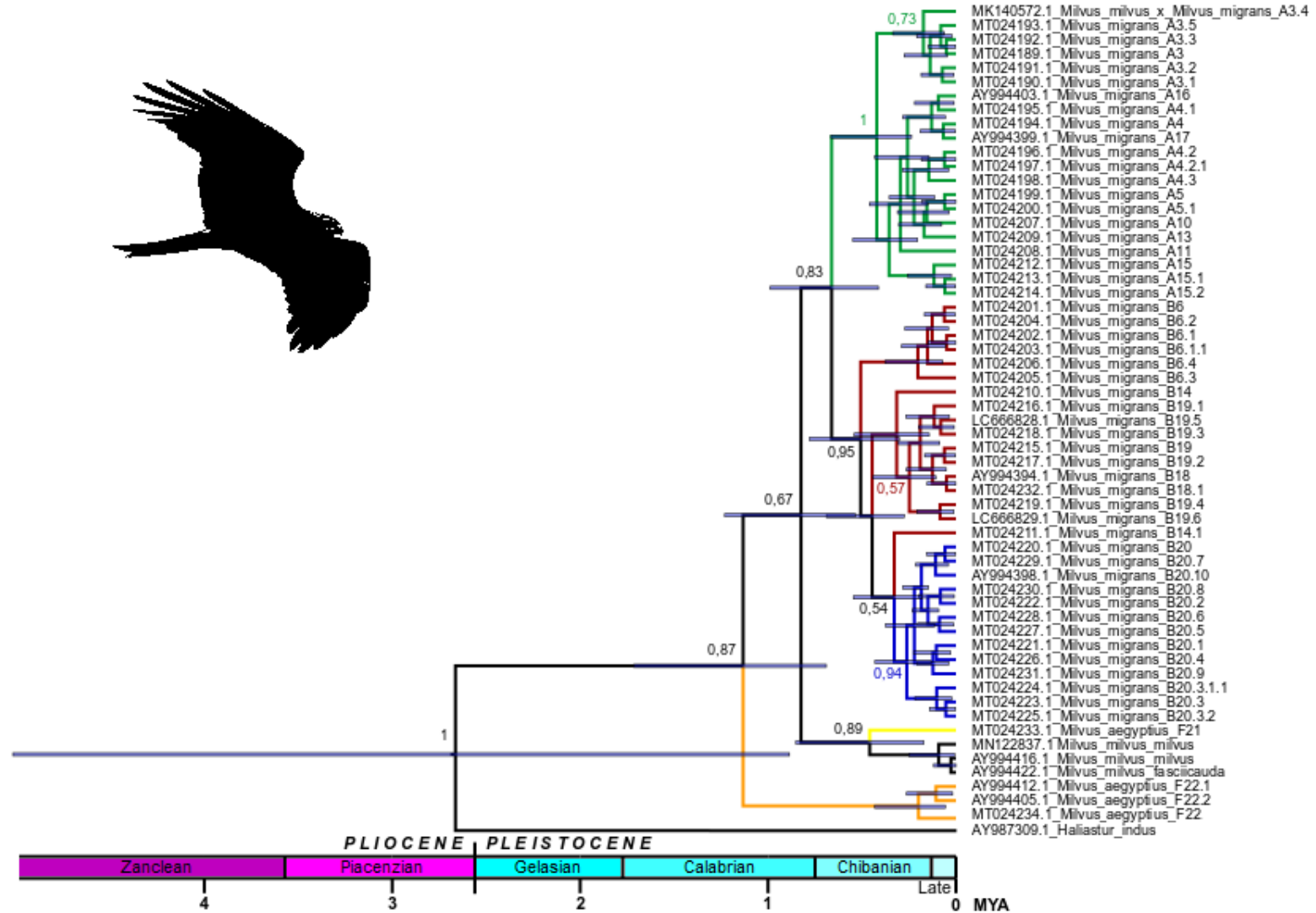


Figure 15. Bayesian phylogenetic tree of Black and Yellow-Billed kites based on Cyt *b* sequences. Colours correspond to these of haplogroups.

Node labels represent posterior Bayesian Inference values >0.5 between clades, the scale represents Pliocene and Pleistocene stages.

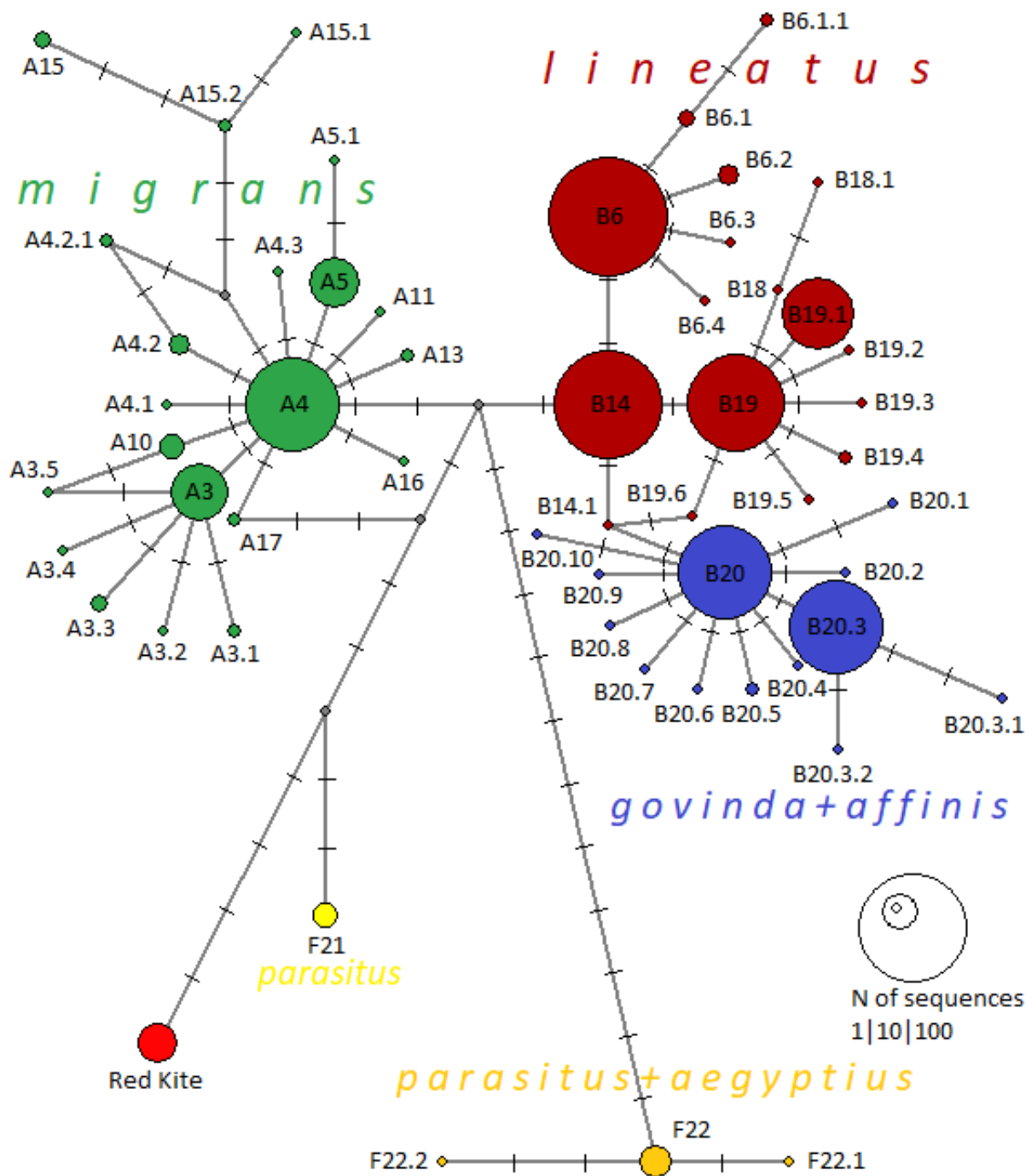


Figure 16. Haplotype network of Black and Yellow-billed kites. Each step represents one mutation, size of the circle corresponds to the number of samples.

major haplotypes. Haplotypes representing the *migrans* breeding territory raise a question. Apart from the three families coming from Czech Republic and Germany, the Black Kites coming from the European mainland (beyond Russia) were, almost exclusively, the haplotype A carriers (111 of 114), while those species that came from the European part of

Russia were represented by nearly the same mixture of haplogroups A and B1, 25 and 21 specimens, respectively. Nearly all the specimens originating from the territory of breeding, which were deemed to be the *lineatus* range, appeared to be the haplogroup B1. Just two of 124 specimens had haplogroup A, and they were found in the Republic of Altai, close to the edge of *migrans* / *lineatus* intergradation zone.

Clade B consists of the haplotypes occurring over the vast territory stretching from Western Russia to Japan, as well as in Southern Asia and Australia (Figure 14). This branch demonstrates distinct divergence, splitting into the two haplogroups: group B1 comprising the haplotypes occurring in the Asian Palearctic and group B2 comprising the haplotypes from South Asia and Australasia (Figure 16). One of the two major haplotypes from group B2 is confined to Indian and Pakistani locations, while the other occurs in Australasia. Group B1 also consisted of the specimens brought from Pakistan and India (Figure 14), and we classify them as representing the local sedentary population (Pakistani locations) or the overwintering species that migrate from the East Palearctic (Indian and partly Pakistani) locations. All 19 specimens coming from Australasia which is considered to be inhabited by *affinis*, had haplotypes from haplogroup B2, one major and 5 minors, which also tend to occur in India (Figure 16).

The Yellow-billed Kite haplotypes from Africa were distinguished from Black Kite haplotypes, just like those of Red Kite (Figure 16). At the same time, the South African haplotype F1 and haplotypes from the locations of Equatorial Africa and Arabia F2 also are considerably distinguished from each other. In African continent, we found representative specimens of two remote haplogroups, with six specimens with haplogroup F1, from South Africa and Madagascar, and 15 specimens with haplogroup F2, from Equatorial Africa and Arabia (Table A4). Three specimens from North Africa, and one specimen from Equatorial Africa, were of clade A. Two of these were collected in the Atlas Mountains, Northwest Africa within the breeding range of Black Kite *M. m. migrans*, on April-May. The two other specimens from Africa, of clade A haplotypes, were collected in Egypt on March and in the Ivory Coast on January during migration time. These bird species relate to migrating *migrans*, both by period and location (Panuccio *et al.* 2014); however, these kites were identified as Yellow-Billed Kite *M. a. aegyptius*, while this species is typical for haplogroups F1 or F2. That could be explained by a mistake that occurred in phenotypic identification, as Yellow-billed Kites and European Black Kites are of the types that can hardly be distinguished, especially in

the immature individuals whose beak colouration have not yet become yellow (Clark & Davies 2018). The migrations of Black Kite in Africa go deep into the continent, overlapping with the range of Yellow-Billed Kite (Figure 17). So, the above birds could be in fact the migrant *migrans*. Another, the alternative, hypothesis might be that Yellow-billed Kites and *migrans* are able to hybridize. However, the fact that there is no data available to support that should be noted. The five specimens from the Cape Verde Islands, which were examined earlier (Johnson *et al.* 2005), also had clade A haplotypes.

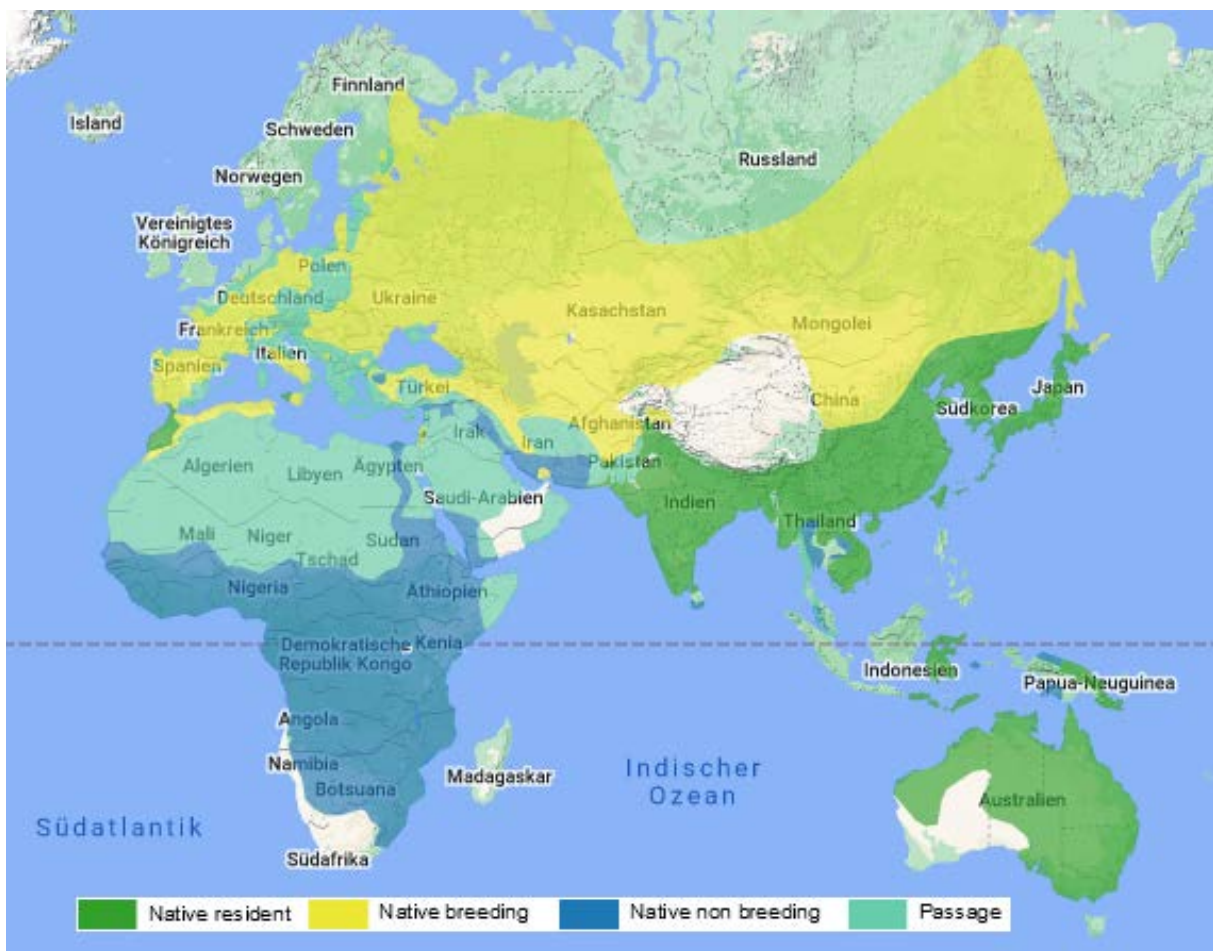


Figure 17. Range of resident and migrant populations of Black Kite (from BirdLife International 2022).

Haplotype diversity indices were the lowest for *govinda* and *affinis* while the highest were those for nominate race, Siberian Kite and zone of their intergradation (Table 10). The values of selection neutrality tests without outgroups are negative for all subspecies, except the mixture zone *migrans/lineatus*, denoting the prevalence of low frequency

Table 9. Kimura 2-parameter distances between Black, Yellow-Billed and Red kite haplotypes in percent, mean values with standard error.

The *migrans/lineatus* means birds from intergradation zone, Brahminy kite values are given for comparison.

	<i>migrans</i>	<i>mig./lin.</i>	<i>lineatus</i>	<i>govinda</i>	<i>affinis</i>	<i>aegyptius</i>	<i>parasitus</i>	<i>milvus</i>	<i>fasciicauda</i>
<i>M. m. migrans/lineatus</i>	0.61±0.06								
<i>M. m. lineatus</i>	0.79±0.06	0.61±0.06							
<i>M. m. govinda</i>	0.96±0.05	0.78±0.06	0.66±0.06						
<i>M. m. affinis</i>	1.02±0.05	0.84±0.05	0.72±0.05	0.35±0.05					
<i>M. a. aegyptius</i>	2.32±0.03	2.29±0.04	2.32±0.04	2.42±0.07	2.49±0.03				
<i>M. a. parasitus</i>	1.80±0.09	1.76±0.12	1.78±0.11	1.88±0.16	1.93±0.17	1.02±0.57			
<i>M. m. milvus</i>	1.55±0.04	1.45±0.04	1.47±0.04	1.61±0.07	1.61±0.06	2.12±0.06	1.58±0.23		
<i>M. m. fasciicauda</i>	1.48±0.04	1.38±0.04	1.39±0.03	1.53±0.08	1.53±0.05	2.04±0.00	1.50±0.28	0.05±0.07	
<i>Haliastur indus</i>	7.33±0.05	7.37±0.06	7.41±0.06	7.19±0.06	7.14±0.05	7.16±0.00	7.10±0.13	6.91±0.06	6.80±0.00

Table 10. Haplotype diversity and neutrality tests values of Black Kite's subspecies and Yellow-Billed Kite. Explanations are given in the text.

Taxon	n	H	S	N _s	N _p	Hd	π	k	θ	TD	MK (NI)	Fu-Li's D*	Fu-Li's F*
<i>M. m. migrans</i>	130	24	26	20	6	0.79	0.0036	2.473	4.779	-1.40	1.05	-0.86	-1.29
<i>M. m. migrans/lineatus</i>	221	12	14	11	3	0.82	0.0040	2.759	2.344	0.44	1.46	-0.42	-0.11
<i>M. m. lineatus</i>	127	16	17	13	4	0.78	0.0026	1.839	3.138	-1.14	1.54	-1.48	-1.62
<i>M. m. govinda</i>	103	7	8	6	2	0.53	0.0010	0.696	1.536	-1.32	3.00	-1.98	-2.08
<i>M. m. affinis</i>	19	6	6	4	2	0.53	0.0010	0.725	1.717	-1.87*	2.63	-2.21	-2.44
<i>M. aegyptius</i>	21	4	17	15	2	0.62	0.0097	6.792	5.123	1.29	0.20	0.69	0.99

* – p<0.05

polymorphisms relative to expectation. NI index of McDonald–Kreitman test's values are >1 except *affinis* meaning possible negative selection for the all other taxa. Almost all are non-significant, however it still means the tendency what the populations expanded recently.

We can observe certain difference not only in genetics but also in morphologic measurements between European and Siberian subspecies of Black Kite as well as kites from intergradations zone of these two subspecies (Table 11). Not all of them are significant, this is may be related with relatively small sample size, most differences are shown for the bill length (Table 12).

4.4. Discussion

4.4.1. Origin and phylogeny of *Milvus* species

As we seen above the divergence of all three existing species of genus *Milvus* begin approximately 1.1 MYA (Figure 15). A close relative fossil species exists, *M. pygmaeus* Tchernov, 1980 from Early Pleistocene of 'Ubeidiya formation in Israel, slightly different in measure being smaller than survived forms (Tchernov 1980). This species was found in sediments dated of 1.4 MYA (Tchernov 1988) which is a bit earlier than the node from which start all currently existing *Milvus* kites. Also *M. brachypterus* Jánossy, 1977 from "Older Pleistocene" which actually corresponds to Calabrian stage (1.8–0.8 MYA) of mounts Villány, Hungary was described. This species was of the same size like recent kites but possessed shorter carpometacarpus (Jánossy 1978). Mlíkovský (2002) consider it as a doubtful form with unclear genus position, but Kessler (2018) accept this kite as valid *Milvus* species. These two ancient kites appear at the time of divergence of modern kite's branches or few hundred thousand years before. The age of the genus *Milvus* may go back to Pliocene, my phylogenetic data do not contradict it but it could be older.

At the same time more ancient findings are unknown, fossils described before as "*Milvus*" *deperditus* Milne-Edwards, 1871 and "*Milvus*" *insertus* Gaillard, 1939 are considered now as *insertae sedis* (Mlíkovský 2002) and probably should be treated as representatives of another genus or genera. According to my reconstruction the Black Kite branch stand apart from 0.8 MYA which is older than we supposed (Andreyenkova *et al.* 2021). Same age based on large datasets of accipitrids with fossil calibration points for other groups was obtained by Nagy and Tökölyi (2014) and Mindell *et al.* (2018). Roques and

Table 11. Morphometric measurements of European, Siberian and Black kites from the intergradation zone.

	Wing		Tail		Tarsus		Bill	
	M	F	M	F	M	F	M	F
<i>migrans</i>	469.3±2.8	471.2±5.8	278.9±2.6	273.0±3.6	63.0±0.0	61.5±0.2	25.3±0.5	26.1±0.6
n	14	12	14	12	3	6	13	10
intergradation zone	469.8±8.3	489.3±6.3	273.7±7.3	291.8±6.6	58.3±1.7	58.5±2.8	26.3±0.3	29.0±0.4
n	6	4	6	4	6	4	6	4
<i>lineatus</i>	481.7±9.3	487.6±4.2	285.2±8.2	289.8±3.0	62.1±2.7	64.2±3.2	29.4±0.8	29.5±0.5
n	7	5	6	4	7	5	7	4

Table 12. Morphometric differences between European, Siberian and Black kites from the intergradation zone.

	Wing			Tail			Tarsus			Bill		
	<i>mig.</i>	int. z.	<i>lin.</i>	<i>mig.</i>	int. z.	<i>lin.</i>	<i>mig.</i>	int. z.	<i>lin.</i>	<i>mig.</i>	int. z.	<i>lin.</i>
Males												
<i>migrans</i>	-			-			-			-		
intergradation zone	ns	-		ns	-		ns	-		*	-	
<i>lineatus</i>	ns	ns	-	ns	ns	-	*	ns	-	***	**	-
Females												
<i>migrans</i>	-			-			-			-		
intergradation zone	*	-		*	-		ns	-		**	-	
<i>lineatus</i>	*	ns	-	**	ns	-	ns	ns	-	***	ns	-

Student's T-test values: ns - non significant, * - p<0.05, ** - p<0.01, *** - p<0.001.

Negro (2005) according to control region data provide more recent date of this event with large interval between 645 and 129 thousand years ago; the authors used small fragment of 357 bp which seems to be too small to provide enough precision.

In the Middle Pleistocene (0.5–0.12 MYA) lived the oldest known *Milvus migrans* from France (Tyrberg 1998) and *M. milvus* from Germany . After separation of European and other Black kites, the last group splits off in Siberian and South Asian Black kites approximately 300 TYA. It is not possible to distinguish Indian *M. migrans govinda* and Australian *M. m. affinis*, both subspecies are merged within their clade. It may be explained by two ways. Black kites possibly recently conquered Indomalaya and Australia and were not yet separated genetically. Or the flux of genes exists in tropic area: these races are not migrant like northern but make movements related to food availability and monsoons (Orta 1994). However, by including additional molecular markers in future analyses will obtain more solid patterns and better resolution of the phylogenetic tree nodes. The significant value of Tajima's *D* test (Table 10) mean that the *affinis* populations exposed not long ago, probably after a bottleneck which may be related with island isolation.

The Yellow-Billed Kite disintegrate to two separate branches, one which represent unique haplotype is related with the Red Kite. Further research with other genetic markers is needed but it is highly likely that we have in Africa two species instead of *Milvus aegyptius* and they do not correspond to existing subspecies, Johnson et al. (2005) showed the same topology of corresponding tree branches.

Interspecific distances are less than the mean inside avian genera (Aliabadian *et al.* 2009), we can conclude that *Milvus* species are relatively close to each other. The difference between *Milvus migrans* and *M. aegyptius* is even greater than between *M. migrans* and *M. milvus*, which confirm that we should consider Black and Yellow-Billed Kites as separate species.

4.4.2. Subspecies and haplotypes of Black Kite

Subspecies genetic differences are up to 1% (Table 9) being in a similar range for most bird subspecies (Aliabadian *et al.* 2009). The K2P-distance between Siberian and other Black kites is 0.66–0.79%, being typical to the normal distance between avian subspecies (Aliabadian *et al.* 2009), also it forms one clade with Australian Black Kite (Figures 15, 16) so

Milvus migrans lineatus fall well into the general totality of *M. migrans* and there is no reason to consider it as separate species as was proposed before (Wells 1998).

During the last series of glaciation, refugia existed in Palearctic realm: Arctic-Alpine, Mediterranean, Siberian-Manchurian (de Lattin 1967). Because north to the Alps existed the refugium of boreal species, the Black Kite as forest-steppe bird should have been conserved in two last, affecting haplogroups A (Mediterranean) and B (Siberian-Manchurian). The refugia influenced the assemblage of modern avifauna in Western Palearctic (Tyrberg 1991; Blondel & Mourer-Chauviré 1998; Finlayson 2011; Holm & Svenning 2014) as well in Eastern (Finlayson 2011; Baranov 2013; Kolbin 2014).

The small subclade A15–15.2 relatively isolated from other *migrans* is of interest. It consists of four German and Czech kites the material from which was sampled in breeding period and two probably migrants from Georgia. It is possible that we observe here the descendants of birds not from Mediterranean refugia but Colchic located here. This refugium was described by Grossheim (1948) for numerous vascular plants and among its occupants different organisms can be found, endemic or not, as symbiotic bacterias (Roy *et al.* 2017), arthropods and oligochaetes (Gegechkori 2011), forest snails (Pokryszko *et al.* 2011), several amphibians and reptiles (Tuniyev 1990), extinct and currently living mammal species (Vereshchagin 1959).

The occurrence of several major haplotypes especially in Asian subspecies (Figure 16) might be explained by the series of glaciations in the Late Pleistocene and changes from forest to tundra-steppe and vice versa, the time when Black Kite populations, following the forest cover dynamics, tended both to expand and disappear, which resulted in a series of bottlenecks (Nazarenko 1982, cited by Andreyenkova *et al.* 2021). The negative values of neutrality tests for all Black Kite subspecies also may confirm this evolutionary scenario (Table 2). During the glaciations the Black Kite range was split, it did not occur in the tundra-steppes habitat of the Northern Palearctic, just like it does not occur in the tundra zone currently.

However mixed A and B1 haplotypes population could have still emerged in the Quaternary, contracting in the southern direction during glacial maxima, and expanding to the north during the periods of warming elevating genetic diversity. As it also could happen, the European and Eastern Black Kite populations would meet and hybridise repeatedly over multiple range expansion waves. *Migrans* and *lineatus* subspecies meet in Western Siberia

during their expansion forming a broad intergradation zone. The phenotypes issued from there may present evidence of full-range variation between those of *migrans* and *lineatus* (Stepanyan 2003; Karyakin 2017). Stepanyan (2003) noted that the Western Siberia is apparently the area of secondary contact between these subspecies considerably diverged.

78% of the haplotypes (173 of 221) carried by the specimens which were sampled in the *migrans/lineatus* zone were those of haplogroup B1. All the other specimens except one had haplogroup A haplotypes, the only outlier specimen showing the haplogroup B2 haplotype (refer to B20.1 haplotype shown in Figure 16). The latter specimen was collected from a secluded nesting site in Central Kazakhstan. Morphometry show the difference in measurements of certain parameters not only between *migrans* and *lineatus* but sometimes between each subspecies and birds from the intergradation zone (Tables 11, 12). In fact, all examined birds issued from this zone are labelled as *lineatus*. The differences are significant mainly for females (Table 12). It is possible to explain that females demonstrate more high level of philopatry (Forero *et al.* 1999) and have less mixing potential among different populations and races respectively.

Westward expansion of *lineatus* since the 1990s has increased, owing to decrease in *migrans* population, while currently *lineatus* population has been rapidly assimilating with the European subspecies over the vast territory covering the area between Ural and Altai (Karyakin 2017). The *lineatus* offense westward appears to be ongoing as Black Kites having the features of *lineatus* have been reportedly last years occurring from across the area of Europe and Middle East (Kralj & Barišić 2013; Karyakin 2017; Skyrpan & Literák 2019; Panter *et al.* 2020; Skyrpan *et al.* 2021). The hybrid issued from *lineatus* male and *migrans* female was found in Ukraine (Literák *et al.* 2020) and belongs to haplogroup A (Figure 15). The data we have obtained on Cyt *b* haplogroup distribution suggests that group A does not spread eastwardly of the main *migrans/lineatus* zone while group B penetrates far westwardly into the presumed range of *migrans* in the Volga region (Figure 15). Even solitary representatives of B1 haplogroup have been found as far as the Central Europe despite absence of the breeding birds having the phenotypic characteristics of *lineatus* (Heneberg *et al.* 2016).

One representative of B2 haplotype was found in Kazakhstan which probably comes from south but we don't have information about genetic structure on these territories, only one old specimen collected on October in Afghanistan (Johnson *et al.*, 2005) belonging to the group A could be a winter migrant *migrans* or a part of the local population. N.

Andreyenkova suggested that isolated *govinda* population may exist in Tajikistan, Afghanistan and mountain Iran (Andreyenkova *et al.* 2021).

In the Pakistani intergradation zone *migrans/lineatus/govinda* were discovered kites belonged to all the main haplogroups A, B1 and B2 (2, 15 and 18 specimens, respectively). While some specimens collected in winter season could be migrants, representatives of haplogroups A, B1 and B2 were discovered in summer season, either. The hybridisation between subspecies here doesn't look impossible, most southern populations of nominate race may be resident and these of *lineatus* probably could effectuate vertical migrations instead of latitudinal (Dementiev 1951b).

In North and Central India three subspecies also exist. Four specimens from Northern India were collected in December or beginning of March when migrants are there and may represent migrating *lineatus* or *lineatus x govinda* hybrids (Table A4). In Goa State I. Karyakin collected samples in March-April when the local sedentary *govinda* usually breed alongside with the non-breeding wintering migrants (*lineatus* and *migrans*) and probably hybrids, all three races were identified by phenotypes (Andreyenkova *et al.* 2021). Haplogroups B1 (n=29) and B2 (n=20) were identified. In South India, typical *govinda* range only B2 was found.

The haplotype network was not completely able to resolve *govinda* and *affinis* subspecies as well as the Bayesian tree, at the same time major haplotype B20 belongs to both races and more isolated B20.3 with minor haplotypes to Indian Small Kite only. This may mean that *govinda* B20.3 branch separated on the Indian subcontinent and other representatives of the clade lived in the wide range from India to Australia, especially taking into account the fact that the sea level decreased during the glaciations of Late Pleistocene and Indochina peninsula extended in glacial maximums till the middle of Indonesia (Voris 2000). The exchange of genes between both races separated by their range can process occasionally today: migrant Black kites were found in continental Malaysia from one side (BirdLife International 2022: Figure 17) and vagrants on Sumatra and Kalimantan (Ferguson-Lees & Christie 2001) from another.

In absence of genetic data from China I cannot say anything about the structure of Eastern intergradation zone *govinda/lineatus* and validity of *formosanus* subspecies. Obtaining of sequences from the region in perspective will shed light on these questions.

4.4.3. Yellow-Billed Kite enigma

Africa is deemed to be inhabited by the two subspecies of the Yellow-billed Kite: *aegyptius* which breed in the Nile Valley and on both coasts of the Red Sea, mainly resident, making movements to south till Tanzania; and *parasitus* which is widespread in sub-Saharan Africa, the Comoros and Madagascar, the latter exercise long intra-continental migrations (Cramp *et al.* 1980; Brown *et al.* 1982; Orta 1994; Ferguson-Lees & Christie 2001). Phylogenetic relationships between the Yellow-billed Kite and other Black Kite subspecies have been studied insufficiently; however, some mitochondrial gene sequences from the Yellow-billed Kite have been used for reconstruction of the phylogenetic tree (Wink & Sauer-Gürth 2000, 2004; Scheider *et al.* 2004, 2009; Johnson *et al.* 2005; Echi *et al.* 2015; Heneberg *et al.* 2016). Based on these data, suggestions have been made that the Yellow-billed Kite might be considered a separate species and *Milvus aegyptius* having two subspecies, *M. a. aegyptius* and *M. a. parasitus*.

In total, 15 specimens from Equatorial Africa and Arabia were carriers of haplogroup F2, which is far from those of the Black and Red Kites. The other six specimens taken from South Africa and Madagascar had haplogroup F1, which forms sister branch to Red Kite (Figures 15, 16). The above data suggest that the sub-Saharan Yellow-billed Kites are represented by the two remote clades having a common ancestor with the Black and Red Kites. Notwithstanding the substantial differences in the Cyt *b* sequence at species level, the phylogenetic and ecological relationships of F1 and F2 representatives remain uncertain, since no data on sub-Saharan Yellow-Billed Kite differentiation for any alternative characteristic is available. There is one noteworthy observation in the present study: geographical distribution of haplogroups F1 and F2 revealed no correlation with the presumed ranges of *aegyptius* and *parasitus* (Figure 14).

As mentioned above both subspecies *aegyptius* and *parasitus* are quite similar in appearance, and hardly identifiable. Moreover, young and even adult Yellow-billed Kites may sometimes be confused with Black Kites. Also, in some areas, Yellow-billed Kite is a seasonal migrant which may occur occasionally beyond its breeding range, such that Egyptian Kite probably meets Parasite on migrations. I don't have information about intraspecific hybridization but it seems probable in view of the fact that the ranges of both races have common border in Eastern Africa (Figure 14). Hypothetically as *parasitus* belongs

to two separate clades (Figures 15, 16) correspond to Central and Southern African birds (Figure 15) we could talk about three forms in traditionally considered Yellow-Billed Kite and perhaps two species according to F1 and F2 haplogroups. Since the research of Johnson *et al.* (2005) who notified this polyphyly after examining Cyt *b* and ND2 sequences, no explanation was proposed. Thereby the phylogenetic relationships with other representatives of the genus *Milvus* remain a challenging goal. The issue will certainly require analyses involving more sequences from new specimens and/or using several genetic markers including nuclear for such analysis.

5. Phylogeny and taxonomic rearrangement of *Athene noctua* complex

5.1. Introduction

The Little Owl *Athene noctua* is a small sedentary nocturnal raptor, widely distributed in the Old World in temperate and Mediterranean Europe, steppes, deserts and mounts of Asia and Northern Africa. Currently the main taxonomic lists accept 13 subspecies of this taxon: nominate *A. n. noctua* (Scopoli, 1769), *A. n. vidalii* A. Brehm, 1857 and *A. n. indigena* C. Brehm, 1855 from Europe, Middle-Eastern *A. n. lilith* Hartert, 1913, Central Asian *A. n. bactriana* Blyth, 1847, *A. n. orientalis* Severtsov, 1873 from Northeastern Kazakhstan and Northwestern China, Himalayan *A. n. ludlowi* E.C. Baker, 1926, *A. n. impasta* Bangs & J.L. Peters, 1928 from Central China, *A. n. plumipes* Swinhoe, 1870 from Southern Siberia, Mongolia and Northeastern China, *A. n. glaux* (Savigny, 1809) from coastal North Africa, Saharan-Arabian *A. n. saharae* (Kleinschmidt, 1909), Sudanese-Eritrean-Northeastern Ethiopian *A. n. spilogastra* Heuglin, 1863, Eastern Ethiopian-Somalian *A. n. somaliensis* Reichenow, 1905 (Holt *et al.* 1999; Dickinson & Remsen 2013; Clements *et al.* 2019; Gill *et al.* 2022). The single extinct subspecies *A. n. lunellensis* Mourer-Chauviré, 1975 is known from the Middle Pleistocene of France. This bird described by several remains was slightly bigger than actual Little Owls (Mourer-Chauviré 1975).

However, the number and composition of subspecies may differ in the literature. The independence of *impasta* is not supported by several researchers considering it as a synonym of *plumipes* (Steinbacher 1936, cited by Vaurie 1960; Dementiev 1951a; Vaurie 1960; Weick 2006; König & Weick 2008). Equally numerous authors confirm the existence of *A. n. sarda* (Kleinschmidt, 1907) as Corsican-Sardinian endemic (Niethammer *et al.* 1938; Dementiev 1951a; Vaurie 1960; Glutz von Blotzheim & Bauer 1980; Mebs & Scherzinger 2000; Prikloonsky 2001) as well as an early version of the modern birds checklist (Peters 1940), more recent checklists consider *sarda* as a synonym of the nominate race. Holt *et al.* (1999) does admit the possibility for *sarda*'s subspecific status. König and Weick (2008) treat *spilogastra* and *somaliensis* as separate species along with *A. spilogastra* as well as *A. lilith*, the last was proposed previously by Wink and Heidrich (1999), equally the possibility of

species level for *plumipes* was suggested (Wink *et al.* 2008). Additionally Weick (2006) sees *saharae* as a synonym of *glaux*.

Several other former Little Owl races are currently considered as described because of geographical clinal variation common for this species and synonymy including in existing taxa: *chiaradiae*, *salentina* and *daciae* in *noctua*; *mira*, *grüni* and *cantabriensis* in *vidalii*; *crytea*, *kessleri* and *caucasica* in *indigena*; *ruficolor* and *solitudinis* in *saharae* (Dementiev 1951a; Vaurie 1960; Priklnsky 2001; Weick 2006).

The range of European subspecies has been discussed: Traditionally the boundary between *vidalii* and nominate race was the Benelux-France/Germany border and the Rhein (Niethammer *et al.* 1938; Peters 1940; Dementiev 1951a; Vaurie 1960; König & Weick 2008) or with an intergradation zone in Western Germany (Glutz von Blotzheim & Bauer 1980). Cramp with coauthors (1985) included the birds from the north Eastern European part of the range as *vidalii*, leaving Italy for the *noctua* subspecies birds with adjacent territories from Southern France to Western Romania which are shared with neighbor subspecies. This was accepted later by several sources (Holt *et al.* 1999; Weick 2006; Clements *et al.* 2019) and is mostly supported with genetic data (Pellegrino *et al.* 2014), here I also follow Cramp's delimitation of these taxonomic forms.

The northern boundary of *indigena* as noted by Dementiev (1951) extends through the steppes in Dnepr and Don Basins. However, Stepanyan (2003) pushes it more south to the Black and Azov Sea and Weick (2006) mentions Ukraine and Russia as the territory where both subspecies mix, without any geographic precision. My observations of numerous bird skins from these areas in Zoological Museum of Moscow University and Zoological Institute in Saint-Petersburg lead me to agree in general with Dementiev's view.

In the Asian part of the Little Owl, range intergradation even of tree species is observed: *noctua*, *indigena* and *bactriana* in Southern Ural, *bactriana*, *orientalis* and *plumipes* in North-Eastern Kazakhstan (Priklnsky 2001). The comparatively more frequent recent records of Little Owls in the north of Kazakhstan and Southern Siberia suggest the range is expanding to the North-East. Though the subspecific affiliation of these birds remains unclear, the intermediate forms between *lilith* and *bactriana* have been clarified for regions within Iraq (Hartert 1925).

Little Owl races differ by size and color; neighbor subspecies may be poorly distinguishable and distant forms are better discernible (Figure 18). The ranges of *A. noctua*



Figure 18. Little Owl races from collection of Zoological Institute of Russian Academy of Sciences, St-Petersburg, males from ventral (**a**) and dorsal (**b**) sides. 1 – *vidalii*; 2 – *noctua*; 3 – *indigena*; 4 – *lilith*; 5 – *bactriana*; 6 – *glaux*; 7 – *orientalis*; 8 – *plumipes*; 9 – *ludlowi*; 10 – *somaliensis*. Photos by the author.

subspecies, based on several sources (Hartert 1925; Dementiev 1951a; Vaurie 1960; Cramp *et al.* 1985; Prikloonsky 2001; Tarasov 2011; Andreyenkov *et al.* 2019; BirdLife International 2019) are presented on Figure 19.

The goal of this work is to analyze DNA sequence data obtained from different subspecies of the Little Owl and correlate it with available morphological and systematic data to clarify its taxonomic status.

5.2. Material and Methods

5.2.1. Sampling and laboratory procedures

I sampled 64 specimens of *Athene noctua* from the IPMB collection (blood, tissue, feathers), Wild bird rehabilitation and Breeding Centers in Russia and Hungary (blood, tissue), Zoological Museum of Moscow University and Hungarian National History Museum (tissue), details are provided in Table 13. The locations are presented on the range map (Figure 19). DNA was extracted with standard phenol/chloroform (dichloromethane) protocol (Sambrook & Russell 2001). PCR amplification, cleaning and sequencing of marker genes were carried as mentioned in Chapter 2. Three loci were amplified, mitochondrial Cyt *b* and COI and nuclear RAG-1 with several primers: COIExtF, Passer F1/R1, Bird1Fd, BirdH_351d, Aves_L288, BirdR1dt for COI; L14764, smt-A, Mt-c2, Mt-Fr, Mt-D, Mt-E for Cyt *b*; R7, R17 and R51 for RAG-1.

5.2.2. Alignment and addition of sequences from databases

Alignments were created in BioEdit 7.2.6 (Hall 1999), nucleotide sequences were aligned using the MUSCLE algorithm (Edgar 2004). Nuclear mitochondrial DNA segments from mitochondrial sequences were rejected. I analyzed the full sequence of Cyt *b* (1143 bp) and partial sequences of COI (565 bp were analysed in concatenated mitochondrial dataset and common 554 bp part was analysed together with GenBank sequences) and RAG-1 (597 bp) genes.

Existing sequences of the Little Owl from GenBank database were added to the analysis; fragments of partial mitochondrial genome MN122903 (Margaryan *et al.* 2021), COI fragment sequences GQ481386 (Kerr *et al.* 2009a), JQ174101, JQ174102

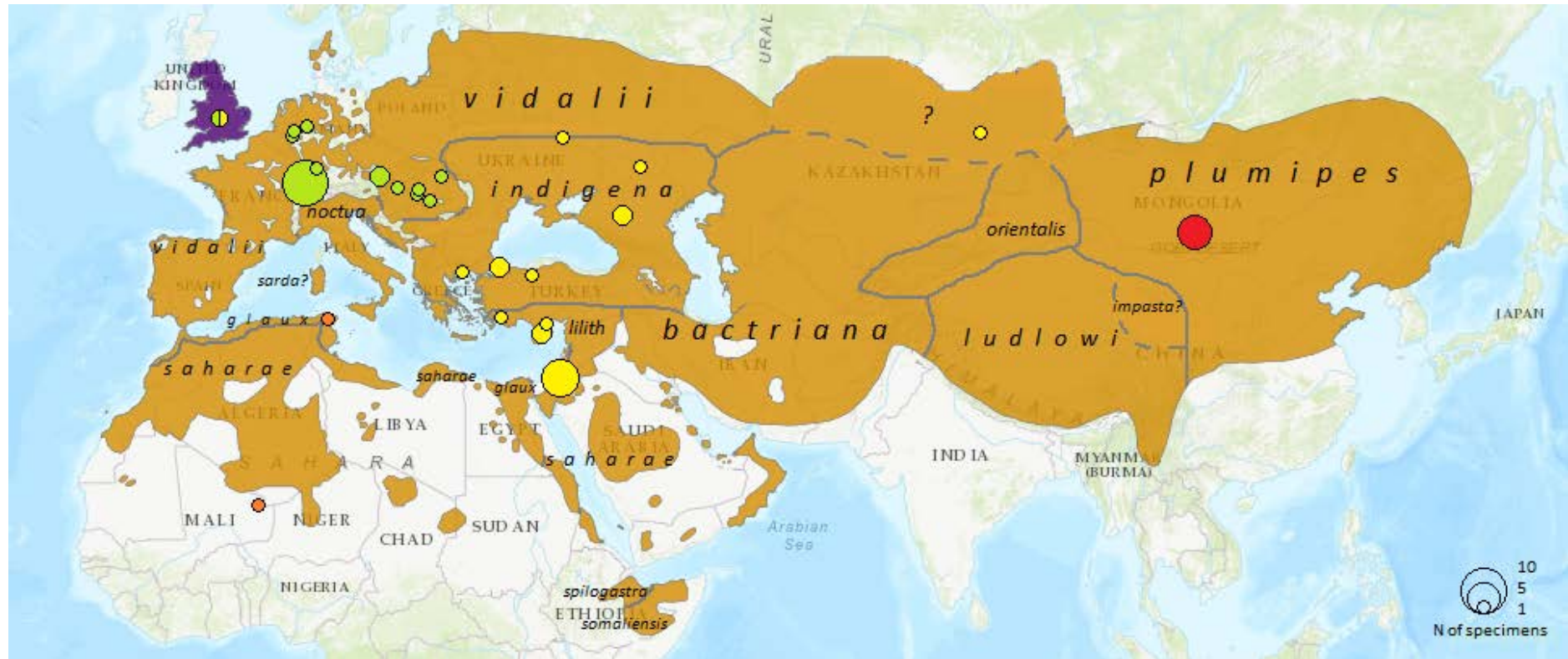


Figure 19. Range of *Athene noctua sensu lato* with subspecies and samples collected for this study. Native range is in brown, introduced in violet (also in New Zealand). Sample colors correspond to major mitochondrial haplotypes (see below).

Table 13. Samples used in the study with obtained sequences.

Taxon	Registration No	Collector	Country	Locality	Tissue	Date	Mt haplotype	Cyt b	COI	RAG-1
<i>Athene noctua lilith</i>	IPMB643		Turkey	Silifke	blood	13.10.1995	A	-	+	-
<i>Athene noctua indigena</i>	IPMB2879		Greece	North-East	muscle		A9	+	+	+
<i>Athene noctua lilith</i>	IPMB3678	O. Hatzofe	Israel		blood	18.11.1997	A3	+	+	+
<i>Athene noctua lilith</i>	IPMB3679	O. Hatzofe	Israel		blood	18.11.1997	A	-	+	+
<i>Athene noctua lilith</i>	IPMB3680	O. Hatzofe	Israel		blood	18.11.1997		-	-	+
<i>Athene noctua lilith</i>	IPMB3681	O. Hatzofe	Israel		blood	07.12.1997	A12	+	+	+
<i>Athene noctua lilith</i>	IPMB3682	O. Hatzofe	Israel		blood	07.12.1997		-	+	+
<i>Athene noctua lilith</i>	IPMB3683	O. Hatzofe	Israel		blood	07.12.1997		-	-	+
<i>Athene noctua lilith</i>	IPMB3684	O. Hatzofe	Israel		blood	07.12.1997	A12	+	+	+
<i>Athene noctua ssp.</i>	IPMB6073	C. König	Germany	Baden-Württemberg	blood			+	+	+
							D6			
<i>Athene noctua lilith</i>	IPMB6087	O. Hatzofe	Israel		blood		A11	+	+	+
<i>Athene noctua lilith</i>	IPMB6088	O. Hatzofe	Israel		blood		A13	+	+	+
<i>Athene noctua ssp.</i>	IPMB6184	K. Niebuhr	Austria	Lower Austria	blood		D4	+	+	+
<i>Athene noctua ssp.</i>	IPMB6185	K. Niebuhr	Austria	Lower Austria	blood		D10	+	+	+
<i>Athene noctua indigena</i>	IPMB6248	H.-H. Witt	Turkey	Karabük	muscle	06.12.1994	A	-	+	+
<i>Athene noctua ssp.</i>	IPMB6307	H.-H. Witt	Turkey		?		A2	+	+	+
<i>Athene noctua indigena</i>	IPMB6932	M. Wink	Greece		feather		A1	+	+	+
<i>Athene noctua lilith x vidalii</i>	IPMB8227	K. Palmer	unknown	captive	?		A7	+	+	+
<i>Athene noctua vidalii</i>	IPMB8228	K. Palmer	unknown	captive	?			-	-	+
<i>Athene noctua ssp.</i>	IPMB8233	K. Palmer	unknown	captive	?			-	-	+
<i>Athene noctua lilith</i>	IPMB20879	P. Flint	Cyprus	Kyrenia (Girne)	feather	03.08.2002	A6	+	+	+
<i>Athene noctua lilith</i>	IPMB20883	P. Flint	Cyprus	Kyrenia (Girne)	feather	22.03.2002	A10	+	+	-
<i>Athene noctua plumipes</i>	IPMB23811	M. Stubbe	Mongolia	South	blood	2002	C1	+	+	+
<i>Athene noctua plumipes</i>	IPMB23812	M. Stubbe	Mongolia	South	blood	2002	C2	+	+	+
<i>Athene noctua plumipes</i>	IPMB23813	M. Stubbe	Mongolia	South	blood	2002	C1	+	+	+
<i>Athene noctua plumipes</i>	IPMB23814	M. Stubbe	Mongolia	South	blood	2002	C1	+	+	+
<i>Athene noctua plumipes</i>	IPMB23815	M. Stubbe	Mongolia	South	blood	2002	C1	+	+	+
<i>Athene noctua plumipes</i>	IPMB23816	M. Stubbe	Mongolia	South	blood	2002	C1	+	+	+
<i>Athene noctua ssp.</i>	IPMB28167	National Birds of Prey Centre, Newent	United Kingdom	England	blood			+	+	+
							A4			
<i>Athene noctua ssp.</i>	IPMB28168	National Birds of Prey Centre, Newent	United Kingdom	England	blood			-	-	+
<i>Athene noctua ssp.</i>	IPMB28169	National Birds of Prey Centre, Newent	United Kingdom	England	blood			+	+	+
							D8			
<i>Athene noctua glaux</i>	IPMB32994		Tunisia	Tunis	blood		B1	+	+	+
<i>Athene noctua ssp.</i>	IPMB37797	Natural History Museum Basel	Switzerland	Basel	blood	11.04.2006		+	+	+
							D7			
<i>Athene noctua ssp.</i>	IPMB37798	Natural History Museum Basel	Switzerland	Basel	blood	11.04.2006		-	+	+
							D			
<i>Athene noctua ssp.</i>	IPMB37799	Natural History Museum Basel	Switzerland	Basel	blood	11.04.2006		+	+	+
							D1			
<i>Athene noctua ssp.</i>	IPMB37800	Natural History Museum Basel	Switzerland	Basel	blood	11.04.2006		+	+	+
							D2			
<i>Athene noctua ssp.</i>	IPMB37801	Natural History Museum Basel	Switzerland	Basel	blood	11.04.2006		+	+	+
							D1			

Table 13. Continued

<i>Athene noctua ssp.</i>	IPMB37802	Natural History Museum Basel	Switzerland	Basel	blood	11.04.2006	D	-	+	+
<i>Athene noctua ssp.</i>	IPMB37803	Natural History Museum Basel	Switzerland	Basel	blood	11.04.2006	D1	+	+	+
<i>Athene noctua ssp.</i>	IPMB37804	Natural History Museum Basel	Switzerland	Basel	blood	11.04.2006	D1	+	+	+
<i>Athene noctua ssp.</i>	IPMB37805	Natural History Museum Basel	Switzerland	Basel	blood	20.04.2006	D12	+	+	+
<i>Athene noctua ssp.</i>	IPMB37806	Natural History Museum Basel	Switzerland	Basel	blood	20.04.2006	D	-	+	+
<i>Athene noctua saharae</i>	IPMB44754	M. Clouet	Mali	Adrar des Ifoghas	muscle	03.2007	B2	+	+	+
<i>Athene noctua saharae</i>	IPMB45908	M. Clouet	Mali		feather		B	-	+	-
<i>Athene noctua saharae</i>	IPMB45909	M. Clouet	Mali		feather		B	-	+	+
<i>Athene noctua indigena</i>	IPMB49372		Turkey	Istanbul	blood		A	+	-	-
<i>Athene noctua indigena</i>	IPMB49373		Turkey	Istanbul	blood		A	+	-	+
<i>Athene noctua liliith</i>	IPMB62442		Turkey	Fethiye	muscle	2011	A	+	-	-
<i>Athene noctua vidalii</i>	IPMB79008	Arbeitsgemeinschaft Biologischer Umweltschutz, Soest	Germany	Soest	muscle		D11	+	+	+
<i>Athene noctua indigena</i>	IPMB92461	K. Kuklin	Russia	Belgorod	blood	05.08.2017	A1	+	+	+
<i>Athene noctua indigena</i>	IPMB92463	K. Kuklin	Russia	Volgograd	blood	05.08.2017	A	+	-	+
<i>Athene noctua ssp.</i>	IPMB92495	I. Starikov	Russia	Altai Kray	blood	19.07.2017	A	+	-	+
<i>Athene noctua vidalii</i>	IPMB93941		Germany	Wachtendonk	blood	20.06.2017	D3	+	+	+
<i>Athene noctua vidalii</i>	IPMB93954		Germany	Rödingen	blood	27.07.2017	D5	+	+	+
<i>Athene noctua ssp.</i>	IPMB97064 Gy/1274	Hungarian Natural History Museum	Hungary		muscle	2016	D1	+	+	-
<i>Athene noctua ssp.</i>	IPMB97068 Gy/1476	Hungarian Natural History Museum	Hungary	Battonya	muscle	30.06.2016	D	-	+	-
<i>Athene noctua ssp.</i>	IPMB97071	I. Starikov	Hungary	Cegléd	blood	04.10.2019	D5	+	+	+
<i>Athene noctua ssp.</i>	IPMB97072	I. Starikov	Hungary	Mátészalka	blood	04.10.2019	D	-	+	+
<i>Athene noctua ssp.</i>	IPMB97073	I. Starikov	Hungary	Kiskunság National Park	blood	04.10.2019	D	-	+	+
<i>Athene noctua ssp.</i>	IPMB97074	I. Starikov	Hungary	Bakony	blood	04.10.2019	D9	+	+	+
<i>Athene noctua indigena</i>	ZMMU_KAN776	Zoological Museum of Moscow University	Russia	Tuguluk	muscle	2020	A2	+	+	+
<i>Athene noctua indigena</i>	ZMMU_KAN777	Zoological Museum of Moscow University	Russia	Tuguluk	muscle	2020	A8	+	+	+
<i>Athene noctua indigena</i>	ZMMU_KAN778	Zoological Museum of Moscow University	Russia	Tuguluk	muscle	2020	A5	+	+	+
<i>Athene brama indica</i>	IPMB40437	M. Arshad	Pakistan	Multan	muscle	04.2006		-	+	+
<i>Athene cunicularia hypugaea</i>	IPMB9027	H.-H. Witt	Mexico	San Quentin neighborhood	muscle	12.11.1999		+	+	+

(Schindel *et al.* 2011), KF946602, KF946603 (Aliabadian *et al.* 2013), KF452050–KF452083 (Pellegrino *et al.* 2014), KT803665 (Dimitriou *et al.* 2017), KJ862133 (Li *et al.* 2017) and KBBI022-07 (Korea Res. Inst. of Bioscience and Biotechnology unpubl.) from BOLD database in the 554 bp common part, RAG-1 fragment sequences EU348872, EU348874, EU348875 (Wink *et al.* 2009). The analyzed species included members of *Athene* F. Boie, 1822 genus: Spotted Owlet *A. brama* (Temminck, 1821) KR779894 (Rawankar *et al.* 2015), MF871705–MF871710, MF871722, MF871725, MF871726, MF871736–MF871738 (Koparde *et al.* 2018), MK932906 (Boonyaparakob & Kasorndorkbua unpubl.); Forest Owlet *A. blewitti* (Hume, 1873) MF871714, MF871731, MF871740; White-Browed Owl *A. superciliaris* (Vieillot, 1817) MF871704, MF871727, MF871739 (Koparde *et al.* 2018); Burrowing Owl *A. cunicularia* (Molina, 1782) MK470730 (Wink & Sauer-Gürth 2021), DQ432754, DQ433340 (Kerr *et al.* 2007), FJ027202, FJ027206 (Kerr *et al.* 2009b); and Boreal Owl *Aegolius funereus* (Linnaeus, 1758) EU348864 (Wink *et al.* 2009) and MN122880 (Margaryan *et al.* 2021) as an outgroup. The sequences MF871723 apparently by mistake named as *A. brama albida* Koelz, 1950 and MF871724 as *A. brama brama* (Temminck, 1821) (Koparde *et al.* 2018) after BLAST examination in GenBank are identical to the same of *Elanus caeruleus* and *A. blewitti* respectively and were removed from the analysis.

5.2.3. Phylogenetic and genetic analyses

For finding the best evolution model, jModelTest 2.1.10 was applied (Guindon & Gascuel 2003; Darriba *et al.* 2012) with the corrected Akaike information criterion (Akaike 1974; Hurvich & Tsai 1993), which showed a Gamma General Time Reversible, GTR+ Γ (Tavaré 1986; Yang 1994) model for Cyt *b*, the same model was used to concatenated mitochondrial dataset for construct a Maximum Likelihood tree, Gamma Hasegawa-Kishino-Yano, HKY+ Γ (Hasegawa *et al.* 1985; Yang *et al.* 1994) for COI and Invariant Sites HKY, HKY+I (Hasegawa *et al.* 1985; Shoemaker & Fitch 1989) for RAG-1 datasets.

ML (500 bootstrap replicates) and Neighbor-joining (10000 replicates, Kimura 2-parameter distances) trees for sequenced loci as well as average pairwise p-distances and K2P distances between taxa were calculated with MEGA 6.06 (Tamura *et al.* 2013).

Bayesian concatenated mitochondrial and nuclear gene trees were calculated using BEAUti/BEAST 1.8.0 package (Drummond *et al.* 2012). Half-value of 2.1% sequence

divergence per million years for *Cyt b* (Weir & Schluter 2008) and 1.8% for COI (Lavinia *et al.* 2016) were taken into account to set the rates of the molecular clock model, the estimated rate for the nuclear alignment. I chose the lognormal relaxed clock model, Birth-Death speciation process (Feller 1939; Gernhard 2008), Markov chain Monte Carlo method with 10 million runs, sampling every 1000th run. Phylogenetic trees were performed in BEAST 1.8.0, the trees with the best likelihood were summarized using TreeAnnotator 1.8.0 (Drummond *et al.* 2012), first 10% of trees were discarded as burn-in.

I constructed the minimum-spanning haplotype network in Network 10.2.0.0 (fluxus-engineering.com 2020). The calculation of the network started by pre-processing with Star Contraction algorithm (Forster *et al.* 2001), continued by Median Joining calculations (Bandelt *et al.* 1999) and finished with post-processing option calculating the Minimum Spanning tree (Polzin & Daneshmand 2003), after that the network was drawn.

Analysis of genetic polymorphism for numerous COI sequences was carried out in DnaSP 6.12.03 (Rozas *et al.* 2017), the haplotype diversity and neutrality test indices are described in Section 2.6. For McDonald-Kreitman test two Spotted Owlet sequences (MK932906, KR779894) were chosen as outgroup.

5.3. Results

The number of variable/parsimony informative sites from all obtained *Athene noctua* sequences is 110/88 for COI (with GenBank data, Table A6), 143/123 for *Cyt b* (Table A7) and only 1/0 for RAG-1 (C-G, position 493) alignments, respectively. A 2305-bp concatenated mitochondrial and nuclear alignment shows strict divergence between different *Athene* species as well as lineages of current *A. noctua* (Figure 20).

The branches between species and main Little Owl groups have very strong support for BI (0.98-1) and relatively good for ML and NJ methods (Figures A12, A13). Inside our target taxa we can delineate separate branch of birds from Western and Central Europe which corresponds to the range of *vidalii* race. In addition, we observe a cluster of Mongolian birds from the race *plumipes* and a large cluster of all other Little Owls in which we can distinguish the African branch (Figure 20). The nuclear part of the analysis proved to be very conservative, among *A. noctua* we observe two haplotypes – *vidalii* clade and all others, differed by only one nucleotide substitution.

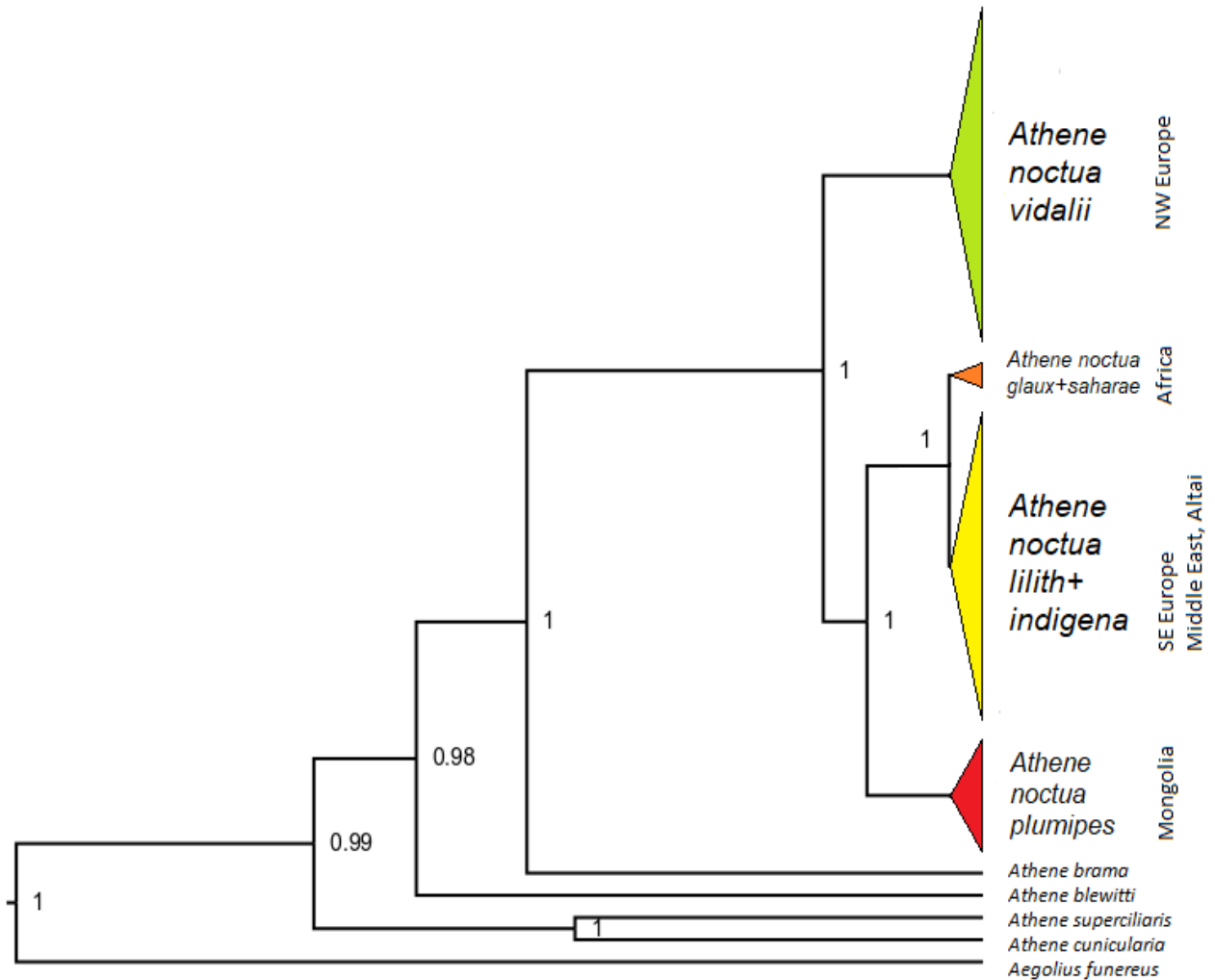


Figure 20. Bayesian phylogeny of *Athene noctua* and relative species based on the three locus dataset (RAG-1+COI+Cyt *b*). Node labels show inference posterior rates.

The Median Joining haplotype network based on mitochondrial sequences revealed the clustering of *Athene noctua sensu lato* clearly into three main groups. We can geographically localize it to the central (haplotypes A, B), eastern (C) and western (D) groups, the first correspond closely to the most accepted subspecies diverge patterns in the Eurasian and the African subgroups (Figure 21).

The Bayesian phylogenetic tree reconstructed from the mitochondrial sequences of Little Owl and other representatives of *Athene* reveals the evolutionary structure of the genus clade. The calculation of evolutionary split between the most distant species show 15.3 MYA in the Middle Miocene (Figure 22). Between our target species *A. noctua* and the nearest known species *A. brama*, divergence was calculated to have occurred 10.5 MYA in the Late Miocene, while the Little Owls of Western European and those of Far Eastern

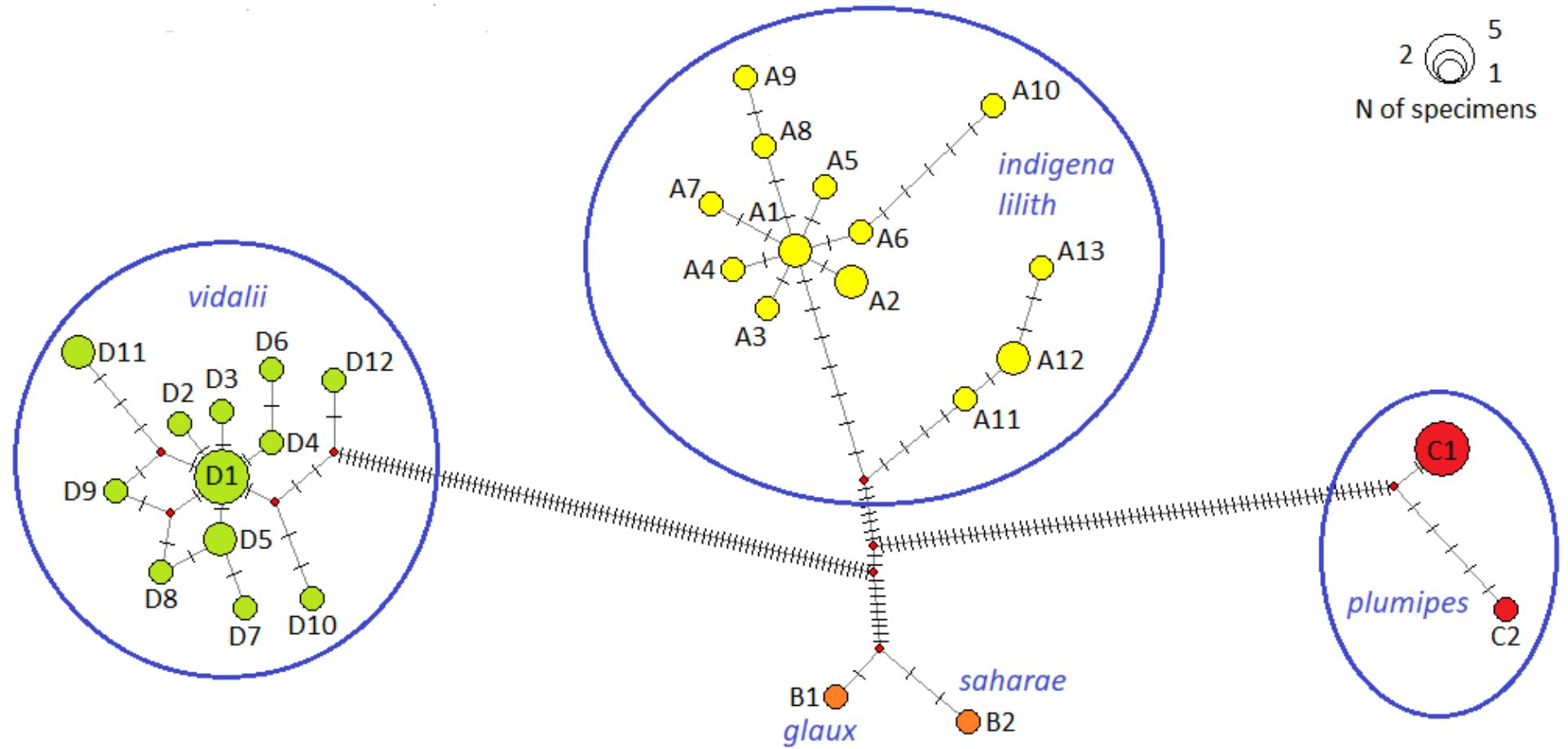


Figure 21. Haplotype network of the Little Owl mitochondrial concatenated sequences (COI+Cyt *b*). Each line represents one substitution.

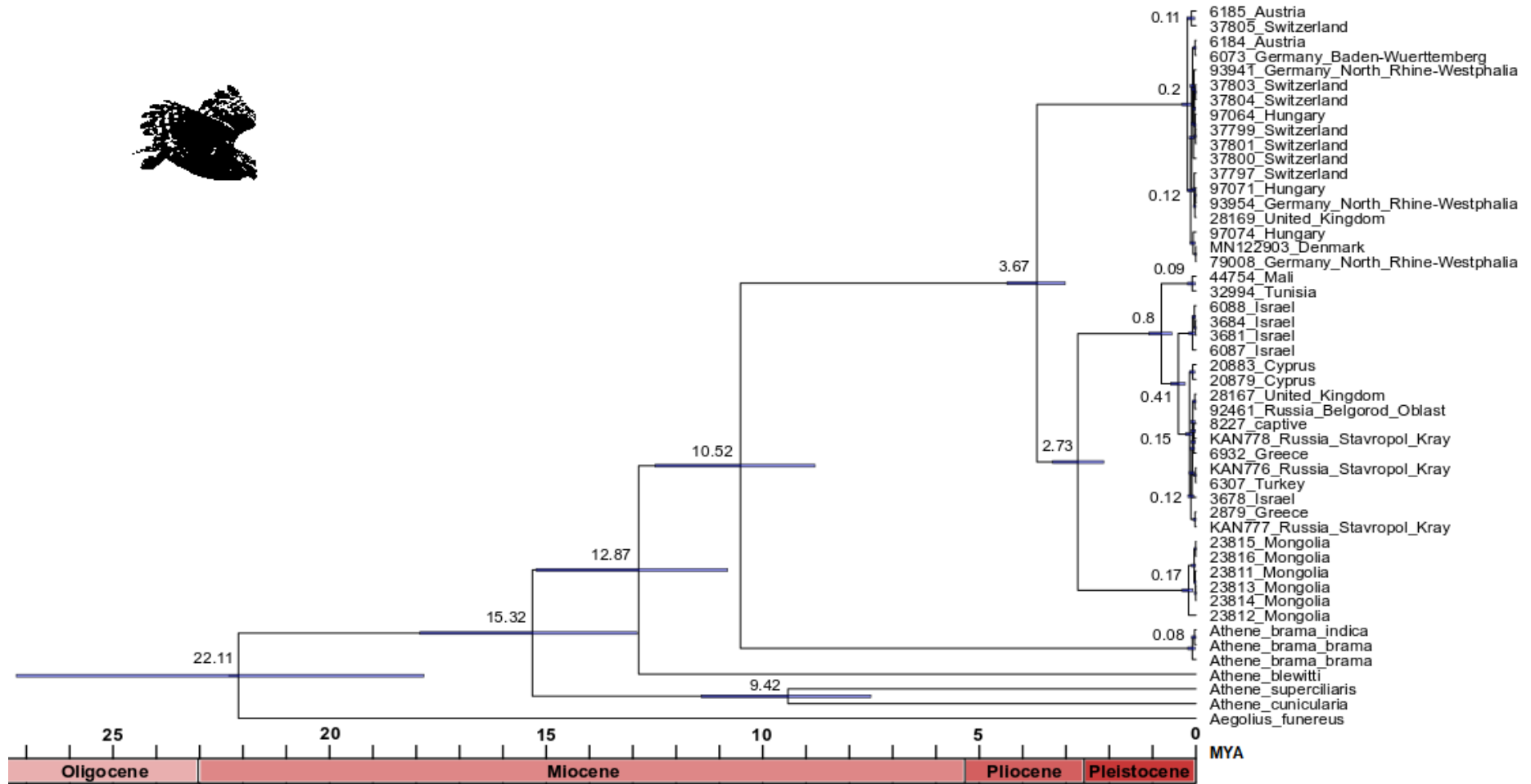


Figure 22. Phylogeny of *Athene noctua* and relative species based on concatenated mitochondrial dataset (COI+Cyt *b*), Bayesian inference tree. Node ages in million years ago are indicated on the branches, node bars show the 95% highest posterior density of nodal age estimates.

groups separated in the Upper Pliocene 3.7 and 2.7 MYA, respectively. The African group split 0.8 MYA on the border of the Calabrian/Chibanian stages of Pleistocene, with all other recent branches appearing at least two times later.

The analysis of the more numerous COI sequences permitted to construct phylogenetic trees with add here birds from *A. n. noctua* and *sarda* ranges (Figures 23 for Bayesian tree, A14 and A15 for ML and NJ trees respectively). I exclude from this analysis the sequences from the birds of intergradation zones between the different subspecies along with the four haplotypes from the owls in this zone which were atypical to other haplotypes in the area. The topology reminds the same for multigene trees but the divergence of *vidalii*

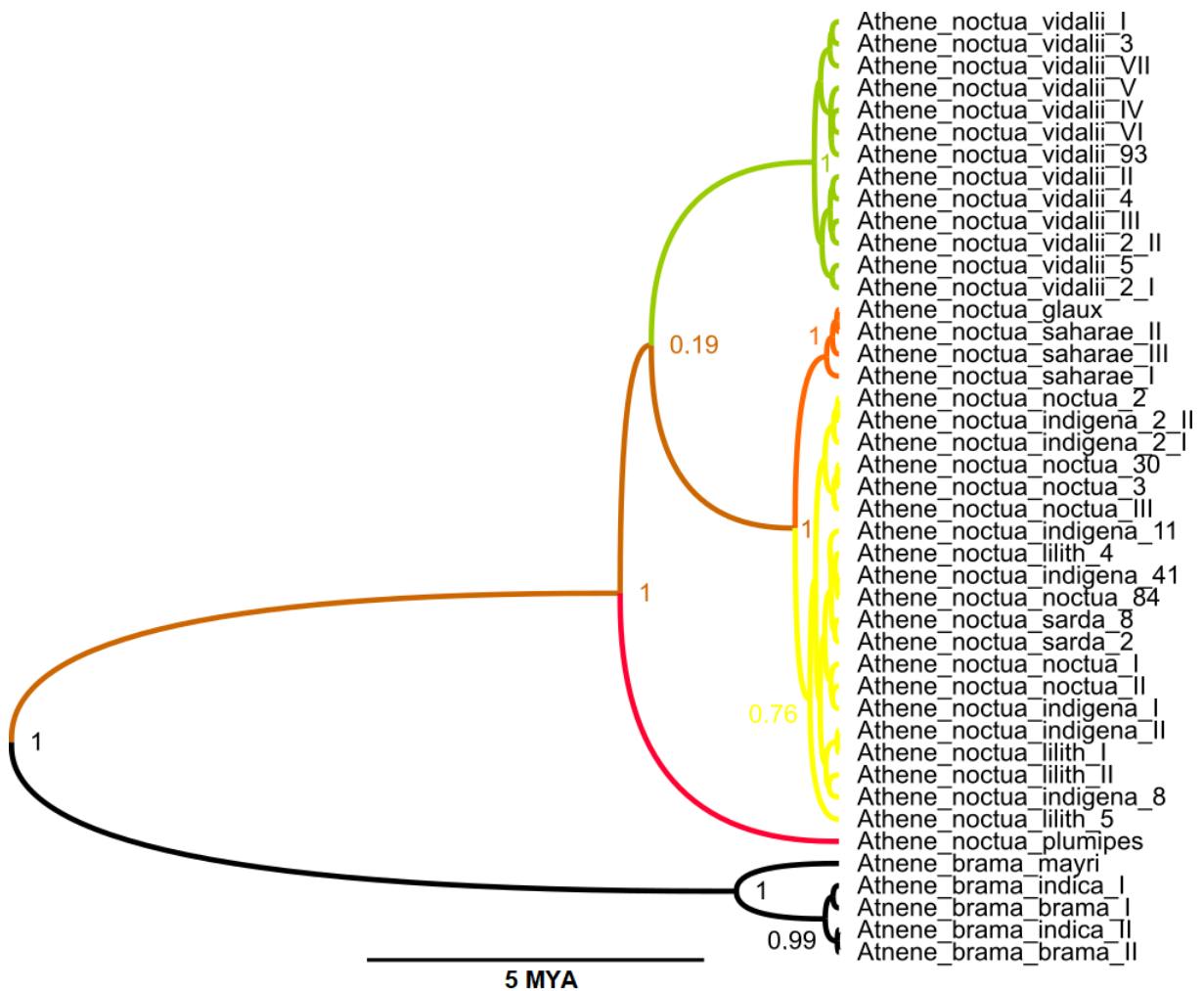


Figure 23. Bayesian phylogenetic tree of the Little Owl taxa COI sequences. Spotted Owlet data are given as outgroup, node labels show posterior rate, Arabic numerals on the right represent number of specimens with same haplotype, Roman numerals distinguish different haplotypes.

and nominate/African major clades are not well supported, at the same time the clades remains stable with no other forms inside.

Also it is possible to calculate COI polymorphism values among the different races of *Athene noctua* (Table 14). The African subspecies were merged to obtain a more manageable number of calculations. The haplotype diversity was found to vary from low to high between the different races, for most the values the genetic neutrality tests without outgroup were negative and insignificant, except for all three tests for *noctua*, which indicates that this population expanded in the past. All the values of neutrality index of McDonald-Kreitman test are greater than one what mean negative selection of the Little Owl taxa, simultaneously this is significant only for *indigena* subspecies.

Calculation of p-distances and K2P distances (Tables 15, 16) derived from mitochondrial data between *Athene* taxa reveals high difference between *vidalii*, *plumipes* and other subspecies of the Little Owl, perceptible between African and other subspecies, and low among African and races from *noctua* cluster.

Table 14. Haplotype diversity and neutrality tests between COI sequences of *Athene noctua* races. n – number of sequences, H – number of haplotypes, S – number of segregating sites, N_s – number of synonymous substitutions, N_p – number of non-synonymous substitutions, Hd – haplotype diversity, π – nucleotide diversity, k – average number of pairwise nucleotide differences, θ – expected number of polymorphic sites between sequences, TD – Tajima’s D test, MK (NI) – neutrality index value of McDonald-Kreitman test. * – p<0.05, *** – p<0.001.

Taxon	n	H	S	N _s	N _p	Hd	π	k	θ	TD	MK (NI)	Fu-Li's D*	Fu-Li's F*
<i>vidalii</i>	61	8	7	6	0	0.35	0.0007	0.38	1.50	-1.89	1.20	-2.81	-2.96
<i>noctua</i>	111	7	33	28	4	0.47	0.0018	1.01	6.25	-2.55***	2.55	-7.85*	-6.89*
<i>sarda</i>	10	2	1	0	1	0.36	0.0006	0.36	0.35	0.01	3.16	0.80	0.68
<i>indigena</i>	64	7	6	3	3	0.57	0.0013	0.73	1.27	-1.03	5.69*	-0.64	-0.90
<i>lilith</i>	15	4	5	4	1	0.64	0.0024	1.35	1.54	-0.41	3.17	-1.00	-0.97
<i>glaux+saharae</i>	4	3	2	1	1	0.83	0.0018	1.00	1.09	-0.71	3.87	-0.71	-0.60
<i>plumipes</i>	9	2	1	1	0	0.22	0.0004	0.22	0.37	-1.09	1.27	-1.19	-1.28

Table 15. Pairwise genetic distance values for *Athene* taxa based on COI sequences, p-distances (below diagonal) and K2P distances (above).

	<i>A. noctua vidalii</i>	<i>A. noctua noctua</i>	<i>A. noctua sarda</i>	<i>A. noctua indigena</i>	<i>A. noctua lilith</i>	<i>A. noctua glaux</i>	<i>A. noctua saharæ</i>	<i>A. noctua plumipes</i>	<i>A. brama indica</i>	<i>A. brama brama</i>	<i>A. brama mayri</i>	<i>A. blewitti</i>	<i>A. superciliaris</i>	<i>A. c. hypugæa</i>	<i>A. c. cunicularia</i>	<i>A. c. juninensis</i>	<i>A. c. partridgei</i>	<i>Aegolius funereus</i>
<i>A. noctua vidalii</i>		0.048-0.055	0.046-0.053	0.043-0.053	0.043-0.050	0.046-0.050	0.046-0.050	0.046-0.050	0.148-0.156	0.148-0.159	0.159-0.165	0.159-0.167	0.214-0.221	0.202-0.215	0.202-0.212	0.199-0.205	0.202-0.215	0.202-0.208
<i>A. noctua noctua</i>	0.044-0.053		0-0.007	0-0.007	0-0.009	0.004-0.009	0.004-0.009	0.032-0.036	0.132-0.140	0.132-0.143	0.149-0.154	0.139-0.147	0.172-0.178	0.170-0.176	0.167-0.176	0.164-0.170	0.167-0.179	0.175-0.181
<i>A. noctua sarda</i>	0.044-0.050	0-0.007		0-0.004	0-0.007	0.004-0.007	0.004-0.007	0.032-0.034	0.132-0.137	0.132-0.140	0.149-0.151	0.142-0.147	0.175-0.178	0.173-0.175	0.170-0.175	0.167-0.169	0.170-0.178	0.178-0.180
<i>A. noctua indigena</i>	0.042-0.050	0-0.007	0-0.004		0-0.007	0.004-0.007	0.004-0.007	0.029-0.034	0.129-0.137	0.129-0.140	0.146-0.152	0.139-0.147	0.172-0.178	0.170-0.176	0.167-0.176	0.164-0.170	0.170-0.179	0.178-0.181
<i>A. noctua lilith</i>	0.042-0.048	0-0.009	0-0.007	0-0.007		0.004-0.009	0.004-0.009	0.032-0.036	0.126-0.140	0.126-0.143	0.146-0.154	0.139-0.145	0.172-0.181	0.170-0.178	0.164-0.178	0.164-0.172	0.164-0.181	0.175-0.181
<i>A. noctua glaux</i>	0.044-0.048	0.004-0.007	0.004-0.007	0.004-0.007	0.004-0.009		0	0.032	0.126-0.129	0.126-0.132	0.143	0.136-0.139	0.172	0.167	0.164-0.167	0.161	0.164-0.167	0.172
<i>A. noctua saharæ</i>	0.044-0.048	0.004-0.009	0.004-0.007	0.004-0.007	0.004-0.009	0		0.032	0.126-0.129	0.126-0.132	0.143	0.136-0.139	0.172	0.167	0.164-0.167	0.161	0.164-0.167	0.172
<i>A. noctua plumipes</i>	0.044-0.048	0.031-0.035	0.031-0.033	0.029-0.033	0.031-0.035	0.031	0.031		0.137-0.140	0.137-0.143	0.154	0.136-0.139	0.200	0.185	0.188-0.191	0.185	0.188-0.194	0.169
<i>A. brama indica</i>	0.132-0.138	0.118-0.125	0.118-0.123	0.116-0.123	0.114-0.125	0.114-0.116	0.114-0.116	0.123-0.125		0-0.004	0.027-0.029	0.142-0.147	0.165-0.168	0.165-0.168	0.177-0.183	0.177-0.180	0.177-0.186	0.163-0.166
<i>A. brama brama</i>	0.132-0.140	0.118-0.127	0.118-0.125	0.116-0.125	0.114-0.127	0.114-0.118	0.114-0.118	0.123-0.127	0-		0.029	0.142-0.150	0.165-0.171	0.165-0.168	0.177-0.183	0.177-0.180	0.177-0.186	0.163-0.169
<i>A. brama mayri</i>	0.140-0.145	0.132-0.136	0.132-0.134	0.129-0.134	0.129-0.136	0.127	0.127	0.136	0.026-0.029	0.029		0.159-0.162	0.174	0.168	0.192-0.195	0.192	0.192-0.198	0.175
<i>A. blewitti</i>	0.140-0.147	0.125-0.132	0.127-0.132	0.125-0.132	0.125-0.129	0.123-0.125	0.123-0.125	0.123-0.125	0.127-0.132	0.127-0.134	0.140-0.143		0.148-0.151	0.172-0.175	0.158-0.164	0.161-0.164	0.158-0.167	0.149-0.152
<i>A. superciliaris</i>	0.182-0.186	0.151-0.156	0.154-0.156	0.151-0.156	0.151-0.158	0.151	0.151	0.171	0.145-0.147	0.145-0.149	0.151	0.134-0.136		0.130	0.116-0.119	0.122	0.116-0.125	0.165
<i>A. cunicularia hypugæa</i>	0.169-0.173	0.149-0.151	0.151-0.154	0.149-0.154	0.149-0.156	0.147	0.147	0.160	0.145-0.147	0.145-0.147	0.147	0.151-0.154	0.116		0.048-0.051	0.053	0.048-0.051	0.183
<i>A. cunicularia cunicularia</i>	0.173-0.180	0.147-0.154	0.149-0.154	0.147-0.154	0.145-0.154	0.145-0.147	0.145-0.147	0.162-0.164	0.154-0.158	0.154-0.158	0.164-0.167	0.140-0.145	0.105-0.107	0.046-0.048		0.013-0.016	0-	0.177-0.180
<i>A. cunicularia juninensis</i>	0.171-0.175	0.145-0.149	0.147-0.149	0.145-0.149	0.143-0.151	0.143	0.143	0.160	0.154-0.156	0.154-0.156	0.164	0.143-0.145	0.110	0.050	0.013-0.015		0.009-0.016	0.186
<i>A. cunicularia partridgei</i>	0.173-0.182	0.147-0.156	0.149-0.156	0.149-0.156	0.147-0.158	0.145-0.149	0.145-0.149	0.162-0.167	0.154-0.160	0.154-0.160	0.164-0.169	0.140-0.145	0.105-0.112	0.046-0.048	0-	0.009-0.015		0.177-0.186
<i>Aegolius funereus</i>	0.173-0.178	0.154-0.158	0.156-0.158	0.156-0.158	0.154-0.158	0.151	0.151	0.149	0.145-0.147	0.145-0.149	0.154	0.147	0.134-0.136	0.160	0.156-0.160	0.162	0.156-0.162	

Table 16. Pairwise genetic distance values for *Athene* taxa based on Cyt *b* sequences, p-distances (below diagonal) and K2P distances (above).

	<i>A. n. vidalii</i>	<i>A. n. indigena</i>	<i>A. n. lilith</i>	<i>A. n. glaux</i>	<i>A. n. saharae</i>	<i>A. n. plumipes</i>	<i>A. b. albida</i>	<i>A. b. indica</i>	<i>A. b. brama</i>	<i>A. blewitti</i>	<i>A. superciliaris</i>	<i>A. c. hypugaea</i>	<i>A. c. cunicularia</i>	<i>Aegolius funereus</i>
<i>Athene noctua vidalii</i>		0.068-0.079	0.068-0.077	0.065-0.069	0.065-0.069	0.076-0.081	0.141-0.144	0.140-0.143	0.136-0.141	0.141-0.145	0.158-0.161	0.167-0.170	0.152-0.156	0.220-0.225
<i>Athene noctua indigena</i>	0.064-0.074		0-0.017	0.019-0.022	0.019-0.022	0.061-0.068	0.148-0.152	0.147-0.151	0.143-0.149	0.152-0.157	0.165-0.170	0.163-0.167	0.156-0.159	0.219-0.226
<i>Athene noctua lilith</i>	0.064-0.072	0-0.016		0.019-0.022	0.019-0.022	0.061-0.068	0.148-0.152	0.147-0.151	0.143-0.149	0.152-0.157	0.165-0.170	0.163-0.167	0.156-0.159	0.220-0.223
<i>Athene noctua glaux</i>	0.062-0.065	0.020-0.024	0.018-0.022		0.002	0.058-0.062	0.148	0.146	0.143-0.145	0.150-0.153	0.165	0.166	0.157	0.225
<i>Athene noctua saharae</i>	0.062-0.065	0.020-0.024	0.018-0.022	0.002		0.058-0.062	0.148	0.146	0.143-0.145	0.150-0.153	0.165	0.166	0.157	0.225
<i>Athene noctua plumipes</i>	0.071-0.075	0.058-0.066	0.058-0.064	0.055-0.059	0.055-0.059		0.146-0.148	0.145-0.147	0.144-0.145	0.154-0.158	0.173-0.175	0.173-0.174	0.163-0.165	0.236-0.238
<i>Athene brama albida</i>	0.126-0.128	0.132-0.137	0.132-0.135	0.132	0.132	0.131-0.132		0.004	0.003-0.007	0.141-0.144	0.163	0.166	0.159	0.216
<i>Athene brama indica</i>	0.125-0.127	0.131-0.136	0.132-0.134	0.131	0.131	0.129-0.131	0.004		0.001-0.005	0.140-0.143	0.162	0.164	0.156	0.216
<i>Athene brama brama</i>	0.122-0.126	0.127-0.135	0.127-0.133	0.127-0.129	0.127-0.129	0.128-0.129	0.003-0.007	0.001-0.005		0.136-0.142	0.159-0.162	0.160-0.162	0.152-0.155	0.212-0.214
<i>Athene blewitti</i>	0.127-0.131	0.135-0.142	0.136-0.140	0.135-0.137	0.135-0.137	0.137-0.140	0.127-0.129	0.126-0.128	0.123-0.127		0.153-0.155	0.162-0.165	0.153-0.155	0.197-0.200
<i>Athene superciliaris</i>	0.140-0.143	0.147-0.152	0.146-0.150	0.146	0.146	0.152-0.153	0.144	0.143	0.140-0.142	0.137-0.138		0.136	0.122	0.214
<i>Athene cunicularia hypugaea</i>	0.148-0.150	0.146-0.151	0.145-0.148	0.147	0.147	0.152-0.153	0.147	0.145	0.142-0.144	0.144-0.146	0.122		0.062	0.223
<i>Athene cunicularia cunicularia</i>	0.136-0.139	0.139-0.143	0.139-0.141	0.140	0.140	0.145-0.146	0.141	0.139	0.136-0.138	0.137-0.138	0.111	0.059		0.200
<i>Aegolius funereus</i>	0.189-0.192	0.188-0.193	0.189-0.191	0.192	0.192	0.200-0.201	0.186	0.186	0.183-0.185	0.173-0.175	0.185	0.191	0.175	

5.4. Discussion

5.4.1. Origin of *Athene*

According to our data all extant species of *Athene* diverged approximately 15 MYA (height 95% high posterior density 16.7–13.9 MYA), so this period may be considered the latest time for the appearance for this genus among other Strigidae which turn out to be older than supposed before. It is an earlier date than has been discovered through paleontological analyses of the most ancient bones of *Athene sp.*, found at the Rudabánya fossil locality in Hungary, which are dated from the Late Miocene 10–11 MYA (Bernor *et al.* 2002).

The first fossil species record of *Athene* is known later from the Upper Pliocene in Kansas, *A. megalopeza* (Ford, 1966). The basal separate branch is formed with American *A. cunicularia* and *A. superciliosus* from Madagascar, all other species belong to the Old World branch (Figure 20). Based on available data I cannot prove that the first divergence happened between Old and New World *Athene* owls. In addition, the diversity of taxonomic forms in Eurasia suggests that this continent is probably the origin of this genus.

During Pleistocene several autochthonous Mediterranean insular species of Little Owl existed which may be compared with extant *Athene noctua*: *A. vallgornerensis* Guerra, Bover, Alcover, 2012 on Mallorca, shorter and more robust (Guerra *et al.* 2012); *A. angelis* Mourer-Chauviré, Salotti, Pereira, Quinif, Courtois, Dubois & La Milza, 1997 on Corsica, taller and more robust (Mourer-Chauviré *et al.* 1997); *A. trinacriae* Pavia, Mourer-Chauviré, 2002 on Sicily, of the same size but with longer legs (Pavia & Mourer-Chauviré 2002); and *A. cretensis* Weesie, 1982 on Crete, slightly larger, with longer wings and disproportionally longer legs, adapted to terrestrial lifestyle (Weesie 1982: Figure 24). All these morphologically distinct forms are not survived till today, disappeared probably in competition with terrestrial predators arrived from the mainland and/or human colonisation of islands (Weesie 1982; Pavia & Mourer-Chauviré 2002). *A. noctua* could partially take their ecological niche and spread own genes on these territories in relatively short time.

Fossils of *Athene noctua* are known from different localities in the Mediterranean Basin since the Early Pleistocene from Italy which dates of 1.3–1.6 MYA (Bedetti & Pavia 2013) and are substantially more recent than our calculations for *A. noctua* in large sense. In spite of this inconsistency, Mediterranean area may be considered as the most likely origin

for the Little Owl because it served like for other avian species as a refuge area during the Quaternary glaciations (Tyrberg 1991).

5.4.2. Population structure of the Little Owl races

The partitioning of all *Athene noctua* in two major clades, North-Western and South-Eastern is confirmed by our data obtained from two mitochondrial loci (Figure 22). The Eastern clade divides clearly into South European-Middle Eastern-African and Far Eastern groupings, and inside the first African branch is well distinguishable (Figure 22). This distribution corresponds well with current classification of Little Owl subspecies as long as I exclude the birds from the zones of intergradation. Previously, the genetic research of

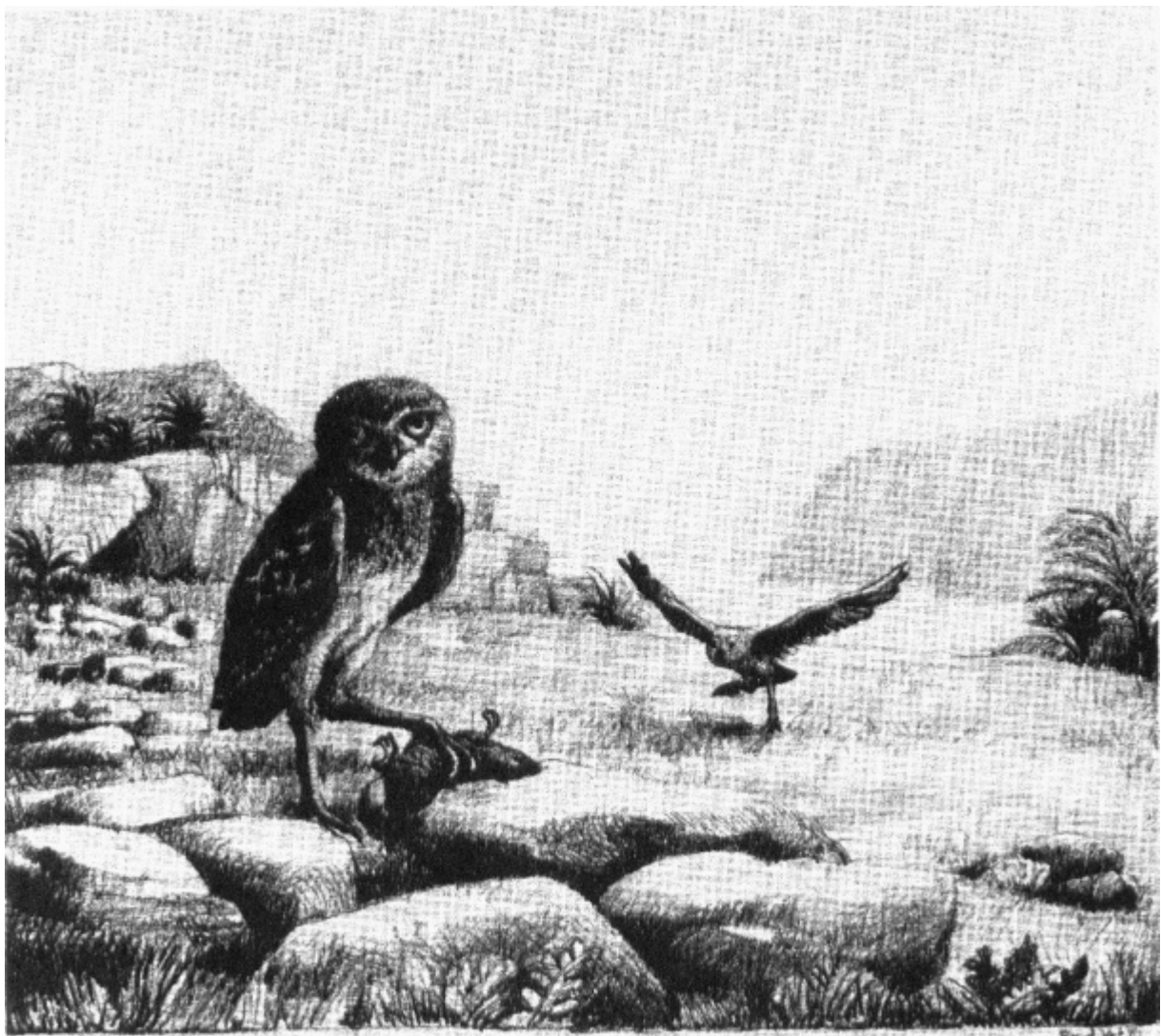


Figure 24. Reconstruction of Cretan Owl *Athene cretensis*†, from Weesie 1982.

European Little owls has shown the same two clades by genetic analysis of COI. Non-covered by my sequencing *noctua* and *sarda* belongs to one clade with *indigena* and *lilith* subspecies (Figures 23, A14, A15; Pellegrino *et al.* 2014). In its turn, the divergence of Eastern group forms Sardinian and South Italian groups by analysis of mitochondrial Control region 1 (Pellegrino *et al.* 2014) and through microsatellite analyses Italian, South-Eastern European and Sardinian groups have been identified by microsatellites (Pellegrino *et al.* 2015).

Thus the Western clade is composed only by *vidalii* race. The proposed Mediterranean group consists of nominate *noctua*, South European *indigena*, and Middle Eastern *lilith*. In this clade we have also located the bird IPMB92495 caught in Russian Altai Kray, the genetic material which was collected by the author. Tarasov (2011) regards last year's numerous cases of *A. noctua* observations in the settlements of North Kazakhstan and Southern parts of Western Siberia as an enlargement of the range to the North-East and considers them to be the nominate form, according to modern delimitation of ranges (Cramp *et al.* 1985) it should correspond to *vidalii*. This is in agreement with Cramp's view that they are not *bactriana* which is related to the desert area and avoid human presence. In contrast Priklonsky (2001) has suggested these birds represent *bactriana* together with *orientalis* and even *plumipes* in the same region, although without any substantial proof. Irisova and Nikulkin (2006) suppose what this range is not related with Altaic which should correspond to mountain subspecies but more probably is continuation of Little Owl range from Kazakhstan which corresponds to *bactriana*. However, my bird belongs to the same clade with *indigena* which is related not to forest as *vidalii*, but to steppe and steppe-forest zone and also breeds in the settlements. If we accept the north-eastern movement hypothesis also for this subspecies this fits into its range which previously was limited by the Ural steppes (Dementiev 1951a). IPMB specimens of *glaux* from Tunisia and *saharae* from Mali belong to African group. Finally, the birds from Mongolia, China and Korea forming distinctive group appertains to *plumipes* race.

The birds of intergradation zones should belong respectively to one of the species: *noctua* or *vidalii* in Central Europe, which is confirmed by my data. This coincides with Cramp's range and other data obtained from mitochondrial DNA (Pellegrino *et al.* 2014; Valterovà *et al.* unpubl.). The bird IPMB92461 from Belgorod Region of Russia is similar to *indigena* with the northern range border of this subspecies being less to the south, in Kharkiv Region of Ukraine (Dementiev 1951a). To conclude, my bird should belong to

indigena particularly if we take into account the extension of the range in North-East as discussed above.

The British birds are *vidalii* according to Dementiev (1951a), at the same time among two sequenced Little owls from England one belongs to *vidalii* and other to *indigena* clade (Figure 22). Perhaps we can observe a mixture of forms in United Kingdom ascending to different birds which were released into the wild here.

Analysis of genetic polymorphism reveals neutrality negative values of the tests without outgroups and values >1 for index of neutrality of McDonald–Kreitman test for almost all Little Owl races (Table 14). For *noctua* and *indigena* statistically significant values were obtained. I could suppose that these taxa expanded largely from few numbers, probably passing a bottleneck. This may be related with Mediterranean refugium where Little Owls survived during the last glaciations. The low positive values are observed only for the *sarda* race if we consider it as a valid taxon, it is not significant because of small number of specimens, but might be relevant and can be explained by the fact that Sardinian birds remained as a stable and relatively isolated insular population not affected by the glaciation and latest recolonizations.

5.4.3. Interracial genetic distances

The highest p-value differences between the races was found between *vidalii*, *plumipes* and all other investigated subspecies of *Athene noctua sensu stricto*. These values, 6.2–7.5% by Cyt *b* and 4.2–5.3% by COI for *vidalii*, 5.5–7.5% and 2.9–4.8% by the same markers for *plumipes* are much higher than genetic distances among other *A. noctua* subspecies, 0–2.4% by Cyt *b* and 0–0.9% by COI, equally between subspecies of *A. brama* 0–2.9% by both markers (Tables 15, 16). Intraspecific p-distances for these genes from owls are 0–1.6% (Wink *et al.* 2008; Jønsson *et al.* 2013; Colihueque *et al.* 2015; Sadanandan *et al.* 2015), and interspecific within the same genus in the wide range from 0.5 to 18% (Wink & Heidrich 1999; Ryu & Park 2003; Wink *et al.* 2008; Jønsson *et al.* 2013; Sadanandan *et al.* 2015; Dantas *et al.* 2016; Uva *et al.* 2018).

Similar values obtained from K2P distances, 6.5–8.1% for *vidalii* and 5.8–8.1% for *plumipes* by Cyt *b*, 4.3–5.0% and 2.9–5.0% by COI respectively (Table 16) significantly exceed the intraspecific average distances from different Strigiformes obtained by these markers

which varies in the range from 0 to 1.9% (Alaie Kakhki & Aliabadian 2012; Nijman & Aliabadian 2013; Aliabadian *et al.* 2016). The highest COI value was found between two specimens of *Aegolius funereus*: 4.1% (Nijman & Aliabadian 2013); this owl has several subspecies distributed in Old and New World which probably may be considered as different species. Intrageneric K2P distance varies from 0.9 to 19% (Ryu & Park 2003; Alaie Kakhki & Aliabadian 2012, Aliabadian *et al.* 2016, Dantas *et al.* 2016).

The small African group is related with the main but distinguish well from it showing distances up to 2.2% (Table 16). At the same time we cannot observe significant distances between the races inside these two groups, the markers used being not sensitive enough. Although including of *lilith* race into *saharae* (Meinertzhagen 1924, 1925; Dementiev 1951a) was not supported after Vaurie (1960), my data confirm it once again. Cypriot birds considered as coastal *glauca* (Niethammer *et al.* 1938) or *indigena* (Vaurie 1960) in the past, after Cramp *et al.* (1985) have been treated as *lilith*. In recent genetic studies using the rapidly evolving mitochondrial Control Region 1 (Pellegrino *et al.* 2014) the data suggests they belong to the same cluster as *indigena* and not *glauca*. Since through our marker analyses we were unable to distinguish *lilith* from *indigena*, I suggest that the question of Little Owls from Cyprus is not fully resolved.

Subspecies of the Barn Owl *Tyto alba* which showed K2P difference 7.2–9.5% from *Cyt b* and 5.5–6.4% from COI (Aliabadian *et al.* 2016) were after this research reclassified as separate species American Barn Owl *T. furcata* and Eastern Barn Owl *T. javanica* by IOC Bird List (Gill *et al.* 2022). The mean K2P distance from *Cyt b* for congeneric birds species is 1.6% (Johns & Avise 1998) and generally the benchmark value of 2% genetic distance is considered enough for a “good” species in owls (Wink *et al.* 2008). In two of the studied Little Owl subspecies my results exceed this value more than twice fold despite the fact that we don’t see differences in the investigated nuclear markers between *plumipes* and the “main” *A. noctua* group. But the nuclear marker shows a very slow evolution.

5.4.4. Taxonomic implications

According to obtained genetic distances between the races of *Athene noctua sensu lato* I recommend to restore two of them to the species level: *Athene vidalii* A. Brehm, 1857 **stat. rest.** which may be called in English Western Little Owl and *Athene plumipes* Swinhoe,

1870 **stat. rest.**, the Eastern Little Owl. In fact the diversity of *Athene* taxa at the species level in Palearctic is not unexpected, at least four currently extinct species inhabited Mediterranean islands (see above). Fossil *A. n. lunellensis* according to the finding places in South France (Mourer-Chauviré 1975) occupied the range of *vidalii*. This owl according to the author of description differs from living *A. noctua* by the size of certain bones. The tarsometatarsus length is 35.5 mm for *lunellensis* (Mourer-Chauviré 1975), 33.0–35.9 mm for *vidalii* and 29.5–33.6 mm for *noctua* (Cramp *et al.* 1985; Weick 2006). Considering its range and measurements of tarsus I recommend to place this form together with *vidalii* as *Athene vidalii lunellensis* (Mourer-Chauviré, 1975) **stat. nov.** conserving nominate extant subspecies.

The taxonomic groupings for Little Owl subspecies distributed in Central Asia from which I don't have genetic material – *bactriana*, *orientalis* and *ludlowi* remains open. At the same time *Athene noctua bactriana* morphologically is very close to *A. n. lilith* (Dementiev 1951a). In addition Hartert (1925) mentions that *lilith* and *bactriana* from Iraq obviously intergrade. *A. n. orientalis* is similar by coloration to *plumipes* (Dementiev 1951a). Vaurie (1960) observed birds from Northwestern Mongolia which had morphologies intermediate between *orientalis* and *plumipes*. This region could possibly be another zone of intergradation. It should be noted that these forms have ecological difference, the first is mountain and *plumipes* is a desert-steppe race (Dementiev 1951a). *A. n. ludlowi* is a mountain race like *orientalis* and its range is located to the south-east. I place provisory *bactriana* to *A. noctua*, *orientalis* and *ludlowi* to *A. plumipes*, but further genetic research on these subspecies is needed. The status of *impasta* is very doubtful, this subspecies is known only by three specimens from Kukuonor and Gansu (Central China). According to the authors descriptions they only differ from one another by darker plumage (Bangs & Peters 1928). Later these findings were disputed, the first birds from this region were collected just after molting while others were collected later in the year and were *plumipes* (Steinbacher 1936, cited by Vaurie 1960; Stresemann *et al.* 1938; Vaurie 1960). So while obtaining genetic material from this race will help answer this question, in the meantime they should be synonymized with *plumipes* as proposed by Steinbacher (1936, cited by Vaurie 1960) and Vaurie (1960).

I recommend conserving subspecies status of *Athene noctua sarda* which is different from nominate subspecies by coloration (Kleinschmidt 1907; Vaurie 1960) and forms its own

cluster after examination of Control Region 1 sequences (Pellegrino *et al.* 2014) and microsatellites (Pellegrino *et al.* 2015). Probably the Little Owls from the south of mainland Italy and Sicily which also form another CR1 clade should be considered as a new separate form, and the form *salentina* once proposed from Apulia remains invalid. Its author distinguishes it only by coloration and contrasts to North Italian and Sicilian birds bringing together with African *glaux* (Trischitta 1939) which is a genetically distant subspecies (Tables 15, 16).

The independence of *Athene lilith* from European Little Owls previously proposed (Wink & Heidrich 1999; König & Weick 2008) can be confirmed for *A. noctua vidalii* but not for *A. n. noctua* (Figures 20–22, Tables 15, 16); this taxon should be treated as a subspecies of *A. noctua* despite certain difference in vocalisation from other forms (Weick 2006). Giving the status of a separate group for *lilith* by Clements *et al.* (2019) who propose this kind of division inside of large species seems equally superfluous.

Finally, in the absence of genetic data I cannot demonstrate proof to support bringing *Athene spilogastra* together with *somaliensis* race as a separate species (König & Weick 2008). However, these owls not only have isolated range, but also they differ morphologically significantly from all other races included in *A. noctua* by their tarsus and wing lengths, whole size and pigmentation (Pellegrino *et al.* 2020). I feel these birds should be considered separately. Summarized proposed taxonomic rearrangements are presented on the Table 17.

Table 17. Systematics of *Athene noctua* complex.

Peters 1940	sp.	<i>Athene noctua</i>			
	ssp.	<i>noctua</i> <i>vidalii</i> <i>sarda</i> <i>indigena</i> <i>?kessleri</i>	<i>?caucasica</i> <i>lilith</i> <i>glaux</i> <i>saharae</i> <i>solitudinis</i>	<i>bactriana</i> <i>orientalis</i> ¹ <i>ludlowi</i> ¹ <i>impasta</i> ¹ <i>plumipes</i> ¹	<i>spilogastra</i> <i>somaliensis</i>
Vaurie 1960	sp.	<i>Athene noctua</i>			
	ssp.	<i>noctua</i> <i>vidalii</i> <i>sarda</i> <i>indigena</i>	<i>lilith</i> <i>glaux</i> <i>saharae</i> <i>bactriana</i>	<i>orientalis</i> <i>ludlowi</i> <i>plumipes</i> <i>spilogastra</i>	<i>somaliensis</i>
König & Weick 2008	sp.	<i>Athene noctua</i>		<i>Athene lilith</i>	<i>Athene spilogastra</i>
	ssp.	<i>noctua</i> <i>vidalii</i> <i>glaux</i> <i>orientalis</i>	<i>ludlowi</i> <i>plumipes</i> ² <i>indigena</i> <i>bactriana</i>	-	<i>spilogastra</i> <i>somaliensis</i>
Dickinson & Remsen 2013 HBW & BirdLife International 2021 Gill et al. 2022	sp.	<i>Athene noctua</i>			
	ssp.	<i>noctua</i> <i>vidalii</i> <i>indigena</i> <i>lilith</i>	<i>glaux</i> <i>saharae</i> <i>bactriana</i> <i>plumipes</i>	<i>orientalis</i> <i>ludlowi</i> <i>impasta</i> <i>spilogastra</i>	<i>somaliensis</i>
Clements et al. 2019	sp.	<i>Athene noctua</i>			
	ssp. group	<i>noctua</i>	<i>bactriana</i>	<i>lilith</i>	<i>spilogastra</i> / <i>somaliensis</i>
	ssp.	<i>noctua</i> <i>vidalii</i> <i>indigena</i> <i>glaux</i> <i>saharae</i> <i>orientalis</i> <i>ludlowi</i> <i>impasta</i> <i>plumipes</i>	<i>bactriana</i>	<i>lilith</i>	<i>spilogastra</i> <i>somaliensis</i>
This study	sp.	<i>Athene noctua</i>	<i>Athene vidalii</i>	<i>Athene plumipes</i>	<i>Athene spilogastra</i> ³
	ssp.	<i>noctua</i> <i>sarda</i> <i>indigena</i> <i>lilith</i> <i>glaux</i> <i>saharae</i> <i>bactriana</i> ⁴	<i>vidalii</i> <i>lunellensis</i> †	<i>plumipes</i> <i>orientalis</i> ⁴ <i>ludlowi</i> ⁴	<i>spilogastra</i> <i>somaliensis</i>

¹ – validity was questioned

² – “perhaps specifically distinct”

³ – species status may be questioned

⁴ – species belonging is provisional

6. Conclusions and future perspectives

In the present study, phylogenetic investigation of several raptor groups was carried out. Obtained results allow drawing the following conclusions.

The project examining the molecular phylogeny of elanin kites confirms their position as ancient taxa sister to other Accipitridae. Based on the cytogenetic, morphological and ecological data is recommended to separate it from accipitrids and elevate to the family Elanidae. Simultaneously, the unique features of the Pearl Kite allow distinguishing it as a monotypic subfamily Gampsonychinae within the family Elanidae, which also contains a second subfamily Elaninae consisting of genera *Elanus* and *Chelictinia*. Further accumulation of genetic data would enable deeper characterization of the phylogeny of this group on a species and subspecies level.

In the second research project a general description of the single-locus phylogeny and phylogeography produced from the large dataset on Black and Yellow-Billed kites was performed. A correlation between the subspecies/geographic distribution and Cyt *b* sequences was found. The radiation of two main branches of *Milvus migrans* occurred in late Pleistocene: first European branch contains subspecies *migrans*, and second Asian/Australian branch divided further into North Asian *lineatus* and South Asian/Australian *govinda/affinis* subspecies. No reproductive isolation was observed, and birds from different branches can interbreed. The genetic structure of Yellow-Billed Kite, which separates into two independent haplogroups not corresponding to existing subspecies, remains unclear and requires further investigation.

The last research project reveals the phylogeny of the Little Owl *sensu lato*. The analysis confirms Pliocene separation of European *Athene noctua vidalii* from other forming own clade by both mitochondrial and nuclear data. Position of Eastern *A. (n.) plumipes* is also distant from the main clade consisting of North African subspecies and large South European/Middle East branches. *A. (n.) lilith* which was previously proposed to be treated as a separate species don't differ from other races belonging to this group. At the same time *vidalii* and *plumipes* taxa should be restored as separate species. Almost all investigated subspecies show expansion in the past probably passed by bottleneck affected by last

glaciations. Accumulation of genetic data from never or insufficiently sequenced Little Owl taxa will extend our knowledge on its systematics and geographical distribution.

Technical progress related to the spread of next-generation and following third-generation sequencing permits to obtain large datasets of genetic information, including full mitogenomes, in a relatively short time compared to the traditional Sanger sequencing. Powerful high-throughput methods provide opportunity to increase research on avian evolution as well as other related topics like bird functional genomics, conservation, phylogeographic and population genetic studies (Kraus & Wink 2015; Wink 2021). Wherein all techniques have their own limits, as we can see today the suggestion that we could have complete genomes of the majority of World bird species by 2022 (Harr & Price 2012) did not come true. Currently we have obtained full genome data from a little more than 5% of avian species (Bravo *et al.* 2021) and this process will take a number of years more. The use of museum specimens occurring in bird evolution studies poses a problem. The DNA from these samples is often old and degraded and readable sequence fragments may be shorter than the resolution of high-throughput technologies (Raxworthy & Smith 2021), as well as the cost of multiple sample sequencing remains rather high. Nevertheless obtaining mitogenomes and nuclear multilocus data from genetically different populations of Yellow-Billed Kite, all subspecies of elanin kites and *Athene noctua* complex would allow answering all taxonomic questions of these groups.

On the other hand, the accumulation of classic paleontological data will improve the molecular dating of the appearance of the particular taxa, including raptors, and the development of palaeornithology contributes significantly to this (Mayr 2007).

All raptors investigated here are globally protected, like almost all other birds of prey (Convention... 2022), and phylogenetic research remains valuable for conservation biology, especially at the population level and species boundaries (Sinclair *et al.* 2005) considering also multiple various phylogenetic metrics (Tucker *et al.* 2017).

Finally, the totality of existing avian species described mainly by morphological criteria does not correspond to evolution species concept, and its real number should be increased approximately twice (Barrowclough *et al.* 2016). There is no doubt that the raptors are an integral part of this general set, thus their species number will exceed a thousand. And even after constructing of ultimate “Avian Tree of Life” with revealed evolutionary

history and position for each species, a more detailed tree at subspecies level will remain a big challenge for future research in the fields of phylogeny and systematics.

7. References

- AKAIKE H. 1974. — A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19 (6): 716–723. <https://doi.org/10.1109/TAC.1974.1100705>
- ALAIIE KAKHKI N. & ALIABADIAN M. 2012. — Mitochondrial DNA (CYTB) divergences in two distinct, Old World and New World Barn Owls. *Iranian Journal of Animal Biosystematics* 8 (1): 47–55.
- ALI S. & RIPLEY S.D. 1968. — *Handbook of the Birds of India and Pakistan. Together with Those of Nepal, Sikkim, Bhutan and Ceylon*. Vol. 1. Bombay, Oxford University Press, i–iv, 1–380.
- ALIABADIAN M., ALAIIE-KAKHKI N., MIRSHAMSI O., NIJMAN V. & ROULIN A. 2016. — Phylogeny, biogeography, and diversification of barn owls (Aves: Strigiformes). *Biological Journal of the Linnean Society* 119: 904–918. <https://doi.org/10.1111/bij.12824>
- ALIABADIAN M., BEENTJES K., ROSELAAR C.S., VAN BRANDWIJK H., NIJMAN V. & VONK R. 2013. — DNA barcoding of Dutch birds. *ZooKeys* 365: 25–48. <https://doi.org/10.3897/zookeys.365.6287>
- ALIABADIAN M., KABOLI M., NIJMAN V. & VENCES M. 2009. — Molecular identification of birds: Performance of distance-based DNA barcoding in three genes to delimit parapatric species. *PLOS ONE* 4 (1): e4119: 1–8. <https://doi.org/10.1371/journal.pone.0004119>
- ALVARENGA H.M.F. & HÖFLING E. 2003. — Systematic revision of the Phorusrhacidae (Aves: Ralliformes). *Papéis Avulsos de Zoologia* 43 (4): 55–91. <https://doi.org/10.1590/S0031-10492003000400001>
- ANDREYENKOV O.V., ANDREYENKOVA N.G., BOXORN A.Y., KASHINSKAYA Y.O. & SHTOL D.A. 2019. — New data on the Little Owl distribution in the Novosibirsk Region and the northern part of the Altai Kray, Russia. *Raptors Conservation* (39): 282–285. <https://doi.org/10.19074/1814-8654-2019-39-282-285>
- ANDREYENKOVA N.G., ANDREYENKOV O.V., KARYAKIN I.V. & ZHIMULEV I.F. 2018. — New haplotypes of the mitochondrial gene *CytB* in the nesting population of the Siberian Black Kite *Milvus migrans lineatus* Gray, 1831 in the territory of the Republic of Tyva. *Doklady Biochemistry and Biophysics* 482: 242–244. <https://doi.org/10.1134/S1607672918050034>
- ANDREYENKOVA N.G., KARYAKIN I.V., STARIKOV I.J., SAUER-GÜRTH H., LITERÁK I., ANDREYENKOV O.V., SHNAYDER E.P., BEKMANSUROV R.H., ALEXEYENKO M.N., WINK M. & ZHIMULEV I.F. 2021. — Phylogeography and demographic history of the black kite *Milvus migrans*, a widespread raptor in Eurasia, Australia and Africa. *Journal of Avian Biology* 52 (10): jav.02822: 1–19. <https://doi.org/10.1111/jav.02822>
- ANSARI H.A. & KAUL D. 1986. — Cytotaxonomic study in the order Falconiformes (Aves). *Zoologica Scripta* 15 (4): 351–356. <https://doi.org/10.1111/j.1463-6409.1986.tb00235.x>

- ARCTANDER P., FOLMER O. & FJELDSÅ J. 1996. — The phylogenetic relationships of Berthelot's Pipit *Anthus berthelotii* illustrated by DNA sequence data, with remarks on the genetic distance between Rock and Water Pipits *Anthus spinoletta*. *Ibis* 138 (2): 263–272. <https://doi.org/10.1111/j.1474-919X.1996.tb04338.x>
- AVISE J.C. 2000. — Cladists in Wonderland. *Evolution* 54 (5): 1828–1832. <https://doi.org/10.1111/j.0014-3820.2000.tb00728.x>
- AVISE J.C., ARNOLD J., BALL R.M., BERMINGHAM E., LAMB T., NEIGEL J.E., REEB C.A. & SAUNDERS N.C. 1987. — Intraspecific phylogeography: The mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics* 18 (1): 489–522. <https://doi.org/10.1146/annurev.es.18.110187.002421>
- AVISE J.C., NELSON W.S. & SIBLEY C.G. 1994. — DNA sequence support for a close phylogenetic relationship between some storks and New World vultures. *Proceedings of the National Academy of Sciences of the United States of America* 91 (11): 5173–5177. <https://doi.org/10.1073/pnas.91.11.5173>
- BANDELT H.J., FORSTER P. & RÖHL A. 1999. — Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution* 16 (1): 37–48. <https://doi.org/10.1093/oxfordjournals.molbev.a026036>
- BANGS O. & PENARD T.E. 1920. — Two new American hawks. *Proceedings of the New England Zoölogical Club* 7: 45–47.
- BANGS O. & PETERS J.L. 1928. — Birds collected by Dr. Joseph F. Rock in Western Kansu and Eastern Tibet. *Bulletin of the Museum of Comparative Zoology* 68 (7): 311–382.
- VAN DER BANK F.H., ENGELBRECHT G.D., SAUER-GÜRTH H., WINK M. & MULDER P.F. 1998. — Allozyme and DNA sequence data support speciation of northern and southern populations of silver catfish, *Schilbe intermedius* (Rüppel, 1832). *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology* 120 (3): 531–543. [https://doi.org/10.1016/s1095-6433\(98\)10063-6](https://doi.org/10.1016/s1095-6433(98)10063-6)
- BANKS J.C., PALMA R.L. & PATERSON A.M. 2006. — Cophylogenetic relationships between penguins and their chewing lice. *Journal of Evolutionary Biology* 19 (1): 156–166. <https://doi.org/10.1111/j.1420-9101.2005.00983.x>
- BARANOV A.A. 2013. — Processes of bird formation in the territory of Middle Siberia. *The Bulletin of Krasnoyarsk State Pedagogical University named after V.P. Astafyev* 25 (3): 212–214. (in Russian with English summary).
- BARROWCLOUGH G.F., CRACRAFT J., KLICKA J. & ZINK R.M. 2016. — How many kinds of birds are there and why does it matter? *PLOS ONE* 11 (11): e0166307: 1–15. <https://doi.org/10.1371/journal.pone.0166307>
- BARTH D., BERNHARD D., FRITZSCH G. & FRITZ U. 2004. — The freshwater turtle genus *Mauremys* (Testudines, Geoemydidae) – a textbook example of an east-west disjunction or a taxonomic

misconcept? *Zoologica Scripta* 33 (3): 213–221. <https://doi.org/10.1111/j.0300-3256.2004.00150.x>

BEDETTI C. & PAVIA M. 2013. — Early Pleistocene birds from Pirro Nord (Puglia, southern Italy). *Palaeontographica Abteilung A* 298 (1–6): 31–53. <https://doi.org/10.1127/pala/298/2013/31>

BED'HOM B., COULLIN P., GUILLIER-GENCIK Z., MOULIN S., BERNHEIM A. & VOLOBOUV V. 2003. — Characterization of the atypical karyotype of the black-winged kite *Elanus caeruleus* (Falconiformes: Accipitridae) by means of classical and molecular cytogenetic techniques. *Chromosome Research* 11 (4): 335–343. <https://doi.org/10.1023/A:1024091923939>

BELON DU MANS P. 1555. — *L'histoire de la natvre des oyseaux, avec levr descriptions, & naïfs portraits retirez du natvrel: escrite en sept livres*. Paris. 382 p. <https://doi.org/10.5962/bhl.title.78886>

BERNOR R., KORDOS L., ROOK L., AGUSTI J., ANDREWS P., ARMOUR-CHELU M., BEGUN D., CAMERON D., DAXNER-HÖCK G., BONIS L., EKART D., FESSAHA N., FORTELIUS M., FRANZEN J.L., GASPARIK M., GENTRY A., HEISSIG K., HERNYAK G., KAISER T., KOUFOS G., KROLOPP E., JANOSSY D., LLENAS M., MESZAROS L., MÜLLER P., RENNE P., ROCEK Z., ŞEN Ş., SCOTT R., SZYNDLAR Z., THEOBALD G., TOPAL G., WERDELIN L., UNGAR P. & ZIEGLER R. 2002. — Recent advances on multidisciplinary research at Rudabánya, Late Miocene (MN9), Hungary: a compendium. *Palaeontographia Italica* 89: 3–36.

BIERREGAARD R.O. JR. & KIRWAN G.M. 2020. — Pearl Kite (*Gampsonyx swainsonii*), in DEL HOYO J., ELLIOTT A., SARGATAL J., CHRISTIE D.A. & DE JUANA E. (eds.), *Handbook of the Birds of the World Alive*. Available from <https://www.hbw.com/node/52965> [accessed 3 May 2020]

BIERREGAARD R.O. JR., MARKS J.S., BOESMAN P. & KIRWAN G.M. 2020. — White-tailed Kite (*Elanus leucurus*), in DEL HOYO J., ELLIOTT A., SARGATAL J., CHRISTIE D.A. & DE JUANA E. (eds.), *Handbook of the Birds of the World Alive*. Available from <https://www.hbw.com/node/52968> [accessed 3 May 2020]

BIRDLIFE INTERNATIONAL 2004. — *Milvus migrans* Black Kite. Available from <http://datazone.birdlife.org/userfiles/file/Species/BirdsInEuropell/BiE2004Sp3355.pdf> [accessed 25 June 2022]

BIRDLIFE INTERNATIONAL 2019. — *Athene noctua* (amended version of 2018 assessment). The IUCN Red List of threatened species 2019: e.T22689328A155470112. Available from <https://www.iucnredlist.org/species/22689328/155470112> [accessed 24 June 2022]

BIRDLIFE INTERNATIONAL 2022. — IUCN Red List for birds. Available from <http://datazone.birdlife.org/> [accessed 2 July 2022]

BLONDEL J. & MOURER-CHAUVIRÉ C. 1998. — Evolution and history of the western Palaeartic avifauna. *Trends in Ecology & Evolution* 13 (12): 488–492. [https://doi.org/10.1016/s0169-5347\(98\)01461-x](https://doi.org/10.1016/s0169-5347(98)01461-x)

BLYTH E. 1850. — Conspectus of the ornithology of India, Burma, and the Malayan peninsula, inclusive of Sindh, Asám, Ceylon, and the Nicobar islands. *The Journal of the Asiatic Society of Bengal* 19 (4): 317–342.

- BONAPARTE C.L. 1840. — A new systematic arrangement of vertebrated animals. *Transactions of the Linnean Society of London* 18 (3): 247–304. <https://doi.org/10.1111/j.1095-8339.1838.tb00177.x>
- BONAPARTE C.L. 1850. — *Conspectus generum avium*. Lugduni Batavorum, E.J. Brill. 543 p. <https://doi.org/10.5962/bhl.title.70841>
- BRANDT J.F. 1853. — Die Gruppen und Gattungen der Raubvögel Russlands in exomorphischer und craniologischer Beziehung. *Journal für Ornithologie* 1 (1; 4): 178–195; 225–240.
- BRAVO G.A., SCHMITT C.J. & EDWARDS S.V. 2021. — What have we learned from the first 500 avian genomes? *Annual Review of Ecology, Evolution, and Systematics* 52 (1): 611–639. <https://doi.org/10.1146/annurev-ecolsys-012121-085928>
- BRISSON [M.J.] 1760. — *Ornithologie ou méthode contenant la division des oiseaux en ordres, sections, genres, especes & leurs variétés*. Vol. 1. Paris, J.-B. Bauche, i–xxiv, 1–526, i–xlix, i–lxxiii.
- BRODERS O., OSBORNE T. & WINK M. 2003. — A mtDNA phylogeny of bustards (family Otididae) based on nucleotide sequences of the cytochrome *b*-gene. *Journal für Ornithologie* 144 (2): 176–185. <https://doi.org/10.1007/BF02465645>
- BRODKORB P. 1960. — The skeleton and systematic position of *Gampsonyx*. *The Auk* 77 (1): 88–89. <https://doi.org/10.2307/4082395>
- BROWN L. 1979. — *Die Greifvögel: ihre Biologie und Ökologie*. Hamburg, Berlin, Paul Parey. 256 p.
- BROWN L. & AMADON D. 1968. — *Eagles, Hawks, and Falcons of the World*. Vol. 1. New York, McGraw-Hill Book Company. 414 p.
- BROWN W., PRAGER E.M., WANG A. & WILSON A. 1982. — Mitochondrial DNA sequences of primates: Tempo and mode of evolution. *Journal of Molecular Evolution* 18: 225–239. <https://doi.org/10.1007/BF01734101>
- BROWN L., URBAN E.K. & NEWMAN K. 1982. — *The Birds of Africa*. Vol. 1. London, New York, Academic Press, i–xiii, 1–521 p.
- BURTON J.A. 1985. — *Owls of the World: Their Evolution, Structure and Ecology*. Sydney, Hodder. 208 p.
- CAI Y., YUE B., JIANG W., XIE S., LI J. & ZHOU M. 2010. — DNA barcoding on subsets of three families in Aves. *Mitochondrial DNA* 21 (3–4): 132–137. <https://doi.org/10.3109/19401736.2010.494726>
- CAVALLI-SFORZA L.L. & EDWARDS A.W.F. 1967. — Phylogenetic analysis models and estimation procedures. *American Journal of Human Genetics* 19 (3): 233–257. <https://doi.org/10.2307/2406616>

- CHO Y.S., JUN J.H., KIM J.A., KIM H.-M., CHUNG O., KANG S.-G., PARK J.-Y., KIM HWA-J., KIM SUN., KIM HEE-J., JANG J., NA K.-J., KIM J., PARK S.G., LEE H.-Y., MANICA A., MINDELL D.P., FUCHS J., EDWARDS J.S., WEBER J.A., WITT C.C., YEO J.-H., KIM SOON. & BHAK J. 2019. — Raptor genomes reveal evolutionary signatures of predatory and nocturnal lifestyles. *Genome Biology* 20 (1): 181: 1–11. <https://doi.org/10.1186/s13059-019-1793-1>
- CHUBB C. 1918. — Descriptions of new forms from South and Central American birds – *Gampsonyx swainsonii magnus*, *G. s. leonæ*, *Falco rufogularis petoensis*, *F. r. pax*. *Bulletin of the British Ornithologists' Club* 39: 21–23.
- CLARK W.S. & BANKS R.C. 1992. — The taxonomic status of the White-tailed Kite. *The Wilson Bulletin* 104 (4): 571–579.
- CLARK W.S. & DAVIES R. 2018. — *African Raptors*. London, Helm. 336 p. (Helm Identification Guides).
- CLAY T. 1958. — Revisions of the Mallophaga genera. *Degeeriella* from the Falconiformes. *Bulletin of the British Museum (Natural History). Entomology* 7 (4): 121–207.
- CLEMENTS J.F., SCHULENBERG T.S., ILIFF M.J., BILLERMAN S.M., FREDERICKS T.A., SULLIVAN B.L. & WOOD C.L. 2019. — The eBird/Clements Checklist of birds of the World: v2019. Available from <https://www.birds.cornell.edu/clementschecklist/download/> [accessed 3 May 2020]
- CLOUET M. & WINK M. 2000. — The buzzards of Cape Verde *Buteo (buteo) bannermani* and Socotra *Buteo (buteo) spp.* : First result of a genetic analysis based on nucleotide sequences of the cytochrome b gene. *Alauda* 68 (1): 55–58.
- COLIHUEQUE N., GANTZ A., RAU J. & PARRAGUEZ M. 2015. — Genetic divergence analysis of the Common Barn Owl *Tyto alba* (Scopoli, 1769) and the Short-eared Owl *Asio flammeus* (Pontoppidan, 1763) from southern Chile using COI sequence. *ZooKeys* 534: 135–146. <https://doi.org/10.3897/zookeys.534.5953>
- CONVENTION ON INTERNATIONAL TRADE IN ENDANGERED SPECIES OF WILD FAUNA AND FLORA 2022. — Appendices I, II and III valid from 22 June 2022. Available from <https://cites.org/eng/app/appendices.php> [accessed 9 July 2022]
- CRACRAFT J. 1972. — The relationships of the higher taxa of birds: Problems in phylogenetic reasoning. *The Condor* 74 (4): 379–392. <https://doi.org/10.2307/1365890>
- CRACRAFT J. 1981. — Toward a phylogenetic classification of the recent birds of the World (class Aves). *The Auk* 98 (4): 681–714.
- CRACRAFT J. 1983. — Species concepts and speciation analysis, in JOHNSTON R.F. (ed.), *Current Ornithology*. New York, Springer US. p. 159–187. https://doi.org/10.1007/978-1-4615-6781-3_6
- CRACRAFT J. 1989. — Speciation and its ontology: The empirical consequences of alternative species concepts for understanding patterns and processes of differentiation, in OTTE D. &

ENDLER J.A. (eds.), *Speciation and its Consequences*. Sunderland, Sinauer Associates, Inc. p. 28–59.

CRAMP S., BROOKS D.J., DUNN E., GILLMOR R., HOLLOM P.A.D., HUDSON R., NICHOLSON E.M., OGILVIE M.A., OLNEY P.J.S., ROSELAAR C.S., SIMMONS K.E.L., VOOUS K.H., WALLACE D.I.M., WATTEL J. & WILSON M.G. 1985. — *Handbook of the Birds of Europe, the Middle East and North Africa*. Vol. 4. Oxford, New York, Oxford University Press. 960 p.

CRAMP S., SIMMONS K.E.L., GILLMOR R., HOLLOM P.A.D., HUDSON R., NICHOLSON E.M., OGILVIE M.A., OLNEY P.J.S., ROSELAAR C.S., VOOUS K.H., WALLACE D.I.M. & WATTEL J. 1980. — *Handbook of the Birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic*. Vol. 2. Oxford, London, New York, Oxford University Press. 695 p.

CUVIER [G.] 1817. — *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Vol. 1. Paris, Deterville, i–xxxvii, 1–588.

DARRIBA D., TABOADA G.L., DOALLO R. & POSADA D. 2012. — jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9 (8): 772. <https://doi.org/10.1038/nmeth.2109>

DE BOER L.E.M. & SINO O R.P. 1984. — A karyological study of Accipitridae (Aves: Falconiformes), with karyotypic descriptions of 16 species new to cytology. *Genetica* 65 (1): 89–107. <https://doi.org/10.1007/BF00056767>

DEBUS S. 2004. — Relationships of the Elanus kites. *Boobook* 22 (1): 8.

DEBUS S., KIRWAN G.M., CHRISTIE D.A. & MARKS J.S. 2020a. — Letter-winged Kite (*Elanus scriptus*), in DEL HOYO J., ELLIOTT A., SARGATAL J., CHRISTIE D.A. & DE JUANA E. (eds.), *Handbook of the Birds of the World Alive*. Available from <https://www.hbw.com/node/52969> [accessed 3 May 2020]

DEBUS S., KIRWAN G.M. & MARKS J.S. 2020b. — Black-shouldered Kite (*Elanus axillaris*), in DEL HOYO J., ELLIOTT A., SARGATAL J., CHRISTIE D.A. & DE JUANA E. (eds.), *Handbook of the Birds of the World Alive*. Available from <https://www.hbw.com/node/52967> [accessed 3 May 2020]

DEMENTIEV G.P. 1936. — [Order Diurnal raptors], in BUTURLIN S.A. & GLADKOV N.A. (eds.), [*Complete Guide of the Birds of USSR*]. Vol. 3. Moskva, Leningrad, KOIZ. p. 42–100. (in Russian).

DEMENTIEV G.P. 1951a. — [Order Owls], in DEMENTIEV G.P. & GLADKOV N.A. (eds.), [*Birds of the Soviet Union*]. Vol. 1. Moskva, Sovetskaja Nauka. p. 342–429. (in Russian).

DEMENTIEV G.P. 1951b. — [Order Raptors], in DEMENTIEV G.P. & GLADKOV N.A. (eds.), [*Birds of the Soviet Union*]. Vol. 1. Moskva, Sovetskaja Nauka. p. 70–341. (in Russian).

DICKINSON E. C. & REMSEN J. V. JR. (eds.). 2013. — *The Howard and Moore Complete Checklist of the Birds of the World. Volume 1: Non-passerines*. Eastbourne, Aves Press. 461 p.

- DIMITRIOU A.C., FORCINA G., PAPAZOGLOU C., PANAYIDES P., GUERRINI M., CRABTREE A., BARBANERA F. & SFENTHOURAKIS S. 2017. — DNA barcoding of bird species in Cyprus: a tool for conservation purposes. *Bird Conservation International* 27 (4): 483–494. <https://doi.org/10.1017/S0959270916000472>
- DOLINAY M. 2015. — *Genetická struktura populací dvou druhů sympatricky se vyskytujících luňáků (Milvus spp.)*. Diplomová práce, Masarykova univerzita, Brno, 67 p.
- DOYLE J.M., KATZNER T.E., BLOOM P.H., JI Y., WIJAYAWARDENA B.K. & DEWOODY J.A. 2014. — The genome sequence of a widespread apex predator, the Golden Eagle (*Aquila chrysaetos*). *PLOS ONE* 9 (4): e95599: 1–11. <https://doi.org/10.1371/journal.pone.0095599>
- DROVETSKI S.V., SEMENOV G., RED'KIN Y.A., SOTNIKOV V.N., FADEEV I.V. & KOBLIK E.A. 2015. — Effects of asymmetric nuclear introgression, introgressive mitochondrial sweep, and purifying selection on phylogenetic reconstruction and divergence estimates in the pacific clade of *Locustella* warblers. *PLOS ONE* 10 (4): e0122590: 1–14. <https://doi.org/10.1371/journal.pone.0122590>
- DRUMMOND A.J., HO S.Y.W., PHILLIPS M.J. & RAMBAUT A. 2006. — Relaxed phylogenetics and dating with confidence. *PLOS Biology* 4 (5): e88: 699–710. <https://doi.org/10.1371/journal.pbio.0040088>
- DRUMMOND A.J., SUCHARD M.A., XIE D. & RAMBAUT A. 2012. — Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* 29 (8): 1969–1973. <https://doi.org/10.1093/molbev/mss075>
- ECHI P.C., SURESH K.U., GEORGE S., RATHEESH R.V., EZEONU I.M., EJERE V.C., EYO J.E. & NWANI C.D. 2015. — Molecular resolution of some West African Birds using DNA barcoding. *Environment Conservation Journal* 16 (1&2): 87–92. <https://doi.org/10.36953/ECJ.2015.161214>
- EDGAR R.C. 2004. — MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32 (5): 1792–1797. <https://doi.org/10.1093/nar/gkh340>
- ETHERINGTON G.J. & MOBLEY J.A. 2016. — Molecular phylogeny, morphology and life-history comparisons within *Circus cyaneus* reveal the presence of two distinct evolutionary lineages. *Avian Research* 7 (1): 17: 1–12. <https://doi.org/10.1186/s40657-016-0052-3>
- FAIN M.G. & HOUDE P. 2004. — Parallel radiations in the primary clades of birds. *Evolution* 58 (11): 2558–2573. <https://doi.org/10.1111/j.0014-3820.2004.tb00884.x>
- FARRIS J.S. 1989. — The retention index and rescaled consistency index. *Cladistics* 5 (4): 417–419. <https://doi.org/10.1111/j.1096-0031.1989.tb00573.x>
- FELLER W. 1939. — Die Grundlagen der Volterraschen Theorie des Kampfes ums Dasein in wahrscheinlichkeitstheoretischer Behandlung. *Acta Biotheoretica* 5 (1): 11–40. <https://doi.org/10.1007/BF01602932>

FELSENSTEIN J. 1981. — Evolutionary trees from DNA sequences: A maximum likelihood approach. *Journal of Molecular Evolution* 17 (6): 368–376. <https://doi.org/10.1007/BF01734359>

FELSENSTEIN J. 1985. — Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39 (4): 783–791. <https://doi.org/10.2307/2408678>

FENG S., STILLER J., DENG Y., ARMSTRONG J., FANG Q., REEVE A.H., XIE D., CHEN G., GUO C., FAIRCLOTH B.C., PETERSEN B., WANG Z., ZHOU Q., DIEKHANS M., CHEN W., ANDREU-SÁNCHEZ S., MARGARYAN A., HOWARD J.T., PARENT C., PACHECO G., SINDING M.-H.S., PUETZ L., CAVILL E., RIBEIRO Â.M., ECKHART L., FIELDSÅ J., HOSNER P.A., BRUMFIELD R.T., CHRISTIDIS L., BERTELSEN M.F., SICHERITZ-PONTEN T., TIETZE D.T., ROBERTSON B.C., SONG G., BORGIA G., CLARAMUNT S., LOVETTE I.J., COWEN S.J., NJOROGÉ P., DUMBACHER J.P., RYDER O.A., FUCHS J., BUNCE M., BURT D.W., CRACRAFT J., MENG G., HACKETT S.J., RYAN P.G., JØNSSON K.A., JAMIESON I.G., DA FONSECA R.R., BRAUN E.L., HOUDE P., MIRARAB S., SUH A., HANSSON B., PONNIKAS S., SIGEMAN H., STERVANDER M., FRANDSEN P.B., VAN DER ZWAN H., VAN DER SLUIS R., VISSER C., BALAKRISHNAN C.N., CLARK A.G., FITZPATRICK J.W., BOWMAN R., CHEN N., CLOUTIER A., SACKTON T.B., EDWARDS S.V., FOOTE D.J., SHAKYA S.B., SHELDON F.H., VIGNAL A., SOARES A.E.R., SHAPIRO B., GONZÁLEZ-SOLÍS J., FERRER-OBIO J., ROZAS J., RIUTORT M., TIGANO A., FRIESEN V., DALÉN L., URRUTIA A.O., SZÉKELY T., LIU Y., CAMPANA M.G., CORVELO A., FLEISCHER R.C., RUTHERFORD K.M., GEMMELL N.J., DUSSEX N., MOURITSEN H., THIELE N., DELMORE K., LIEDVOGEL M., FRANKE A., HOEPPNER M.P., KRONE O., FUDICKAR A.M., MILÁ B., KETTERSON E.D., FIDLER A.E., FRIIS G., PARODY-MERINO Á.M., BATTLE P.F., COX M.P., LIMA N.C.B., PROSDOCIMI F., PARCHMAN T.L., SCHLINGER B.A., LOISELLE B.A., BLAKE J.G., LIM H.C., DAY L.B., FUXJAGER M.J., BALDWIN M.W., BRAUN M.J., WIRTHLIN M., DIKOW R.B., RYDER T.B., CAMENISCH G., KELLER L.F., DACOSTA J.M., HAUBER M.E., LOUDER M.I.M., WITT C.C., MCGUIRE J.A., MUDGE J., MEGNA L.C., CARLING M.D., WANG B., TAYLOR S.A., DEL-RIO G., ALEIXO A., VASCONCELOS A.T.R., MELLO C.V., WEIR J.T., HAUSSLER D., LI Q., YANG H., WANG J., LEI F., RAHBEK C., GILBERT M.T.P., GRAVES G.R., JARVIS E.D., PATEN B. & ZHANG G. 2020. — Dense sampling of bird diversity increases power of comparative genomics. *Nature* 587 (7833): 252–257. <https://doi.org/10.1038/s41586-020-2873-9>

FERGUSON-LEES J. & CHRISTIE D.A. 2001. — *Raptors of the World*. Boston, Houghton Mifflin. 992 p.

FINLAYSON C. 2011. — *Avian Survivors: The History and Biogeography of Palearctic Birds*. London, Bloomsbury Publishing. 321 p. (Poyser Monographs).

FITZINGER L.J. 1856. — *Über das System und die Charakteristik der natürlichen Familien der Vögel*. Wien, Kais. Kön. Hof- und Staatsdruckerei. 38 p. <https://doi.org/10.5962/bhl.title.14130>

FLUXUS-ENGINEERING.COM 2020. — Free phylogenetic Network software. Available from <https://fluxus-engineering.com/sharenet.htm> [accessed 5 June 2022]

FORERO M.G., DONÁZAR J.A., BLAS J. & HIRALDO F. 1999. — Causes and consequences of territory change and breeding dispersal distance in the Black Kite. *Ecology* 80 (4): 1298–1310. <https://doi.org/10.2307/177076>

- FORSTER P., TORRONI A., RENFREW C. & RÖHL A. 2001. — Phylogenetic star contraction applied to Asian and Papuan mtDNA evolution. *Molecular Biology and Evolution* 18 (10): 1864–1881. <https://doi.org/10.1093/oxfordjournals.molbev.a003728>
- FRIEDMANN H. 1950. — *The Birds of North and Middle America*. Vol. 11. Washington, U.S. Government Printing Office, i–vi, 1–793. (United States National Museum; 50).
- FRIEDMANN V.S. 2012. — Hardship of the biological species concept and ways of its overcoming (on example of birds). *Berkut* 21 (1–2): 127–182. (in Russian with English summary).
- FRITZ U., AUER M., BERTOLERO A., CHEYLAN M., FATTIZZO T., HUNSDORFER A.K., MARTIN SAMPAYO M., PRETUS J.L., ŠIROKÝ P. & WINK M. 2006. — A rangewide phylogeography of Hermann's tortoise, *Testudo hermanni* (Reptilia: Testudines: Testudinidae): implications for taxonomy. *Zoologica Scripta* 35 (5): 531–543. <https://doi.org/10.1111/j.1463-6409.2006.00242.x>
- FU Y.X. & LI W.H. 1993. — Statistical tests of neutrality of mutations. *Genetics* 133 (3): 693–709. <https://doi.org/10.1093/genetics/133.3.693>
- FÜRBRINGER M. 1888. — *Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane*. Vol. 2. Amsterdam, Van Holkema, 837–1751.
- GADOW H. 1893. — *Dr. H.G. Bronn's Klassen und Ordnungen des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bild*. Vol. 6, 4, II. Leipzig, C. F. Winter'sche Verlagshandlung, I–VI, 1–304.
- GALUSHIN V.M. 1971. — A huge urban population of birds of prey in Delhi, India. *Ibis* 113 (4): 522. <https://doi.org/10.1111/j.1474-919X.1971.tb05189.x>
- GARROD A.H. 1874. — On certain muscles of birds and their value in classification. Part II. *Proceedings of the Zoological Society of London*: 111–123. <https://doi.org/10.1111/j.1096-3642.1874.tb02459.x>
- GEGECHKORI A.M. 2011. — The results of biogeographical study of Arcto-Tertiary refugia (Colchis and Talysh) of the Southern Caucasus. *Annals of Agrarian Science* 9 (1): 16–33.
- GERNHARD T. 2008. — The conditioned reconstructed process. *Journal of Theoretical Biology* 253 (4): 769–778. <https://doi.org/10.1016/j.jtbi.2008.04.005>
- GILL F.B. & DONSKER D.B. (eds.) 2020. — IOC World Bird List 10.1. <https://doi.org/10.14344/IOC.ML.10.1>
- GILL, F. B., DONSKER, D. B. & RASMUSSEN, P. (eds.). 2022. — IOC World Bird List – Version 12.1 <https://doi.org/10.14344/IOC.ML.12.1>
- GLUTZ VON BLOTZHEIM U.N. & BAUER K.M. 1980. — *Handbuch der Vögel Mitteleuropas*. Vol. 9. Wiesbaden, Akademische Verlagsgesellschaft. 1148 p.

GMELIN J.F. 1788. — *Caroli a Linné, systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Vol. 1. Lipsiae, G.E. Beer. 500 p. <https://doi.org/10.5962/bhl.title.36932>

GRAY G.R. 1840. — *A List of the Genera of Birds, With Their Synonyma an Indication of the Typical Species of Each Genus*. [London], R. and J.E. Taylor, i-vii, i-ii, 1–80. <https://doi.org/10.5962/bhl.title.13777>

GRAY G.R. 1869. — *Hand-List of Genera and Species of Birds, Distinguishing Those Contained in the British Museum*. Vol. 1. London, Taylor and Francis, i-xx, 1–404. <https://doi.org/10.5962/bhl.title.54948>

GRIFFITHS C.S. 1994. — Monophyly of the Falconiformes based on syringeal morphology. *The Auk* 111 (4): 787–805. <https://doi.org/10.2307/4088811>

GRIFFITHS C.S. 1997. — Correlation of functional domains and rates of nucleotide substitution in cytochrome *b*. *Molecular Phylogenetics and Evolution* 7 (3): 352–365. <https://doi.org/10.1006/mpev.1997.0404>

GRIFFITHS C.S., BARROWCLOUGH G.F., GROTH J.G. & MERTZ L.A. 2007. — Phylogeny, diversity, and classification of the Accipitridae based on DNA sequences of the RAG-1 exon. *Journal of Avian Biology* 38 (5): 587–602. <https://doi.org/10.1111/j.0908-8857.2007.03971.x>

GROSSHEIM A.A. 1948. — [*The Vegetation Cover of the Caucasus*]. Moskva, Izdatel'stvo Moskovskogo obshchestva ispytateley prirody. 267 p. (New Series. Botany Branch; 4 (XII)). (in Russian).

GROTH J.G. & BARROWCLOUGH G.F. 1999. — Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. *Molecular Phylogenetics and Evolution* 12 (2): 115–123. <https://doi.org/10.1006/mpev.1998.0603>

GUERRA C., BOVER P. & ALCOVER J.A. 2012. — A new species of extinct little owl from the Pleistocene of Mallorca (Balearic Islands). *Journal of Ornithology* 153 (2): 347–354. <https://doi.org/10.1007/s10336-011-0749-3>

GUINDON S., DUFAYARD J.-F., LEFORT V., ANSIMOVA M., HORDIJK W. & GASCUEL O. 2010. — New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology* 59 (3): 307–321. <https://doi.org/10.1093/sysbio/syq010>

GUINDON S. & GASCUEL O. 2003. — A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood, in RANNALA B. (ed.). *Systematic Biology* 52 (5): 696–704. <https://doi.org/10.1080/10635150390235520>

HACKETT S.J., KIMBALL R.T., REDDY S., BOWIE R.C.K., BRAUN E.L., BRAUN M.J., CHOJNOWSKI J.L., COX W.A., HAN K.-L., HARSHMAN J., HUDDLESTON C.J., MARKS B.D., MIGLIA K.J., MOORE W.S., SHELDON F.H., STEADMAN D.W., WITT C.C. & YURI T. 2008. — A phylogenomic study of birds reveals their evolutionary history. *Science* 320 (5884): 1763–1768. <https://doi.org/10.1126/science.1157704>

- HAECKEL E. 1866. — *Generelle Morphologie der Organismen*. Vol. 2. Berlin, G. Reimer, I–CLX, 1–462.
- HALL T.A. 1999. — BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- HARR B. & PRICE T. 2012. — Speciation: Clash of the genomes. *Current Biology* 22 (24): R1044–R1046. <https://doi.org/10.1016/j.cub.2012.11.005>
- HARRIS T. & WALTERS C. 1982. — Chromosomal sexing of the Black Shouldered Kite (*Elanus caeruleus*) (Aves: Accipitridae). *Genetica* 60: 19–20.
- HARRISON C.J.O. & WALKER C.A. 1976. — Birds of the British Upper Eocene. *Zoological Journal of the Linnean Society* 59 (4): 323–351. <https://doi.org/10.1111/j.1096-3642.1976.tb01017.x>
- HARTERT E. 1914. — *Die Vögel der paläarktischen Fauna. Systematische Übersicht der in Europa, Nord-Asien und der Mittelmeerregion vorkommenden Vögel*. Vol. 9. Berlin, R. Friedländer und Sohn, 1089–1216.
- HARTERT E. 1925. — Types of birds in the Tring Museum. B. Types in the general collection. VI. *Novitates Zoologicae* 32 (3): 259–276.
- HASEGAWA M., KISHINO H. & YANO T. 1985. — Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution* 22 (2): 160–174. <https://doi.org/10.1007/BF02101694>
- HBW & BIRDLIFE INTERNATIONAL 2021. — Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world. Version 6. Available from http://datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife_Checklist_v6_Dec21.zip [accessed 2 July 2022]
- HEIDRICH P. & WINK M. 1998. — Phylogenetic relationships in holarctic owls (Order Strigiformes): Evidence from nucleotide sequences of the mitochondrial cytochrome b gene, in CHANCELLOR R.D., MEYBURG B.-U. & FERRERO J.J. (eds.), *Holarctic birds of prey: Proceedings of an international conference; Actas del Congreso Internacional sobre Rapaces del Holártico; Badajoz, Extremadura (Spain), 17-22 Abril 1995*. Berlin, Mérida. WWGBP, ADENEX. p. 73–87.
- HELBIG A.J., KOCUM A., SEIBOLD I. & BRAUN M.J. 2005. — A multi-gene phylogeny of aquiline eagles (Aves: Accipitriformes) reveals extensive paraphyly at the genus level. *Molecular Phylogenetics and Evolution* 35 (1): 147–164. <https://doi.org/10.1016/j.ympev.2004.10.003>
- HELLMAYR C.E. & CONOVER B. 1949. — *Catalogue of Birds of the Americas and the Adjacent Islands in Field Museum of Natural History and Including all Species and Subspecies Known to Occur in North America, Mexico, Central America, South America, the West Indies, and Islands of the Caribbean Sea, the Galapagos Archipelago, and Other Islands Which May Be Included on Account of Their Faunal Affinities*. Vol. 13. Chicago, Field Museum Press, i–vi, 1–358. (Zoological series; 1, 4). <https://doi.org/10.5962/bhl.title.5570>

- HENEBERG P., DOLINAY M., MATUŠÍK H., PFEIFFER T., NACHTIGALL W., BIZOS J., ŠIMČÍKOVÁ D. & LITERÁK I. 2016. — Conservation of the Red Kite *Milvus milvus* (Aves: Accipitriformes) is not affected by the establishment of a broad hybrid zone with the Black Kite *Milvus migrans migrans* in Central Europe. *PLOS ONE* 11 (7): e0159202: 1–22. <https://doi.org/10.1371/journal.pone.0159202>
- HENNIG W. 1950. — *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin Ost, Deutscher Zentralverlag. 396 p.
- HILLE S. & THIOLLAY J. 2000. — The imminent extinction of the Kites *Milvus milvus fasciicauda* and *Milvus m. migrans* on the Cape Verde Islands. *Bird Conservation International* 10 (4): 361–369. <https://doi.org/10.1017/S0959270900000319>
- HOLDER M. & LEWIS P.O. 2003. — Phylogeny estimation: traditional and Bayesian approaches. *Nature Reviews Genetics* 4 (4): 275–284. <https://doi.org/10.1038/nrg1044>
- HOLM S.R. & SVENNING J.-C. 2014. — 180,000 years of climate change in Europe: Avifaunal responses and vegetation implications. *PLOS ONE* 9 (4): e94021: 1–14. <https://doi.org/10.1371/journal.pone.0094021>
- HOLT D.W., BERKLEY R., DEPPE C., ENRÍQUEZ ROCHA P.L., PETERSEN J.L., RANDEL SALAZAR J.L., SEGARS K.P. & WOOD K.L. 1999. — Little Owl *Athene noctua*, in DEL HOYO J., ELLIOTT A. & SARGATAL J. (eds.), *Handbook of the Birds of the World*. Vol. 5. Barcelona, Lynx Edicions. p. 225–226.
- HOWARD R. & MOORE A. 1980. — *A Complete Checklist of the Birds of the World*. Oxford, Oxford University Press. 728 p.
- DEL HOYO J., ELLIOTT A. & SARGATAL J. (eds.). 1994. — *Handbook of the Birds of the World*. Vol. 2. Barcelona, Lynx Edicions. 638 p.
- DEL HOYO J., ELLIOTT A. & SARGATAL J. (eds.). 1999. — *Handbook of the Birds of the World*. Vol. 5. Barcelona, Lynx Edicions. 760 p.
- HUGHES J., KENNEDY M., JOHNSON K.P., PALMA R.L. & PAGE R.D.M. 2007. — Multiple cophylogenetic analyses reveal frequent cospeciation between pelecaniform birds and *Pectinopygus* lice. *Systematic Biology* 56 (2): 232–251. <https://doi.org/10.1080/10635150701311370>
- HURVICH C.M. & TSAI C.-L. 1993. — A corrected Akaike Information Criterion for vector autoregressive model selection. *Journal of Time Series Analysis* 14 (3): 271–279. <https://doi.org/10.1111/j.1467-9892.1993.tb00144.x>
- HUSAIN K.Z. 1959. — Notes on the taxonomy and zoogeography of the genus *Elanus*. *The Condor* 61 (2): 153–154.
- HUXLEY T.H. 1867. — On the classification of birds; and on the taxonomic value of the modifications of certain of the cranial bones observable in that class. *Proceedings of the Zoological Society of London*: 415–472.

ILLIGER C. 1811. — *Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis, eorumque versione germanica*. Berolini, C. Salfeld, I–XVIII, 1–301. <https://doi.org/10.5962/bhl.title.106965>

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE 1999. — *International code of zoological nomenclature = Code internationale de nomenclature zoologique*. London, International Trust for Zoological Nomenclature, Natural History Museum. 306 p.

IONSTONUS I. 1650. — *Historiæ naturalis de auibus libri VI. Cum æneis figuris*. Francofurti ad Moenvm, M. Merian. 227 p.

IRESTEDT M., JOHANSSON U.S., PARSONS T.J. & ERICSON P.G.P. 2001. — Phylogeny of major lineages of suboscines (Passeriformes) analysed by nuclear DNA sequence data. *Journal of Avian Biology* 32 (1): 15–25. <https://doi.org/10.1034/j.1600-048X.2001.320103.x>

IRISOVA N.L. & NIKULKIN V.N. 2006. — [To the distribution of the Little Owl in Western Siberia], in RIABITSEV V.K. (ed.), [*Materials for the Distribution of birds in the Ural, Preural and Western Siberia*]. Yekaterinburg, Izdatel'stvo Ural'skogo universiteta. p. 123–124. (in Russian).

JÁNOSSY D. 1978. — Plio-Pleistocene bird remains from the Carpathian Basin III. Strigiformes, Falconiformes, Caprimulgiformes, Apodiformes. *Aquila* 84: 9–36.

JARVIS E.D., MIRARAB S., ABERER A.J., LI B., HOUDE P., LI C., HO S.Y.W., FAIRCLOTH B.C., NABHOLZ B., HOWARD J.T., SUH A., WEBER C.C., FONSECA R.R.D., LI J., ZHANG F., LI H., ZHOU L., NARULA N., LIU L., GANAPATHY G., BOUSSAU B., BAYZID M.S., ZAVIDOVYCH V., SUBRAMANIAN S., GABALDÓN T., CAPELLA-GUTIÉRREZ S., HUERTA-CEPAS J., REKEPALLI B., MUNCH K., SCHIERUP M., LINDOW B., WARREN W.C., RAY D. & GREEN R.E. 2014. — Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* 346 (6215): 1320–1331. <https://doi.org/10.1126/science.1253451>

JEON H.S., MYEONG H., KANG S.-G., KIM J.A., LEE S.-H., LEE M.-Y. & AN J. 2018. — The mitochondrial genome of *Milvus migrans* (Aves, Accipitriformes, Accipitridae), an endangered species from South Korea. *Mitochondrial DNA Part B* 3 (2): 498–499. <https://doi.org/10.1080/23802359.2018.1450678>

JOHNS G.C. & AVISE J.C. 1998. — A comparative summary of genetic distances in the vertebrates from the mitochondrial cytochrome *b* gene. *Molecular Biology and Evolution* 15 (11): 1481–1490. <https://doi.org/10.1093/oxfordjournals.molbev.a025875>

JOHNSEN A., RINDAL E., ERICSON P.G.P., ZUCCON D., KERR K.C.R., STOECKLE M.Y. & LIFJELD J.T. 2010. — DNA barcoding of Scandinavian birds reveals divergent lineages in trans-Atlantic species. *Journal of Ornithology* 151 (3): 565–578. <https://doi.org/10.1007/s10336-009-0490-3>

JOHNSON J.A., WATSON R.T. & MINDELL D.P. 2005. — Prioritizing species conservation: does the Cape Verde kite exist? *Proceedings of the Royal Society B: Biological Sciences* 272 (1570): 1365–1371. <https://doi.org/10.1098/rspb.2005.3098>

JOLLIE M. 1977a. — A contribution to the morphology and phylogeny of the Falconiformes (part II). *Evolutionary Theory* 2: 115–208.

- JOLLIE M. 1977b. — A contribution to the morphology and phylogeny of the Falconiformes (part III). *Evolutionary Theory* 2: 209–300.
- JOLLIE M. 1977c. — A contribution to the morphology and phylogeny of the Falconiformes (part IV). *Evolutionary Theory* 3: 1–141.
- JØNSSON K.A., POULSEN M.K., HARYOKO T., REEVE A.H. & FABRE P.-H. 2013. — A new species of masked-owl (Aves: Strigiformes: Tytonidae) from Seram, Indonesia. *Zootaxa* 3635 (1): 51–61. <https://doi.org/10.11646/zootaxa.3635.1.5>
- KANG H., LI B., MA X. & XU Y. 2018. — Evolutionary progression of mitochondrial gene rearrangements and phylogenetic relationships in Strigidae (Strigiformes). *Gene* 674: 8–14. <https://doi.org/10.1016/j.gene.2018.06.066>
- KARTASHYOV N.N. 1974. — [*Systematics of the Birds*]. Moskva, Vysshaya Shkola. 362 p. (in Russian).
- KARYAKIN I.V. 2017. — Problem of identification of Eurasian subspecies of the Black Kite and records of the Pariah Kite in Southern Siberia, Russia. *Raptors Conservation* (34): 49–67. <https://doi.org/10.19074/1814-8654-2017-34-49-67>
- KAUP J.J. 1844. — *Classification der Säugethiere und Vögel*. Darmstadt, C. W. Leske, I–X, 1–144, I–VI, 1–14. <https://doi.org/10.5962/bhl.title.51492>
- KAUSHIK T.K. & GUPTA R.C. 2014. — Black Kite populations are suffering declining trends in Kurukshetra and likely to get further depleted: An analysis of causes. *Journal of Tropical Life Science* 4 (1): 14–18. <https://doi.org/10.11594/jtls.04.01.03>
- KEMP A.C., KIRWAN G.M., MARKS J.S., MOTIS A. & GARCIA E.F.J. 2020. — Black-winged Kite (*Elanus caeruleus*), in DEL HOYO J., ELLIOTT A., SARGATAL J., CHRISTIE D.A. & DE JUANA E. (eds.), *Handbook of the Birds of the World Alive*. Available from <https://www.hbw.com/node/52966> [accessed 3 May 2020]
- KERR K.C.R., BIRKS S.M., KALYAKIN M.V., RED’KIN Y.A., KOBLIK E.A. & HEBERT P.D.N. 2009a. — Filling the gap – COI barcode resolution in eastern Palearctic birds. *Frontiers in Zoology* 6 (1): 29: 1–13. <https://doi.org/10.1186/1742-9994-6-29>
- KERR K.C.R., LIJMAER D.A., BARREIRA A.S., HEBERT P.D.N. & TUBARO P.L. 2009b. — Probing evolutionary patterns in neotropical birds through DNA barcodes. *PLOS ONE* 4 (2): e4379, 1–6. <https://doi.org/10.1371/journal.pone.0004379>
- KERR K.C.R., STOECKLE M.Y., DOVE C.J., WEIGT L.A., FRANCIS C.M. & HEBERT P.D.N. 2007. — Comprehensive DNA barcode coverage of North American birds. *Molecular Ecology Notes* 7 (4): 535–543. <https://doi.org/10.1111/j.1471-8286.2007.01670.x>
- KESSLER J.E. 2018. — Evolution and presence of diurnal predatory birds in the Carpathian Basin. *Ornis Hungarica* 26 (1): 102–123. <https://doi.org/10.1515/orhu-2018-0008>
- KIMURA M. 1979. — The neutral theory of molecular evolution. *Scientific American* 241 (5): 98–126. <https://doi.org/10.1038/scientificamerican1179-98>

- KIMURA M. 1980. — A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16 (2): 111–120. <https://doi.org/10.1007/BF01731581>
- KL[EINSCHMIDT] O. 1907. — Zum geographischen Variieren von *Strix Athene*. *Falco* 3: 63–67.
- KOCUM A. 2006. — *Phylogenie der Accipitriformes (Greifvögel) anhand verschiedener nuklearer und mitochondrialer DNA-Sequenzen*. Inauguraldissertation zur Erlangung des akademischen Grades doctor rerum naturalium (Dr. rer. nat.), Greifswald, Ernst-Moritz-Arndt-Universität Greifswald, i–iv, 1–249.
- KOLBIN V.A. 2014. — [Some aspects of the formation of avifauna of the Palearctic]. *The Russian Journal of Ornithology* 23 (1053): 3028–3037. (in Russian).
- KÖNIG C. & WEICK F. 2008. — *Owls of the World*. London, Cristopher Helm. 528 p.
- KOPARDE P., MEHTA P., REDDY S., RAMAKRISHNAN U., MUKHERJEE S. & ROBIN V.V. 2018. — The critically endangered forest owlet *Heteroglaux blewitti* is nested within the currently recognized *Athene* clade: A century-old debate addressed. *PLOS ONE* 13 (2): e0192359. <https://doi.org/10.1371/journal.pone.0192359>
- KRALJ J. & BARIŠIĆ S. 2013. — Rare birds in Croatia. Third report of the Croatian rarities committee. *Natura Croatica* 22 (2): 375–396.
- KRAUS R.H.S. & WINK M. 2015. — Avian genomics: fledging into the wild! *Journal of Ornithology* 156 (4): 851–865. <https://doi.org/10.1007/s10336-015-1253-y>
- KUHLMAN F. 1987. — The demise of the Black-eared Kite *Milvus migrans* in Kobe, Japan. *Japanese Journal of Ornithology* 36 (2/3): 79–86. <https://doi.org/10.3838/jjo.36.79>
- KUNZ F., GAMAUF A., ZACHOS F.E. & HARING E. 2019. — Mitochondrial phylogenetics of the goshawk *Accipiter [gentilis]* superspecies. *Journal of Zoological Systematics and Evolutionary Research* 57 (4): 942–958. <https://doi.org/10.1111/jzs.12285>
- LA CEPEDE [B.G.E.] [1799]. — *Discours d'ouverture et de clôture du cours d'histoire naturelle des animaux vertébrés et à sang rouge*. Paris, Plassan. 57 p. <https://doi.org/10.5962/bhl.title.127486>
- DE LATTIN G. 1967. — *Grundriss der Zoogeographie*. Jena, Gustav Fischer. 602 p.
- LAVINIA P.D., KERR K.C.R., TUBARO P.L., HEBERT P.D.N. & LIJMAER D.A. 2016. — Calibrating the molecular clock beyond cytochrome *b*: assessing the evolutionary rate of COI in birds. *Journal of Avian Biology* 47 (1): 84–91. <https://doi.org/10.1111/jav.00766>
- LEFORT V., LONGUEVILLE J.-E. & GASCUEL O. 2017. — SMS: Smart Model Selection in PhyML. *Molecular Biology and Evolution* 34 (9): 2422–2424. <https://doi.org/10.1093/molbev/msx149>

- LEKUONA J.M. & URSUA C. 2009. — Mortalidad de aves en parques eólicos de Navarra (norte de España), in DE LUCAS M., JANSS G.F.E. & FERRER M. (eds.), *Aves y parques eólicos. Valoración del riesgo y atenuantes*. Quercus: 187–202.
- LERNER H.R.L. & MINDELL D.P. 2005. — Phylogeny of eagles, Old World vultures, and other Accipitridae based on nuclear and mitochondrial DNA. *Molecular Phylogenetics and Evolution* 37 (2): 327–346. <https://doi.org/10.1016/j.ympev.2005.04.010>
- LI JING, CUI Y., JIANG J., YU J., NIU L., DENG J., SHEN F., ZHANG L., YUE B. & LI JING. 2017. — Applying DNA barcoding to conservation practice: a case study of endangered birds and large mammals in China. *Biodiversity and Conservation* 26 (3): 653–668. <https://doi.org/10.1007/s10531-016-1263-y>
- LINNÆUS C. 1735. — *Systema naturæ, sive regna tria naturæ systematice proposita per classes, ordines, genera, & species*. Lugduni Batavorum, T. Haak. [12 p.]
- LINNÆUS C. 1758. — *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Vol. 1. Holmiæ, L. Salvius. 823 p.
- LITERÁK I., SKYRPAN M. & ANDREYENKOVA N.G. 2020. — A mixed pair of black and red kites in Ukraine, including DNA analysis of hybrid offspring. *Biologia* 75 (7): 115–120. <https://doi.org/10.2478/s11756-019-00268-1>
- LOHMAN D.J., PRAWIRADILAGA D.M. & MEIER R. 2009. — Improved COI barcoding primers for Southeast Asian perching birds (Aves: Passeriformes). *Molecular Ecology Resources* 9 (1): 37–40. <https://doi.org/10.1111/j.1755-0998.2008.02221.x>
- LOUETTE M., HERREMANS M., NAGY Z., ROLAND L.-A.R., JORDAENS K., VAN HOUTD J., SONET G. & BREMAN F. 2011. — Frances's Sparrowhawk radiation on the Comoro Islands, in: SCHUCHMANN K.-L. (ed.), *Tropical Vertebrates in a Changing World*. Bonn, Zoologisches Forschungsmuseum Alexander Koenig: 133–143. (Bonner Zoologische Monographien; 57).
- LUO H., FANG W., LIN Q., CHEN X. & ZHOU X. 2022. — Characterization of the complete mitochondrial genome of *Elanus caeruleus* Desfontaines, 1789 (Accipitriformes: Accipitridae). *Mitochondrial DNA. Part B, Resources* 7 (4): 627–628. <https://doi.org/10.1080/23802359.2022.2060769>
- MAHMOOD M.T., MCLENACHAN P.A., GIBB G.C. & PENNY D. 2014. — Phylogenetic position of avian nocturnal and diurnal raptors. *Genome Biology and Evolution* 6 (2): 326–332. <https://doi.org/10.1093/gbe/evu016>
- MARGARYAN A., NOER C.L., RICHTER S.R., RESTRUP M.E., BÜLOW-HANSEN J.L., LEERHØI F., LANGKJÆR E.M.R., GOPALAKRISHNAN S., CARØE C., GILBERT M.T.P. & BOHMANN K. 2021. — Mitochondrial genomes of Danish vertebrate species generated for the national DNA reference database, DNAMark. *Environmental DNA* 3 (2): 472–480. <https://doi.org/10.1002/edn3.138>

- MAYR E. 1974. — Cladistic analysis or cladistic classification? *Journal of Zoological Systematics and Evolutionary Research* 12 (1): 94–128. <https://doi.org/10.1111/j.1439-0469.1974.tb00160.x>
- MAYR E. 1989. — A new classification of the living birds of the World. *Auk* 106 (3): 508–512. <https://doi.org/10.1093/auk/106.3.508>
- MAYR E. 1993. — Fifty years of progress in research on species and speciation. *Proceedings of the California Academy of Sciences* 48 (6): 131–140.
- MAYR E. 1996. — What is a species, and what is not? *Philosophy of Science* 63 (2): 262–277. <https://doi.org/10.1086/289912>
- MAYR E. 2000. — The biological species concept, in WHEELER Q.D. & MEIER R. (eds.), *Species concepts and phylogenetic theory: A debate*. New York, Columbia University Press: 17–29.
- MAYR E. & SHORT L.L. 1970. — *Species Taxa of North American birds. A Contribution to Comparative Systematics*. Cambridge, Nuttall Ornithological Club. 127 p. (Publications of the Nuttall Ornithological Club; 9). <https://doi.org/10.5962/bhl.title.155019>
- MAYR G. 2007. — The renaissance of avian paleontology and its bearing on the higher-level phylogeny of birds. *Journal of Ornithology* 148 (S2): 455–458. <https://doi.org/10.1007/s10336-007-0159-8>
- MAYR G. 2009. — *Paleogene Fossil Birds*. Berlin, Heidelberg, Springer-Verlag. 262 p.
- MAYR G. & SMITH T. 2019. — A diverse bird assemblage from the Ypresian of Belgium furthers knowledge of early Eocene avifaunas of the North Sea Basin. *Neues Jahrbuch für Geologie und Paläontologie* 291 (3): 253–281. <https://doi.org/10.1127/njgpa/2019/0801>
- MAZUMDAR S. 2013. — *Ecology and conservation issues of Black Kite Milvus migrans govinda (Sykes) in Kolkata municipal corporation area*. Thesis submitted for the Degree of Doctor of Philosophy (Science) in Biology, University of Calcutta, [Kolkata], i–x, 1–226.
- MCDONALD J.H. & KREITMAN M. 1991. — Adaptive protein evolution at the *Adh* locus in *Drosophila*. *Nature* 351 (6328): 652–654. <https://doi.org/10.1038/351652a0>
- MCKITRICK M.C. & ZINK R.M. 1988. — Species concepts in ornithology. *The Condor* 90 (1): 1–14. <https://doi.org/10.2307/1368426>
- MEBS T. & SCHERZINGER W. 2000. — *Die Eulen Europas: Biologie, Kennzeichen, Bestände*. Stuttgart, Kosmos. 410 p. (Kosmos-Naturführer).
- MEES G.F. 1970. — On some birds from southern Mexico. *Zoologische Mededelingen* 44: 237–245.
- MEES G.F. 1982. — Birds from the lowlands of southern New Guinea (Merauke and Koembe). *Zoologische Verhandelingen* 191: 1–188.

- MEINERTZHAGEN R. 1924. — Notes on a small collection of birds made in Iraq in the winter of 1922–23. *Ibis* Ser. 11, 6 (4): 601–625. <https://doi.org/10.1111/j.1474-919X.1924.tb05346.x>
- MEINERTZHAGEN R. 1925. — A further contribution to the ornithology of Palestine, Transjordan, and Petra. *Ibis* Ser. 12, 1 (2): 305–324. <https://doi.org/10.1111/j.1474-919X.1925.tb02927.x>
- MENDELSON J.M. 1983. — Social behaviour and dispersion of Blackshouldered Kite. *Ostrich* 54 (1): 1–18. <https://doi.org/10.1080/00306525.1983.9634437>
- MEYER DE SCHAUENSEE R. 1971. — *A Guide to the Birds of South America*. Edinburgh, Oliver & Boyd. 470 p.
- MINDELL D.P., FUCHS J. & JOHNSON J.A. 2018. — Phylogeny, taxonomy, and geographic diversity of diurnal raptors: Falconiformes, Accipitriformes, and Cathartiformes, in SARASOLA J.H., GRANDE J.M. & NEGRO J.J. (eds.), *Birds of Prey. Biology and conservation in the XXI century*. Springer: 3–32. <https://doi.org/10.1007/978-3-319-73745-4>
- MITROPOL'SKIY O.V., FOTTELER E.V. & TRET'YAKOV G.P. 1987. — [Order Falconiformes], in MATCHANOV N.M. (ed.), [*Birds of Uzbekistan*]. Vol. 1. Tashkent, Fan. p. 123–247. (in Russian).
- MLÍKOVSKÝ J. 2002. — *Cenozoic Birds of the World*. Vol. 1. Praha, NINOX Press. 417 p.
- MONROE B.L. JR. & SIBLEY C.G. 1993. — *A World Checklist of Birds*. New Haven, London, Yale University Press. 414 p.
- MORIYAMA E.N. & POWELL J.R. 1997. — Synonymous substitution rates in *Drosophila*: Mitochondrial versus nuclear genes. *Journal of Molecular Evolution* 45 (4): 378–391. <https://doi.org/10.1007/PL00006243>
- MOURER-CHAUVIRE C. 1975. — *Les oiseaux du Pléistocène moyen et supérieur de France*. Université de Lyon. 262 p. (Documents des laboratoires de géologie de la Faculté des sciences de Lyon; 64, 1).
- MOURER-CHAUVIRE C., SALOTTI M., PEREIRA E., QUINIF Y., COURTOIS J., DUBOIS J. & LA MILZA J.-C. 1997. — *Athene angelis* n. sp. (Aves, Strigiformes), nouvelle espèce endémique insulaire éteinte du Pléistocène moyen et supérieur de Corse (France). *Comptes rendus de l'Académie des sciences* 324: 677–684.
- MUNDY P.J. 2011. — Yellow-billed kites from Arabia. Available from <http://ir.nust.ac.zw/xmlui/handle/123456789/562> [accessed 24 November 2018]
- NAGY J. & TÖKÖLYI J. 2014. — Phylogeny, historical biogeography and the evolution of migration in accipitrid birds of prey (Aves: Accipitriformes). *Ornis Hungarica* 22 (1): 15–35. <https://doi.org/10.2478/orhu-2014-0008>
- NEGRO J.J., PERTOLDI C., RANDI E., FERRERO J.J., LÓPEZ-CABALLERO J.M., RIVERA D. & KÖRPIMÄKI E. 2006. — Convergent evolution of *Elanus* kites and the owls. *Journal of Raptor Research* 40 (3): 222–225. [https://doi.org/10.3356/0892-1016\(2006\)40\[222:CEOEKA\]2.0.CO;2](https://doi.org/10.3356/0892-1016(2006)40[222:CEOEKA]2.0.CO;2)

- NEI M. & LI W.-H. 1979. — Mathematical model for studying genetic variation in terms of restriction endonucleases. *Proceedings of the National Academy of Sciences of the United States of America* 76 (10): 5269–5273. <https://doi.org/10.1073/pnas.76.10.5269>
- NEI M. & TAJIMA F. 1981. — DNA polymorphism detectable by restriction endonucleases. *Genetics* 97 (1): 145–163. <https://doi.org/10.1093/genetics/97.1.145>
- NIELSEN R. 2001. — Statistical tests of selective neutrality in the age of genomics. *Heredity* 86 (6): 641–647. <https://doi.org/10.1046/j.1365-2540.2001.00895.x>
- NIETHAMMER G., VON BOXBERGER L., DATHE H., EICHLER W., FRIELING H., HILDEBRANDT H., KUMMERLÖWE H., MEISE W., STEINBACHER J. & STRESEMANN E. 1938. — *Handbuch der deutschen Vogelkunde*. Vol. 2. Leipzig, Akademische Verlagsgesellschaft M. B. H., I–X, 1–545.
- NIJMAN V. & ALIABADIAN M. 2013. — DNA barcoding as a tool for elucidating species delineation in wide-ranging species as illustrated by owls (Tytonidae and Strigidae). *Zoological Science* 30 (11): 1005–1009. <https://doi.org/10.2108/zsj.30.1005>
- O'BRIEN S.J. & MAYR E. 1991. — Bureaucratic mischief: Recognizing endangered species and subspecies. *Science* 251 (4998): 1187–1188. <https://doi.org/10.1126/science.251.4998.1187>
- ORTA J. 1994. — Black Kite *Milvus migrans*, in DEL HOYO J., ELLIOTT A. & SARGATAL J. (eds.), *Handbook of the Birds of the World*. Vol. 2. Barcelona, Lynx Edicions. p. 118–119.
- PAGE R.D.M., LEE P.L.M., BECHER S.A., GRIFFITHS R. & CLAYTON D.H. 1998. — A different tempo of mitochondrial DNA evolution in birds and their parasitic lice. *Molecular Phylogenetics and Evolution* 9 (2): 276–293. <https://doi.org/10.1006/mpev.1997.0458>
- PANTER C.T., XIROUCHAKIS S., DANKO Š., MATUŠÍK H., PODZEMNÝ P., OVČIARIKOVÁ S. & LITERÁK I. 2020. — Kites (*Milvus* spp.) wintering on Crete. *The European Zoological Journal* 87 (1): 591–596. <https://doi.org/10.1080/24750263.2020.1821801>
- PANUCCIO M., AGOSTINI N., MELLONE U. & BOGLIANI G. 2014. — Circannual variation in movement patterns of the Black Kite (*Milvus migrans migrans*): a review. *Ethology Ecology & Evolution* 26 (1): 1–18. <https://doi.org/10.1080/03949370.2013.812147>
- PARKES K.C. 1958. — Specific relationships in the genus *Elanus*. *The Condor* 60 (2): 139–140.
- PATTEN M.A. 2015. — Subspecies and the philosophy of science. *The Auk* 132 (2): 481–485. <https://doi.org/10.1642/AUK-15-1.1>
- PAVIA M. & MOURER-CHAUVIRÉ C. 2002. — An overview of the genus *Athene* in the Pleistocene of the Mediterranean islands, with the description of *Athene trinacriae* n. sp. (Aves: Strigidae), in ZHOU Z. & ZHANG F. (eds.), *Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution, Beijing, 1-4 June 2000*. Beijing. Science Press. p. 13–27.
- PELLEGRINO I., CUCCO M., CALÀ E., BOANO G. & PAVIA M. 2020. — Plumage coloration and morphometrics of the Little Owl *Athene noctua* in the Western Palearctic. *Journal of Ornithology* 161 (4): 1071–1081. <https://doi.org/10.1007/s10336-020-01792-7>

- PELLEGRINO I., NEGRI A., BOANO G., CUCCO M., KRISTENSEN T.N., PERTOLDI C., RANDI E., ŠÁLEK M. & MUCCI N. 2015. — Evidence for strong genetic structure in European populations of the little owl *Athene noctua*. *Journal of Avian Biology* 46: 462–475. <https://doi.org/10.1111/jav.00679>
- PELLEGRINO I., NEGRI A., CUCCO M., MUCCI N., PAVIA M., ŠÁLEK M., BOANO G. & RANDI E. 2014. — Phylogeography and Pleistocene refugia of the Little Owl *Athene noctua* inferred from mtDNA sequence data. *Ibis* 156 (3): 639–657. <https://doi.org/10.1111/ibi.12162>
- PETERS J.L. 1931. — *Check-list of Birds of the World*. Vol. 1. Cambridge, Harvard University Press. i–xviii, 1–345.
- PETERS J.L. 1934. — *Check-list of Birds of the World*. Vol. 2. Cambridge, Harvard University Press. i–vii, 1–401.
- PETERS J.L. 1940. — *Check-list of Birds of the World*. Vol. 4. Cambridge, Harvard University Press. i–vii, 1–291.
- PINTO O.M.D.O. 1938. — *Catalogo das aves do Brasil e lista dos exemplares que as representam no Museu Paulista*. São Paulo, Museu Paulista, 1938. 598 p.
- PFANDER P.V. 2012. — Reform of the zoological nomenclature – Solution for the “species problem”. *Raptors Conservation* 24: 165–177.
- PFANDER P.V. 2018. — [The tragedy of species-level systematics]. *The Russian Journal of Ornithology* 27 (1558): 301–335. (in Russian).
- POKRYSZKO B., CAMERON R., MUMLADZE L. & TARKHNISHVILI D. 2011. — Forest snail faunas from Georgian Transcaucasia: Patterns of diversity in a Pleistocene refugium. *Biological Journal of the Linnean Society* 102 (2): 239–250. <https://doi.org/10.1111/j.1095-8312.2010.01575.x>
- POLZIN T. & DANESHMAND S.V. 2003. — On Steiner trees and minimum spanning trees in hypergraphs. *Operations Research Letters* 31 (1): 12–20. [https://doi.org/10.1016/S0167-6377\(02\)00185-2](https://doi.org/10.1016/S0167-6377(02)00185-2)
- POTIER S., BONADONNA F., MARTIN G.R., ISARD P.-F., DULAURENT T., MENTEK M. & DURIEZ O. 2018. — Visual configuration of two species of Falconidae with different foraging ecologies. *Ibis* 160 (1): 54–61. <https://doi.org/10.1111/ibi.12528>
- PRIKLONSKY S.G. 2001. — [The birds of Russia and adjacent territories: the little owl *Athene noctua* (Scopoli, 1769)]. *The Russian Journal of Ornithology* (158): 763–779. (in Russian).
- PRUM R.O., BERV J.S., DORNBURG A., FIELD D.J., TOWNSEND J.P., LEMMON E.M. & LEMMON A.R. 2015. — A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* 526 (7574): 569–573. <https://doi.org/10.1038/nature15697>
- PYCRAFT W.P. 1902. — Contribution to the osteology of birds. Part V. Falconiformes. *Proceedings of the General Meetings for Scientific Business of the Zoological Society of London* 1 (19): 277–320.

- RAND D.M. & KANN L.M. 1996. — Excess amino acid polymorphism in mitochondrial DNA: contrasts among genes from *Drosophila*, mice, and humans. *Molecular Biology and Evolution* 13 (6): 735–748. <https://doi.org/10.1093/oxfordjournals.molbev.a025634>
- RANNALA B. & YANG Z. 1996. — Probability distribution of molecular evolutionary trees: A new method of phylogenetic inference. *Journal of Molecular Evolution* 43 (3): 304–311. <https://doi.org/10.1007/BF02338839>
- RAWANKAR A., WAGH G. & WADATKAR J. 2015. — DNA barcoding and phylogenetic analysis of *Tyto alba*, *Otus bakkamoena* and *Athene brama* from Indian subcontinent. *International Journal of Zoology and Research* 5 (5): 7–14
- RAXWORTHY C.J. & SMITH B.T. 2021. — Mining museums for historical DNA: advances and challenges in museomics. *Trends in Ecology & Evolution* 36 (11): 1049–1060. <https://doi.org/10.1016/j.tree.2021.07.009>
- REICHENOW A. 1882. — *Die Vögel der zoologischen Gärten. Leitfaden zum Studium der Ornithologie mit besonderer Berücksichtigung der in Gefangenschaft gehaltenen Vögel. Ein Handbuch für Vogelwirthe*, Vol. 1, Leipzig, L.A. Kittler, I–XXX, 1–278.
- REMSEN J.V. JR. 2005. — Pattern, process, and rigor meet classification. *The Auk* 122 (2): 403–413. <https://doi.org/10.1093/auk/122.2.403>
- RENSCH B. 1931. — Die Vogelwelt von Lombok, Sumbawa und Flores. *Mitteilungen aus dem Zoologischen Museum in Berlin* 17: 451–637.
- RETNANINGTYAS R.W., HERMADHIYANTI W. & LISTYORINI D. 2017. — The phylogenetic study of the White-Bellied Sea Eagle [*Haliaeetus leucogaster* (Gmelin, 1788)] based on DNA barcoding cytochrome-c oxidase subunit I (COI), in *ICBS Conference Proceedings, International Conference on Biological Science (2015), 18–19 September 2015*. KnE Life Sciences. p. 208–212. <https://doi.org/10.18502/kls.v3i4.706>
- RICH P.V. & BOHASKA D.J. 1976. — The World's oldest owl: A new strigiform from the Paleocene of southwestern Colorado. *Smithsonian Contributions to Paleobiology* 27: 87–93.
- RIDGWAY R. 1873. — Catalogue of the ornithological collection of the Boston Society of Natural History. Part II. Falconidae. *Proceedings of the Boston Society of Natural History* 16: 43–72
- RIDGWAY R. 1876. — Studies of the American Falconidae. *Bulletin of the United States Geological and Geographical Survey of the Territories* 2 (1): 91–182.
- RONQUIST F. & HUELSENBECK J.P. 2003. — MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19 (12): 1572–1574. <https://doi.org/10.1093/bioinformatics/btg180>
- ROQUES S. & NEGRO J.J. 2005. — MtDNA genetic diversity and population history of a dwindling raptorial bird, the red kite (*Milvus milvus*). *Biological Conservation* 126 (1): 41–50. <https://doi.org/10.1016/j.biocon.2005.04.020>

ROY M., POZZI A.C., GAREIL R., NAGATI M., MANZI S., NOUIOUI I., SHARIKADZE N., JARGEAT P., GRUYA H., MOREAU P.-A., FERNANDEZ M.P. & GARDES M. 2017. — Alder and the Golden Fleece: high diversity of *Frankia* and ectomycorrhizal fungi revealed from *Alnus glutinosa* subsp. *barbata* roots close to a Tertiary and glacial refugium. *PeerJ* 5: e3479: 1–21. <https://doi.org/10.7717/peerj.3479>

ROZAS J., FERRER-MATA A., SÁNCHEZ-DELBARRIO J.C., GUIRAO-RICO S., LIBRADO P., RAMOS-ONSINS S.E. & SÁNCHEZ-GRACIA A. 2017. — DnaSP 6: DNA sequence polymorphism analysis of large data sets. *Molecular Biology and Evolution* 34 (12): 3299–3302. <https://doi.org/10.1093/molbev/msx248>

RUBINOFF D. & HOLLAND B.S. 2005. — Between two extremes: Mitochondrial DNA is neither the panacea nor the nemesis of phylogenetic and taxonomic inference. *Systematic Biology* 54 (6): 952–961. <https://doi.org/10.1080/10635150500234674>

RUBTSOV A.S. 2015. — Reproductive isolation and the notion of species in birds. *Biology Bulletin* 42 (9): 793–807. <https://doi.org/10.1134/S1062359015090101>

RYU S.H. & PARK H.C. 2003. — Molecular phylogeny of the family Strigidae (Aves) based on mitochondrial cytochrome *b* gene. *Animal Systematics, Evolution and Diversity* 19 (2): 297–304. (in Korean with English summary).

SADANANDAN K.R., TAN D.J.X., SCHJØLBERG K., ROUND P.D. & RHEINDT F.E. 2015. — DNA reveals long-distance partial migratory behavior in a cryptic owl lineage. *Avian Research* 6 (1): 25: 1–7. <https://doi.org/10.1186/s40657-015-0035-9>

SAITOU N. & NEI M. 1987. — The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution* 4 (4): 406–425. <https://doi.org/10.1093/oxfordjournals.molbev.a040454>

SAMBROOK J. & RUSSELL D.W. 2001. — *Molecular Cloning: A Laboratory Manual*. Vol. 2. Cold Spring Harbor, Cold Spring Harbor Laboratory Press, 8.1–I.44.

SANGSTER G. 2014. — The application of species criteria in avian taxonomy and its implications for the debate over species concepts. *Biological Reviews* 89 (1): 199–214. <https://doi.org/10.1111/brv.12051>

SANSOM R.S. & WILLS M.A. 2017. — Differences between hard and soft phylogenetic data. *Proceedings of the Royal Society B: Biological Sciences* 284 (1869): 20172150: 1–7. <https://doi.org/10.1098/rspb.2017.2150>

SCHEIDER J., WINK M., STUBBE M., HILLE S. & WILTSCHKO W. 2004. — Phylogeographic relationships of the Black Kite *Milvus migrans*, in CHANCELLOR R.D. & MEYBURG B.-U. (eds.), *Raptors Worldwide, Proceedings of the 6th World Conference on birds of prey and owls, Budapest, Hungary, May 2003*. Berlin, WWGBP; Budapest, MME. p. 467–472.

SCHEIDER J., WINK M., WILTSCHKO W. & STUBBE M. 2009. — Zur Phylogenie und Taxonomie der Schwarzmilan-Subspezies, in STUBBE M. (ed.), *Fachbeiträge des 6. Internationalen Symposiums Populationsökologie von Greifvogel- und Eulenarten 19.-22.10.2006 in*

Meisdorf/Harz mit allen Beiträgen des Symposiums. *Populationsökologie Greifvogel- und Eulenarten* 6: 233–242.

SCHINDEL D., STOECKLE M., MILENSKY C., TRIZNA M., SCHMIDT B., GEBHARD C. & GRAVES G. 2011. — Project description: DNA barcodes of bird species in the National Museum of Natural History, Smithsonian Institution, USA. *ZooKeys* 152: 87–91. <https://doi.org/10.3897/zookeys.152.2473>

SCHLEGEL H. 1844. — *Kritische Übersicht der europäischen Vögel. Revue critique des oiseaux d'Europe*. Leiden, A. Arnz & Co, I–CXXXV, 1–116. <https://doi.org/10.5962/bhl.title.96043>

SCHREIBER A., STUBBE M. & STUBBE A. 2000. — Red kite (*Milvus milvus*) and black kite (*M. migrans*): Minute genetic interspecies distance of two raptors breeding in a mixed community (Falconiformes: Accipitridae). *Biological Journal of the Linnean Society* 69: 351–365. <https://doi.org/10.1111/j.1095-8312.2000.tb01210.x>

SEEBOHM H. 1890. — *Classification of birds; an attempt to diagnose the subclasses, orders, suborders, and some of the families of existing birds*. London, R.H. Porter, i–xi, 1–53. <https://doi.org/10.5962/bhl.title.13287>

SEIBOLD I., HELBIG A.J. & WINK M. 1993. — Molecular systematics of falcons (family Falconidae). *Naturwissenschaften* 80 (2): 87–90. <https://doi.org/10.1007/BF01140425>

SEIBOLD I. 1994. — *Untersuchungen zur molekularen Phylogenie der Greifvögel anhand von DNA-Sequenzen des mitochondrialen Cytochrom-b-Gens*. Konstanz, Hartung-Gorre. 238 p.

SEIBOLD I. & HELBIG A.J. 1995. — Evolutionary history of New and Old World vultures inferred from nucleotide sequences of the mitochondrial cytochrome *b* gene. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 350 (1332): 163–178. <https://doi.org/10.1098/rstb.1995.0150>

SHARPE R.B. 1891. — *A Review of Recent Attempts to Classify Birds*. Budapest, International Ornithological Congress. 90 p. <https://doi.org/10.5962/bhl.title.13335>

SHARPE R.B. 1899. — *A Hand-list of the Genera and Species of Birds*. Vol. 1. London, British Museum (Natural History), i–xxi, 1–303, 1–20.

SHOEMAKER J.S. & FITCH W.M. 1989. — Evidence from nuclear sequences that invariable sites should be considered when sequence divergence is calculated. *Molecular Biology and Evolution* 6: 270–289. <https://doi.org/10.1093/oxfordjournals.molbev.a040550>

SHUFELDT R.W. 1891. — Some comparative osteological notes on the North-American kites. *Ibis Ser. 6, 3* (2): 228–232. <https://doi.org/10.1111/j.1474-919X.1891.tb08572.x>

SIBLEY C.G. 1960. — The electrophoretic patterns of egg-white proteins as taxonomic characters. *Ibis* 102 (2): 215–284. <https://doi.org/10.1111/j.1474-919X.1960.tb07114.x>

SIBLEY C.G. & AHLQUIST J.E. 1972. — *A Comparative Study of the Egg White Proteins of Non-passerine Birds*. New Haven, Yale University, i–vi, 1–276. (Bulletins of Peabody Museum of Natural History; 39).

SIBLEY C.G. & AHLQUIST J.E. 1990. — *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. New Haven, Yale University Press, i–xxiii, 1–976.

SIBLEY C.G., AHLQUIST J.E. & MONROE B.L. JR. 1988. — A Classification of the living birds of the world based on DNA-DNA hybridization studies. *The Auk* 105 (3): 409–423. <https://doi.org/10.1093/auk/105.3.409>

SIBLEY C.G. & MONROE B.L. 1990. — *Distribution and Taxonomy of Birds of the World*. New Haven, London, Yale University Press, i–xxiv, 1–1111.

SIMAKOV M.D., KOREPOV M.V., KUZMIN A.A. & TITOV S.V. 2021. — Genetic diversity of mtDNA in the Volga black kite population (*Milvus migrans* Boddaert, 1783). *Russian Journal of Ecosystem Ecology* 6 (1): 1–10. (in Russian with English summary). <https://doi.org/10.21685/2500-0578-2021-1-5>

SIMONSEN K.L., CHURCHILL G.A. & AQUADRO C.F. 1995. — Properties of statistical tests of neutrality for DNA polymorphism data. *Genetics* 141 (1): 413–429. <https://doi.org/10.1093/genetics/141.1.413>

SINCLAIR E.A., PÉREZ-LOSADA M. & CRANDALL K.A. 2005. — Molecular phylogenetics for conservation biology, in PURVIS A., GITTLEMAN J.L. & BROOKS T. (eds.), *Phylogeny and Conservation*. Cambridge, Cambridge University Press. p. 19–56. <https://doi.org/10.1017/CBO9780511614927.002>

SKYRPAN M. & LITERÁK I. 2019. — A kite *Milvus migrans migrans/lineatus* in Ukraine. *Biologia* 74 (12): 1669–1673. <https://doi.org/10.2478/s11756-019-00270-7>

SKYRPAN M., PANTER C., NACHTIGALL W., RIOLS R., SYSTAD G., ŠKRÁBAL J. & LITERÁK I. 2021. — Kites *Milvus migrans lineatus* (*Milvus migrans migrans/lineatus*) are spreading west across Europe. *Journal of Ornithology* 162 (2): 317–323. <https://doi.org/10.1007/s10336-020-01832-2>

SOKAL R.R. & MICHENER C.D. 1958. — A statistical method for evaluating systematic relationships. *The University of Kansas Science Bulletin* 38, 2 (22): 1409–1438.

SORENSEN M.D., AST J.C., DIMCHEFF D.E., YURI T. & MINDELL D.P. 1999. — Primers for a PCR-based approach to mitochondrial genome sequencing in birds and other vertebrates. *Molecular Phylogenetics and Evolution* 12 (2): 105–114. <https://doi.org/10.1006/mpev.1998.0602>

STARIKOV I.J. & WINK M. 2020. — Old and cosmopolite: Molecular phylogeny of tropical–subtropical kites (Aves: Elaninae) with taxonomic implications. *Diversity* 12 (9): 327: 1–21. <https://doi.org/10.3390/d12090327>

ŠTEFKA J., HOECK P.E., KELLER L.F. & SMITH V.S. 2011. — A hitchhikers guide to the Galápagos: co-phylogeography of Galápagos mockingbirds and their parasites. *BMC Evolutionary Biology* 11 (1): 284: 1–18. <https://doi.org/10.1186/1471-2148-11-284>

- STEPANYAN L.S. 2003. — *Conspectus of the Ornithological Fauna of Russia and Adjacent Territories (Within the Borders of the USSR as a Historic Region)*. Moskva, Akademkniga. 806 p. (in Russian with English summary).
- STRESEMANN E. & AMADON D. 1979. — Order Falconiformes, in MAYR E. & COTTRELL G.W. (eds.), *Check-list of Birds of the World*. Vol. 1. Cambridge, Museum of Comparative Zoology. p. 271–425.
- STRESEMANN E., MEISE W. & SCHÖNWETTER M. 1938. — Aves Beickianae. Beiträge zur Ornithologie von Nordwest-Kansu nach den Forschungen von Walter Beick (†) in den Jahren 1926–1933. *Journal für Ornithologie* 86 (2): 171–221. <https://doi.org/10.1007/BF02001019>
- STRESEMANN V. 1959. — The wing molt and systematic position of the genus *Gampsonyx*. *The Auk* 76 (3): 360–361. <https://doi.org/10.2307/4081819>
- STUDIER J.A. & KEPPLER K.J. 1988. — A note on the neighbor-joining algorithm of Saitou and Nei. *Molecular Biology and Evolution* 5 (6): 729–731. <https://doi.org/10.1093/oxfordjournals.molbev.a040527>
- SUNDEVALL C.J. 1872. — *Methodi naturalis avium disponendarum tentamen. Försök till fogelklassens naturenliga uppställning*. Stockholm, Samson & Wallin, A–F, I–LXIX, 1–187, 1*–12*. <https://doi.org/10.5962/bhl.title.122988>
- SUSCHKIN P. 1899. — Beiträge zur Classification der Tagraubvögel mit Zugrundelegung der osteologischen Merkmale. *Zoologischer Anzeiger* 22: 500–518.
- SUSCHKIN P. 1905. — *Zur Morphologie des Vogelskelets: Vergleichende Osteologie der normalen Tagraubvögel (Accipitres) und die Fragen der Classification*. Moscou, J. N. Kouchnéreff et C-ie. I–IV, 1–247. (Nouveaux mémoires de la Société impériale des naturalistes de Moscou; XVI, 4). <https://doi.org/10.5962/bhl.title.66842>
- SWAINSON W. 1837. — *On the Natural History and Classification of Birds*. Vol. 2. London, Longman, Rees, Orme, Brown, Green, & Longman; John Taylor. 398 p.
- SWANN H.K. 1922. — *A Synopsis of the Accipitres (Diurnal Birds of Prey), Comprising Species and Subspecies Described up to 1920, With Their Characters and Distribution*. London, i–viii, 1–233, i–iii. <https://doi.org/10.5962/bhl.title.64220>
- TAJIMA F. 1983. — Evolutionary relationship of DNA sequences in finite populations. *Genetics* 105 (2): 437–460. <https://doi.org/10.1093/genetics/105.2.437>
- TAJIMA F. 1989. — Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* 123 (3): 585–595. <https://doi.org/10.1093/genetics/123.3.585>
- TAMBUSSI C.P. & DEGRANGE F. 2013. — *South American and Antarctic Continental Cenozoic Birds: Paleobiogeographic Affinities and Disparities*. Springer, i–xi, 1–113.
- TAMURA K., STECHER G., PETERSON D., FILIPSKI A. & KUMAR S. 2013. — MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution* 30 (12): 2725–2729. <https://doi.org/10.1093/molbev/mst197>

- TARASOV V.V. 2011. — Distribution of the Little Owl in Western Siberia. *Vestnik OSU* 5 (124): 93–95. (in Russian with English summary).
- TAVARÉ S. 1986. — Some probabilistic and statistical problems in the analysis of DNA sequences, in MIURA R.M. (ed.), *Some Mathematical Questions in Biology: DNA Sequence Analysis*. Providence, American Mathematical Society. p. 57–86. (Lectures in Mathematics in the Life Sciences; 17).
- TAVARES E.S., GONÇALVES P., MIYAKI C.Y. & BAKER A.J. 2011. — DNA barcode detects high genetic structure within Neotropical bird species. *PLOS ONE* 6 (12): e28543: 1–13. <https://doi.org/10.1371/journal.pone.0028543>
- TCHERNOV E. 1980. — *The Pleistocene Birds of 'Ubeidiya, Jordan Valley*. Jerusalem, Israel Academy of Sciences and Humanities. 83 p.
- TCHERNOV E. 1988. — The age of 'Ubeidiya formation (Jordan Valley, Israel) and the earliest hominids in the Levant. *Paléorient* 14 (2): 63–65. <https://doi.org/10.3406/paleo.1988.4455>
- TEMMINCK C.-J. 1840. — *Manuel d'ornithologie, ou tableau systématique des oiseaux qui se trouvent en Europe; précédé d'une analyse du système général d'ornithologie et suivi d'une table alphabétique des espèces*. Vol. 1. Paris, G. Dufour, i–cxv, 1–439.
- TRISCHITTA A. 1939. — *Alcune nuove forme di uccelli italiani*. Bagheria. 5 p.
- TUCKER C.M., CADOTTE M.W., CARVALHO S.B., DAVIES T.J., FERRIER S., FRITZ S.A., GRENYER R., HELMUS M.R., JIN L.S., MOOERS A.O., PAVOINE S., PURSCHKE O., REDDING D.W., ROSAUER D.F., WINTER M. & MAZEL F. 2017. — A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews* 92 (2): 698–715. <https://doi.org/10.1111/brv.12252>
- TUNIYEV B.S. 1990. — [Herpetofauna of unique Colchis forests and its modern refugia], in SNAKIN V.V. (ed.), *[Soil and Biogeocenological Research in the North-West Caucasus]*. Pushchino. p. 55–70. (in Russian).
- TYRBERG T. 1991. — Arctic, montane and steppe birds as glacial relicts in the West Palearctic. *Verhandlungen der Ornithologischen Gesellschaft in Bayern* 25: 29–49.
- TYRBERG T. 1998. — *Pleistocene Birds of the Palearctic: A Catalogue*. Cambridge, Nuttall Ornithological Club. 720 p. (Publications of the Nuttall Ornithological Club; 27).
- VAURIE C. 1960. — Systematic notes on Palearctic birds. No. 42. Strigidae: The genus *Athene*. *American Museum Novitates* (2015): 1–21.
- VERESHCHAGIN N.K. 1959. — *[Mammals of the Caucasus]*. Izdatel'stvo Akademii nauk SSSR. 704 p. (Proceedings of the Zoological Institute of the USSR Academy of Sciences). (in Russian).
- VIEILLOT L.P. 1816. — *Analyse d'une nouvelle ornithologie élémentaire*. Paris, Deterville. 70 p.
- VIGORS N.A. JR. 1825. — Sketches in ornithology; or observations on the leading affinities of some of the more extensive groups of birds. *The Zoological Journal* 2 (V): 37–70.

- Voous K.H. 1973. — List of recent holarctic bird species non-passerines. *Ibis* 115 (4): 612–638. <https://doi.org/10.1111/j.1474-919X.1973.tb02004.x>
- VORIS H.K. 2000. — Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* 27 (5): 1153–1167. <https://doi.org/10.1046/j.1365-2699.2000.00489.x>
- WANG X., SUN Y., YUAN X., TANG M.-Q., WANG L., YU Y.-F. & LI Q.-W. 2004. — Comparative study of mitochondrial tRNA gene sequence and secondary structure among fifteen predatory birds. *Yi chuan xue bao = Acta Genetica Sinica* 31: 411–419. (in Chinese with English summary).
- WATTERSON G.A. 1975. — On the number of segregating sites in genetical models without recombination. *Theoretical Population Biology* 7 (2): 256–276. [https://doi.org/10.1016/0040-5809\(75\)90020-9](https://doi.org/10.1016/0040-5809(75)90020-9)
- WEESIE P.D.M. 1982. — A Pleistocene endemic island form within the genus *Athene*: *Athene cretensis* n.sp. (Aves, Strigiformes) from Crete. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series B* 85 (3): 323–336.
- WEICK F. 2006. — *Owls (Strigiformes): Annotated and Illustrated Checklist*. Berlin, Heidelberg, Springer, I–XXXIV, 1–350.
- WEIR J.T. & SCHLUTER D. 2008. — Calibrating the avian molecular clock. *Molecular Ecology* 17 (10): 2321–2328. <https://doi.org/10.1111/j.1365-294X.2008.03742.x>
- WELLS M.G. 1998. — *World Bird Species Checklist: With Alternative English and Scientific Names*. Marsworth, Worldlist. 671 p.
- WILLUGHBEI F. & RAIUS J. 1676. — *Ornithologiæ libri tres: In quibus aves omnes hactenus cognitæ in methodum naturis suis convenientem redactæ accurate describuntur, descriptiones iconibus elegantissimis & vivarum avium simillimis, æri incisus illustrantur*. Londini, J. Martyn. 502 p.
- WINK M. 1995. — Phylogeny of Old and New World vultures (Aves: Accipitridae and Cathartidae) inferred from nucleotide sequences of the mitochondrial cytochrome *b* gene. *Zeitschrift Fur Naturforschung. C, Journal of Biosciences* 50 (11–12): 868–882. <https://doi.org/10.1515/znc-1995-11-1220>
- WINK M. 2000. — Advances in DNA studies of diurnal and nocturnal raptors, in CHANCELLOR R.D. & MEYBURG B.-U. (eds.), *Raptors at Risk, Proceedings of the 5th World Conference on birds of prey and owls, Midrand, South Africa, 4-11 August 1998*. WWGBP, Hancock House. p. 831–844.
- WINK M. 2021. — DNA analyses have revolutionized studies on the taxonomy and evolution in birds, in MIKKOLA H. (ed.), *Birds. Challenges and Opportunities for Business, Conservation and Research*. IntechOpen. p. 1–19. <https://doi.org/10.5772/intechopen.97013>

- WINK M., EL-SAYED A.-A., SAUER-GÜRTH H. & GONZALEZ J. 2009. — Molecular phylogeny of owls (Strigiformes) inferred from DNA sequences of the mitochondrial cytochrome *b* and the nuclear *RAG-1* gene. *Ardea* 97 (4): 581–591. <https://doi.org/10.5253/078.097.0425>
- WINK M. & HEIDRICH P. 1999. — Molecular evolution and systematics of owls (Strigiformes), in KÖNIG C., WEICK F. & BECKING J.-H., *Owls of the World*. Pica Press. p. 39–57.
- WINK M. & HEIDRICH P. 2000a. — Fortschritte in der molekularen Systematik der Eulen (Strigiformes). *Kauzbrief* 13 (9): 15–25.
- WINK M. & HEIDRICH P. 2000b. — Molecular systematics of owls (Strigiformes) based on DNA sequences of the mitochondrial cytochrome *b* gene, in CHANCELLOR R.D. & MEYBURG B.-U. (eds.), *Raptors at Risk, Proceedings of the 5th World Conference on Birds of Prey and Owls, Midrand, Johannesburg, South Africa, 4-11 August 1998*. WWGBP & Hancock House. p. 819–828.
- WINK M., HEIDRICH P., SAUER-GÜRTH H., ELSAYED A.-A. & GONZALEZ J. 2008. — Molecular evolution and systematics of owls (Strigiformes), in KÖNIG C. & WEICK F., *Owls of the World*. London, Christopher Helm. p. 42–63.
- WINK M. & SAUER-GÜRTH H. 2000. — Advances in the molecular systematics of African raptors, in CHANCELLOR R.D. & MEYBURG B.-U. (eds.), *Raptors at Risk, Proceedings of the 5th World Conference on Birds of Prey and Owls, Midrand, Johannesburg, South Africa, 4-11 August 1998*. WWGBP & Hancock House. p. 135–147.
- WINK M. & SAUER-GÜRTH H. 2004. — Phylogenetic relationships in diurnal raptors based on nucleotide sequences of mitochondrial and nuclear marker genes., in CHANCELLOR R.D. & MEYBURG B.-U. (eds.), *Raptors Worldwide, Proceedings of the 6th World Conference on Birds of Prey and Owls, Budapest, Hungary, May 2003*. Berlin, WWGBP; Budapest, MME. p. 483–498.
- WINK M. & SAUER-GÜRTH H. 2021. — Molecular taxonomy and systematics of owls (Strigiformes) - An update. *AIRO* 29: 487–500.
- WINK M., SAUER-GÜRTH H. & FUCHS J. 2004. — Phylogenetic relationships in owls based on nucleotide sequences of mitochondrial and nuclear marker genes, in CHANCELLOR R.D. & MEYBURG B.-U. (eds.), *Raptors Worldwide, Proceedings of the 6th World Conference on Birds of Prey and Owls, Budapest, Hungary, May 2003*. Berlin, WWGBP; Budapest, MME. p. 517–526.
- WINK M. & SEIBOLD I. 1996. — Molecular phylogeny of Mediterranean raptors (Families Accipitridae and Falconidae), in MUNTANER J. & MAYOL J. (eds.), *Biología y conservación de las rapaces mediterráneas, 1994; Actas del VI Congreso de Biología y Conservación de las Rapaces Mediterráneas, Palma de Mallorca, 22-25 de septiembre de 1994 = Biology and Conservation of Mediterranean raptors, 1994: Proceedings of the VI Congress on Biology and Conservation of Mediterranean Raptors, Palma de Mallorca, 22-25 September, 1994*. Pozuelo de Alarcón, SEO; Birdlife. p. 335–344.

- WINK M., SEIBOLD I., LOTFIKHAH F. & BEDNAREK W. 1998. — Molecular systematics of holarctic raptors (Order Falconiformes), in CHANCELLOR R.D., MEYBURG B.-U. & FERRERO J.J. (eds.), *Holarctic Birds of Prey: Proceedings of an International Conference; Actas del Congreso Internacional sobre Rapaces del Holártico; Badajoz, Extremadura (Spain), 17-22 Abril 1995*. Berlin, Mérida. WWGBP, ADENEX. p. 29–48.
- WOLTERS H.E. 1982. — *Die Vogelarten der Erde: eine systematische Liste mit Verbreitungsangaben sowie deutschen und englischen Namen*. Hamburg, Berlin, Paul Parey. 745 p.
- YANG Z. 1994. — Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: Approximate methods. *Journal of Molecular Evolution* 39 (3): 306–314. <https://doi.org/10.1007/BF00160154>
- YANG Z., GOLDMAN N. & FRIDAY A. 1994. — Comparison of models for nucleotide substitution used in maximum-likelihood phylogenetic estimation. *Molecular Biology and Evolution* 11 (2): 316–324. <https://doi.org/10.1093/oxfordjournals.molbev.a040112>
- YANG Z. & RANNALA B. 2012. — Molecular phylogenetics: principles and practice. *Nature Reviews Genetics* 13 (5): 303–314. <https://doi.org/10.1038/nrg3186>
- [ZARUDNY N.A.] 1881. — [What is Blue-legged Kite (*Milvus glaucopus* Evm)]. *Priroda i okhota* 3 (9): 156–158. (in Russian).
- ZEIN M.S.A. 2018. — Barkoding DNA burung Elang (Famili Accipitridae) di Indonesia. *Berita Biologi* 17 (2): 165–173. <https://doi.org/10.14203/beritabiologi.v17i2.3108>
- ZELENKOV N.V. & KUROCHKIN E.N. 2014. — [Class Aves], in [Fossil Vertebrates of Russia and Neighboring Countries. Fossil Reptiles and Birds]. Vol. 3. Moskva, GEOS. p. 92–291. (in Russian).
- ZHAI W., NIELSEN R. & SLATKIN M. 2009. — An investigation of the statistical power of neutrality tests based on comparative and population genetic data. *Molecular Biology and Evolution* 26 (2): 273–283. <https://doi.org/10.1093/molbev/msn231>
- ZHANG H., DOU H., YANG X., ZHAO C., LIU G. & ZHANG J. 2014. — The complete mitochondrial genome sequence of the Sparrowhawk (*Accipiter nisus*). *Mitochondrial DNA*: 1648–1649. <https://doi.org/10.3109/19401736.2014.958711>
- ZHOU C., JIN J., PENG C., WEN Q., WANG G., WEI W., JIANG X., PRICE M., CUI K., MENG Y., SONG Z., LI J., ZHANG X., FAN Z. & YUE B. 2019. — Comparative genomics sheds light on the predatory lifestyle of accipitrids and owls. *Scientific Reports* 9: 2249: 1–10. <https://doi.org/10.1038/s41598-019-38680-x>
- ZINK R.M. 1996. — Species concepts, speciation, and sexual selection. *Journal of Avian Biology* 27 (1): 1–6. <https://doi.org/10.2307/3676954>

- ZINK R.M. 2004. — The role of subspecies in obscuring avian biological diversity and misleading conservation policy. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271 (1539): 561–564. <https://doi.org/10.1098/rspb.2003.2617>
- ZINK R.M. 2006. — Rigor and species concepts. *The Auk* 123 (3): 887–891. <https://doi.org/10.1093/auk/123.3.887>
- ZINK R.M. & DAVIS J.I. 1999. — New perspectives on the nature of species, in ADAMS N.J. & SLODOW R.H. (eds.), *Proceedings of the 22nd International Ornithological Congress, 16-22 August 1998, Durban*. Johannesburg, BirdLife South Africa. p. 1505–1518.
- ZINK R.M. & KLICKA J. 2018. — Species concepts and speciation analysis, in MORRISON M.L., RODEWALD A.D., VOELKER G., COLÓN M.R. & PRATHER J.F. (eds.), *Ornithology: Foundation, Analysis, and Application*. Baltimore, Johns Hopkins University Press. p. 39–60.
- ZINK R.M. & MCKITRICK M.C. 1995. — The debate over species concepts and its implications for ornithology. *The Auk* 112 (3): 701–719. <https://doi.org/10.1093/auk/112.3.701>
- ZUCKERKANDL E. & PAULING L. 1965. — Evolutionary divergence and convergence in proteins, in BRYSON V. & VOGEL H.J. (eds.), *Evolving Genes and Proteins*. New York, Academic Press. p. 97–166. <https://doi.org/10.1016/B978-1-4832-2734-4.50017-6>

8. Appendices

Table A1. Variable sites of RAG-1 sequences of elanin kites.

	4	5	5	6	7	7	8	3	3	5	8	8	8	3	4	4	5	5	6	6	6	6
Specimen/Position	6	7	8	0	3	9	8	0	9	9	0	6	9	4	2	5	0	1	2	1	7	6
Elanus_caeruleus_373_Egypt	A	G	T	A	T	G	G	G	G	A	A	G	C	T	A	A	G	T	A	T	T	T
Elanus_caeruleus_4251_Morocco	.	.	C
Elanus_caeruleus_9965_South_Africa	C
Elanus_caeruleus_9966_South_Africa	C
Elanus_caeruleus_9967_South_Africa
Elanus_caeruleus_20593_Namibia_Okavuejo	C
Elanus_caeruleus_47115_Namibia_Windhoek	C
Elanus_caeruleus_47116_Namibia_Windhoek
Elanus_caeruleus_47117_Namibia_Windhoek
Elanus_caeruleus_47118_Namibia_Windhoek
Elanus_caeruleus_47119_Namibia_Windhoek	.	.	C	C
Elanus_caeruleus_58999_Benin_Cotonou
Elanus_caeruleus_75231_Benin_Bohicon
Elanus_caeruleus_EF078724.1_unknown_origin	Y	Y
Elanus_axillaris_8050_Australia	T	C	.	C	.	C	A
Elanus_axillaris_29917_Australia
Elanus_axillaris_29920_Australia
Chelictinia_riocourii_47157_Nigeria	A	.	.	.	T	.	C	.	.	G	.	C	C	.
Gampsonyx_swainsonii_EF078725.1_unknown_origin	A	A	G	G	A	T	G	.	G	A	.	G	.	.	.

Table A2. Variable sites of COI sequences of elanin kites.

Specimen/Position	1	1	2	2	3	3	3	3	4	4	5	6	6	6	6	7	7	7	8	9	0	0	0	1	1	1	2	2	2	3	3	4	4	4	4	5	5	6	6	6	7	7	7	8	8	9						
Elanus_caeruleus_373_ Egypt	A	T	C	A	A	C	A	A	C	A	C	T	C	C	A	A	C	T	C	T	C	C	C	G	C	G	G	C	G	C	C	G	C	G	C	A	C	T	C	A	T	A	G	C	C	C	T					
Elanus_caeruleus_4251_ Morocco	A			
Elanus_caeruleus_9965_ South_Africa	C		
Elanus_caeruleus_9966_ South_Africa	C		
Elanus_caeruleus_9967_ South_Africa	G	C		
Elanus_caeruleus_20593_ Namibia_Okavuejo	C		
Elanus_caeruleus_47115_ Namibia_Windhoek	
Elanus_caeruleus_47116_ Namibia_Windhoek	
Elanus_caeruleus_47117_ Namibia_Windhoek	
Elanus_caeruleus_47118_ Namibia_Windhoek
Elanus_caeruleus_58999_ Benin_Cotonou	C
Elanus_caeruleus_75231_ Benin_Bohicon	G	C
Elanus_caeruleus_ MK932886.1_Thailand	.	.	T	C	T	.	.	G	A	.	.	.	A	.	.	A	.	.	.	G	
Elanus_axillaris_29920_ Australia	.	C	.	.	.	T	T	G	.	.	C	T	A	.	A	.	T	A	.	T	A	T	.	.	C	.	.	.	C			
Elanus_leucurus_BOLD_5_USA_Panama_Argentina	T	C	.	.	.	T	C	C	.	C	.	T	T	A	A	A	.	.	A	.	.	T	C	.	C	.	G	C	T	A	T	
Chelictinia_riocourii_4715_7_Nigeria	C	.	T	C	.	C	.	.	.	C	.	T	A	T	.	T	.	T	T	A	A	A	A	T	A	.	.	A	A	.	T	.	.	.	C	C	.	C	.	A	T	C					
Gampsonyx_swainsonii_BOLD_6_Panama_Colombia_Brazil_Argentina	G	.	.	C	.	A	C	.	.	C	.	C	.	T	.	T	C	.	C	.	T	T	A	A	A	A	.	.	A	A	.	A	T	A	.	.	T	C	.	C	.	G	C	T	A	T						
Gampsonyx_swainsonii_BOLD_2_Guyana	G	.	.	C	.	A	C	.	.	C	.	C	.	T	.	T	C	.	C	.	T	T	A	A	A	A	.	.	A	A	.	A	T	A	.	.	T	C	.	C	.	G	C	T	A	T						

Table A3. End

									1	1	1
	9	9	9	9	9	9	9	0	0	0	
	8	8	8	9	9	9	9	0	0	1	
Specimen/Position	5	8	9	1	4	7	0	9	2		
Elanus_caeruleus_373_											
Egypt	C	T	G	C	C	C	C	G	T		
Elanus_caeruleus_4251_											
Morocco		
Elanus_caeruleus_9965_											
South_Africa		
Elanus_caeruleus_9966_											
South_Africa		
Elanus_caeruleus_9967_											
South_Africa		
Elanus_caeruleus_20593_											
Namibia_Okavuejo		
Elanus_caeruleus_47115_											
Namibia_Windhoek		
Elanus_caeruleus_47116_											
Namibia_Windhoek		
Elanus_caeruleus_47117_											
Namibia_Windhoek		
Elanus_caeruleus_47118_											
Namibia_Windhoek		
Elanus_caeruleus_47119_											
Namibia_Windhoek		
Elanus_caeruleus_58999_											
Benin_Cotonou		
Elanus_caeruleus_75231_											
Benin_Bohicon		
Elanus_axillaris_29920_											
Australia	T	.	.
Elanus_leucurus_											
AY987233.1_USA	T	C	A	A	.		
Chelictinia_riocourii_47157_											
Nigeria	.	.	A	.	T	.	.	A	.		

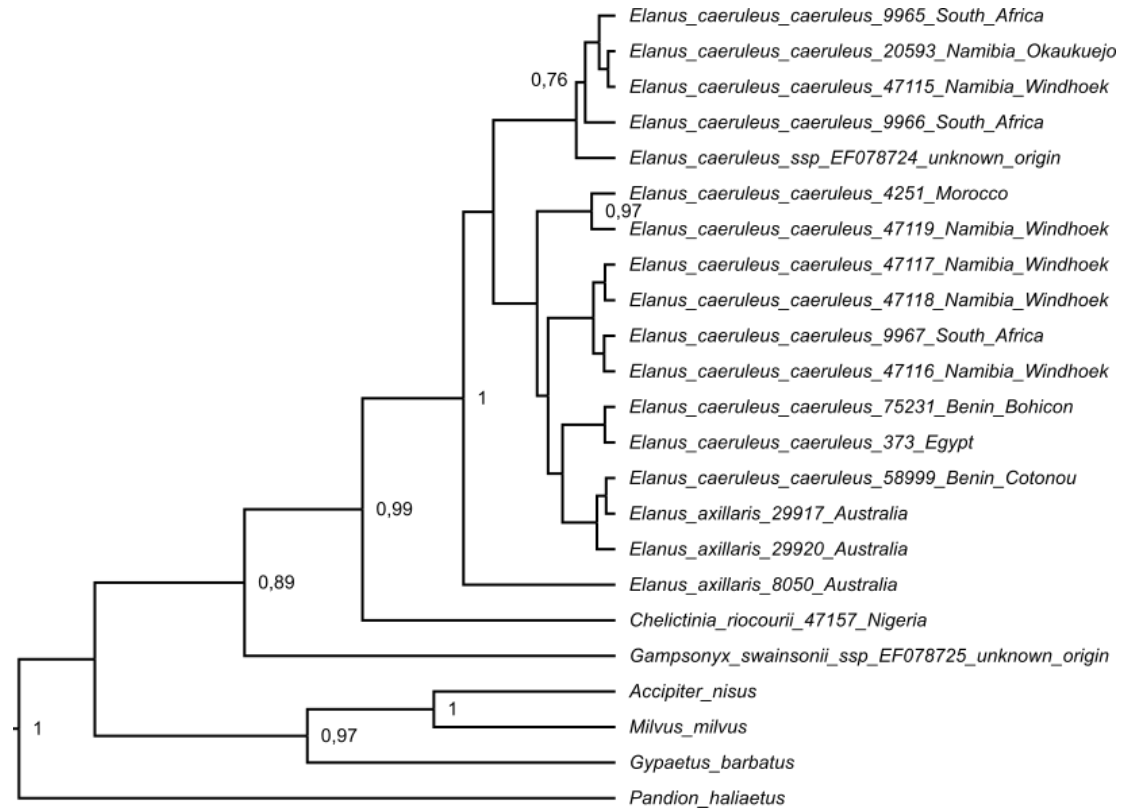


Figure A1. Bayesian phylogenetic tree of RAG-1 sequences of elanin kites. Here and below node labels show posterior rates >50%.

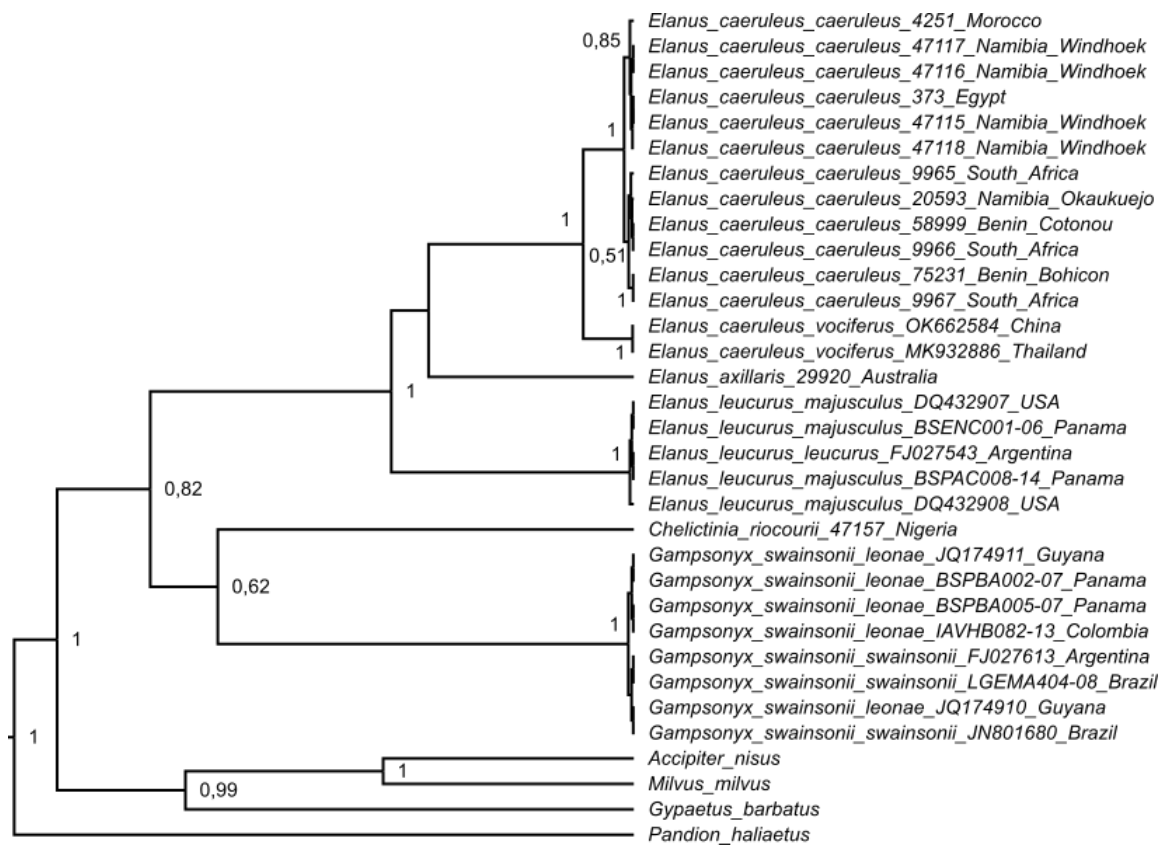


Figure A2. Bayesian phylogenetic tree of COI sequences of elanin kites.

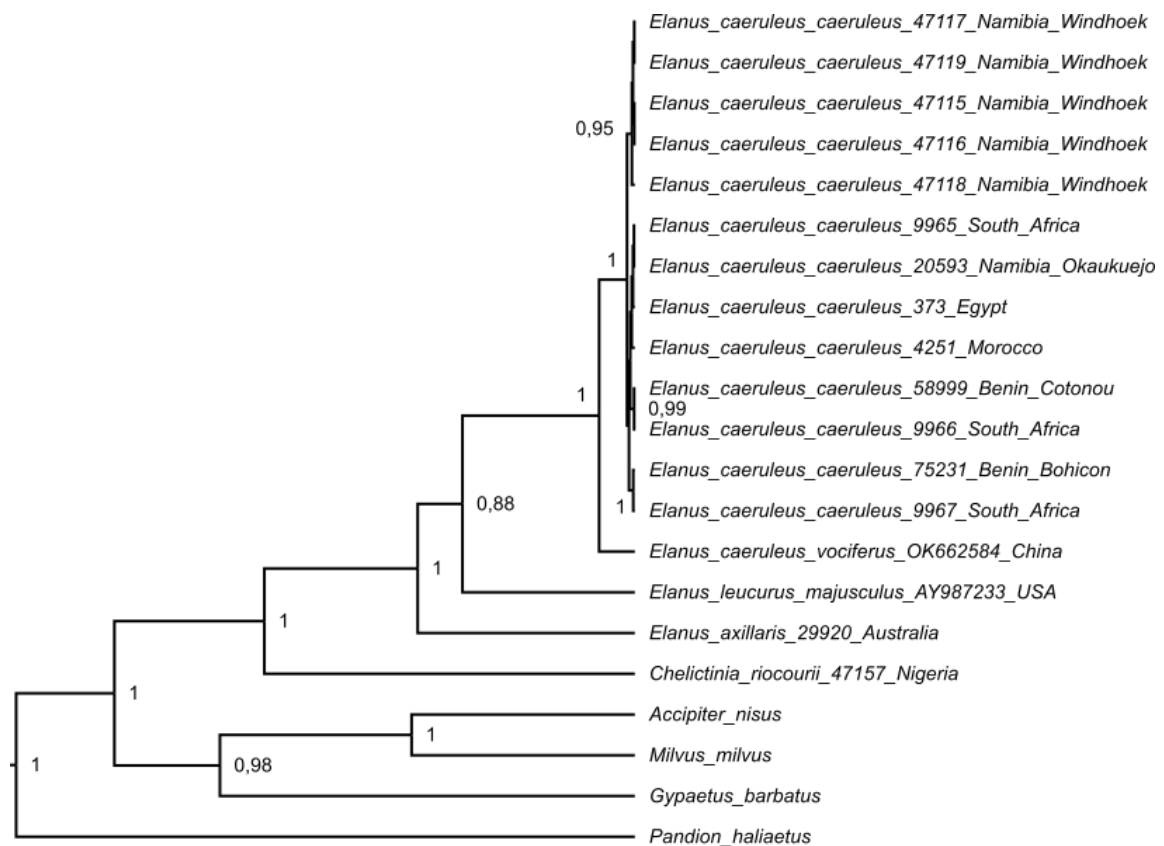


Figure A3. Bayesian phylogenetic tree of Cyt *b* sequences of elanin kites.

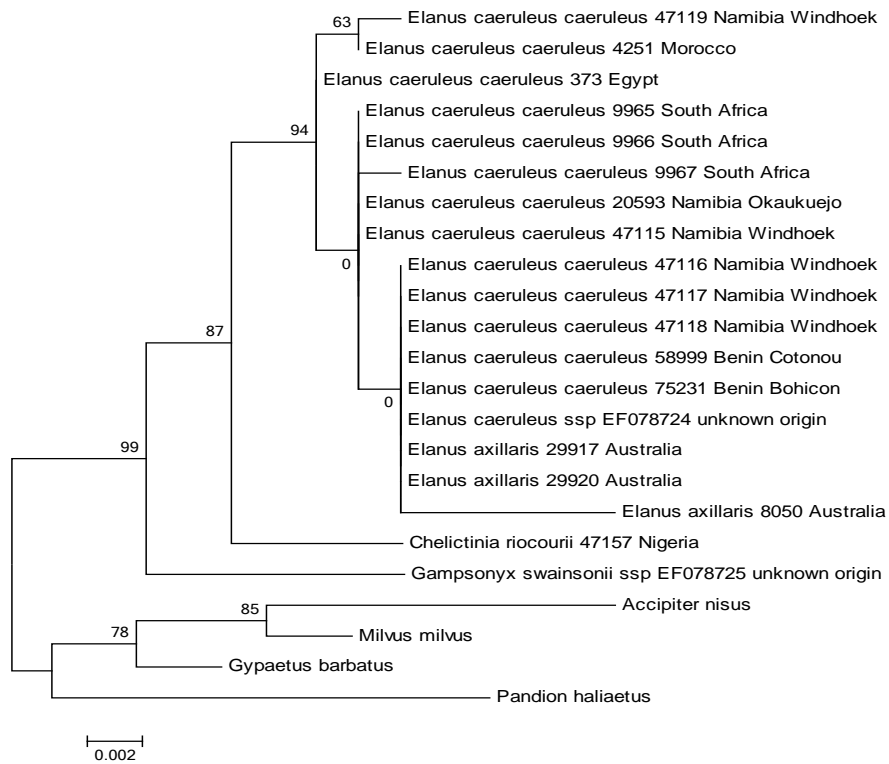


Figure A4. Maximum likelihood tree of RAG-1 sequences of elanin kites. Here and below bootstrap values are indicated as the node labels, last line represents number of substitutions per site.

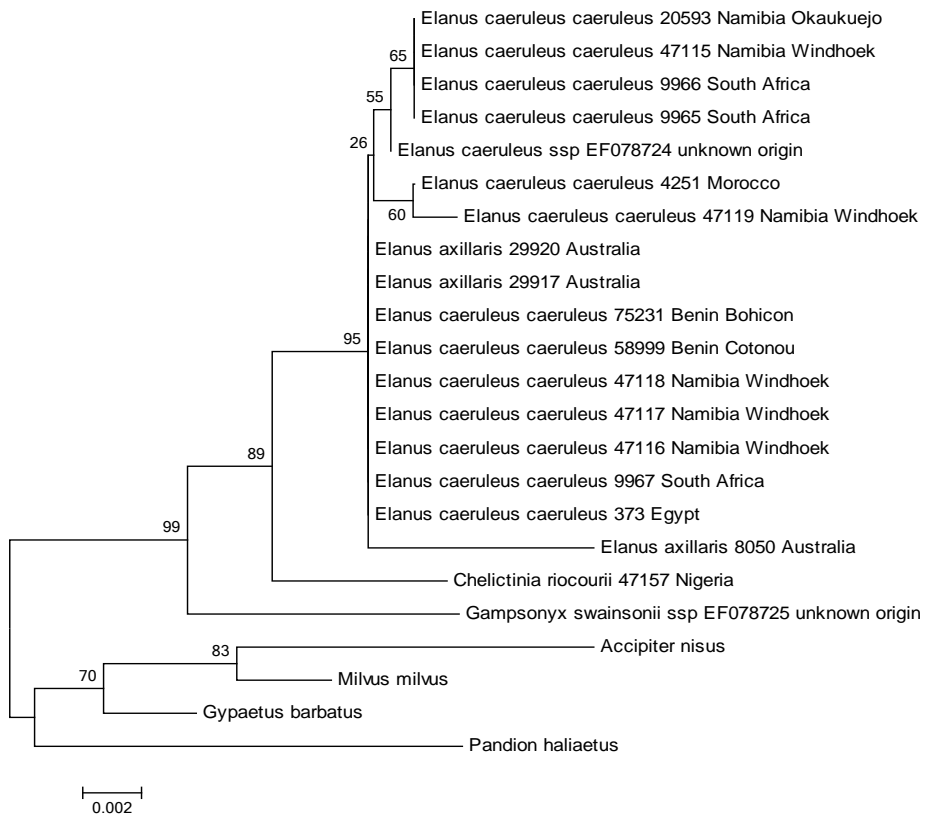


Figure A5. Neighbor-joining tree of RAG-1 sequences of elanin kites.

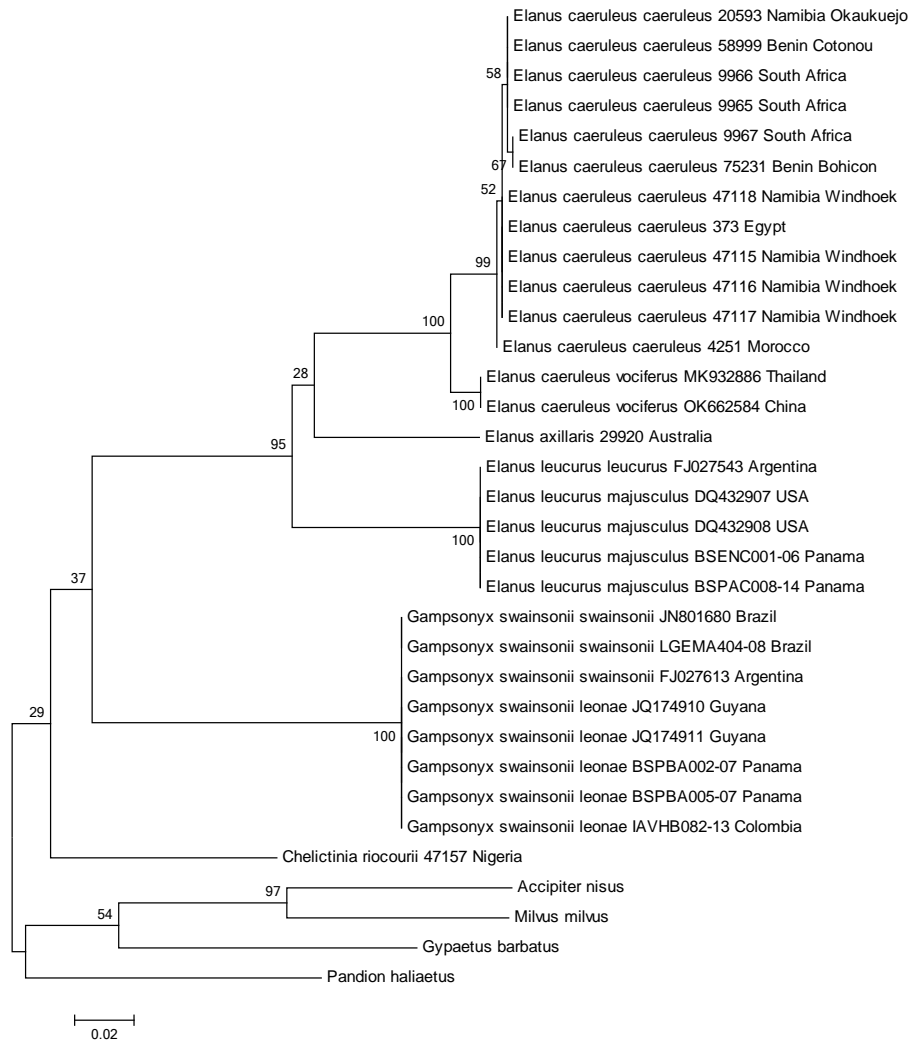


Figure A6. Maximum likelihood tree of COI sequences of elanin kites.

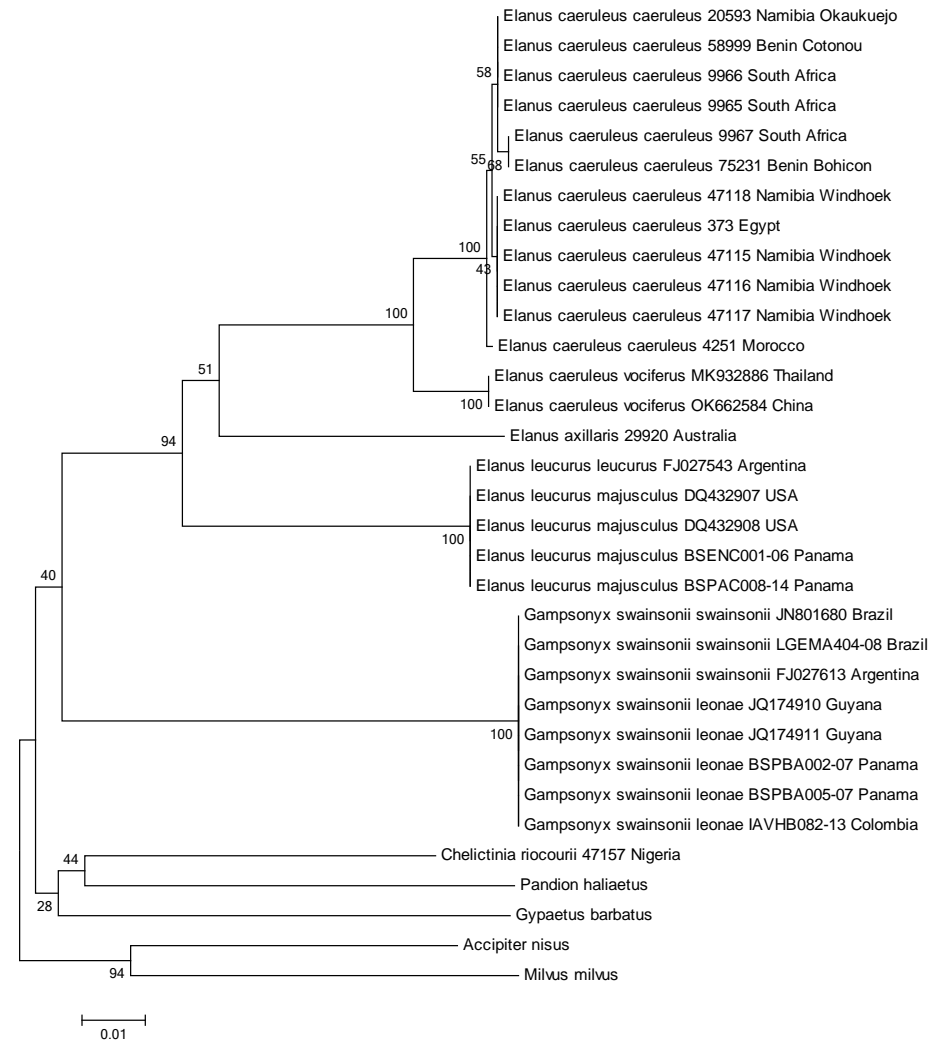


Figure A7. Neighbor-joining tree of COI sequences of elanin kites.

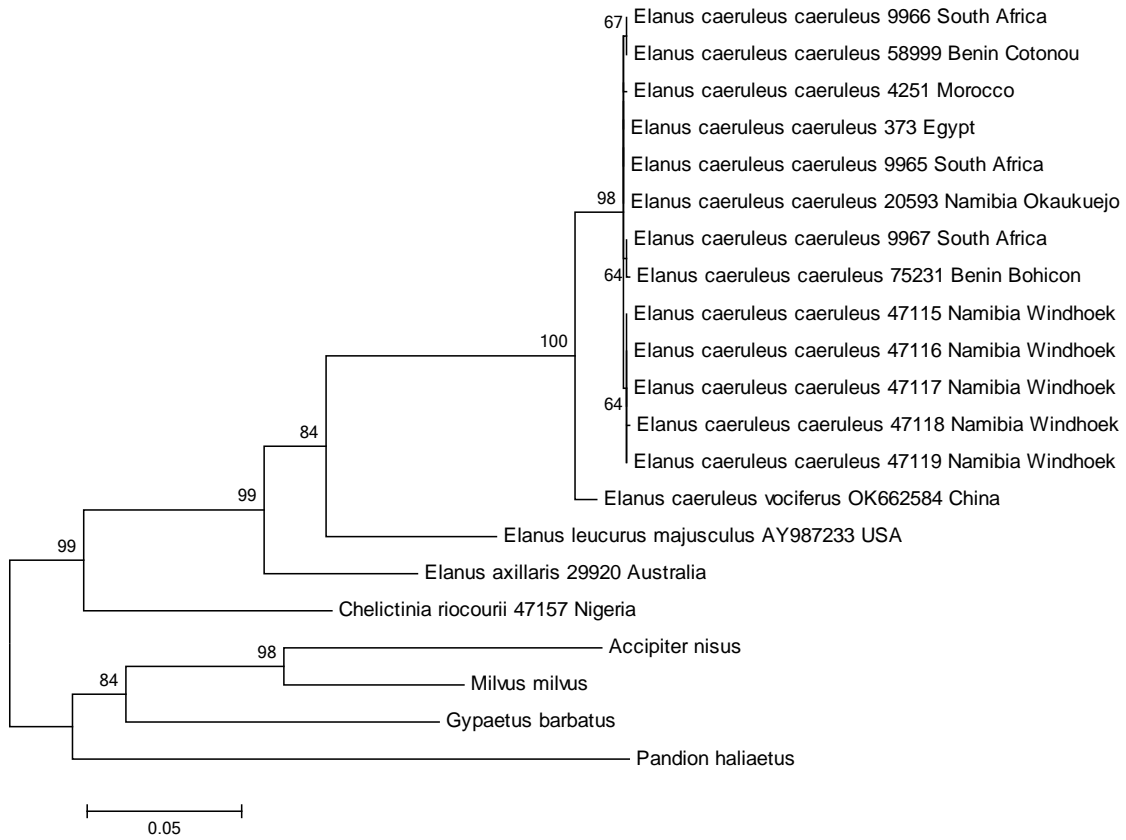


Figure A8. Maximum likelihood tree of *Cyt b* sequences of elanin kites.

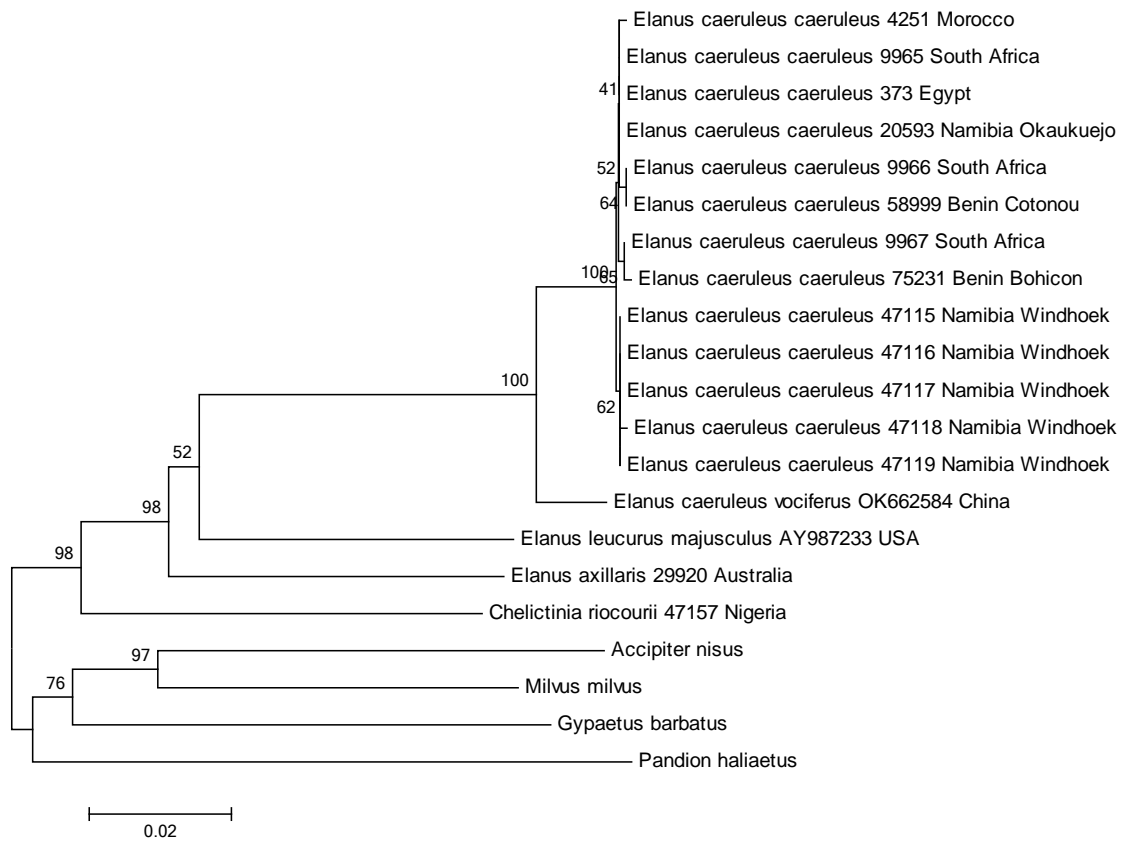


Figure A9. Neighbor-joining tree of *Cyt b* sequences of elanin kites.

Table A4. Samples of Black, Yellow-Billed and Red kites, used in genetic analyses. Originally filled by N. Andreyenkova, modified by I. Starikov.

Species	Latitude	Longitude	Cyt b haplotype	Haplogroup	Collection / museum catalogue No	Country (region) of collection	Date of collection	GenBank No	Range of subspecies, according to Karyakin 2017	Reference	Collector / source	Tissue	Haplogroup map Network & trees
<i>M. migrans</i>	52.239	85.869	A3	A	IMCB 115	Russia (Altai Republic)	30.07.2017	MT024189	lineatus	Andreyenkova <i>et al.</i> 2021	E. Nikolenko	feather	+ +
<i>M. migrans</i>	50.929	84.762	A4	A	IMCB 602	Russia (Altai Republic)	10.09.2018	MT024194	lineatus	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+ +
<i>M. migrans</i>	51.389	94.632	B19.1	B1	IMCB 48	Russia (Tyva Republic)	01.07.2017	MT024216	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	feather	+ +
<i>M. migrans</i>	51.425	94.889	B14	B1	IMCB 50	Russia (Tyva Republic)	02.07.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.438	94.864	B14	B1	IMCB 51	Russia (Tyva Republic)	02.07.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.5	94.665	B19	B1	IMCB 52	Russia (Tyva Republic)	30.06.2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.517	94.694	B6	B1	IMCB 53	Russia (Tyva Republic)	30.06.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.382	94.582	B6.2	B1	IMCB 54	Russia (Tyva Republic)	01.07.2017	MT024204	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.401	94.68	B6	B1	IMCB 55	Russia (Tyva Republic)	01.07.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	egg shell	+ +
<i>M. migrans</i>	51.394	94.588	B14	B1	IMCB 56	Russia (Tyva Republic)	01.07.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.415	94.661	B19	B1	IMCB 57	Russia (Tyva Republic)	01.07.2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.392	94.58	B6	B1	IMCB 58	Russia (Tyva Republic)	01.07.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.422	94.67	B6	B1	IMCB 59	Russia (Tyva Republic)	01.07.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.387	94.632	B6	B1	IMCB 60	Russia (Tyva Republic)	01.07.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.576	94.64	B6	B1	IMCB 61	Russia (Tyva Republic)	01.07.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.408	94.913	B6.1	B1	IMCB 62	Russia (Tyva Republic)	02.07.2017	MT024202	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.384	94.92	B19	B1	IMCB 63	Russia (Tyva Republic)	02.07.2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.373	94.618	B19	B1	IMCB 64	Russia (Tyva Republic)	02.07.2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	51.519	94.686	B14	B1	IMCB 65	Russia (Tyva Republic)	30.06.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.519	94.686	B14	B1	IMCB 66	Russia (Tyva Republic)	30.06.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	51.449	94.834	B6	B1	IMCB 68	Russia (Tyva Republic)	02.07.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.491	94.671	B14	B1	IMCB 69	Russia (Tyva Republic)	30.06.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	51.382	94.582	B6.2	B1	IMCB 70	Russia (Tyva Republic)	01.07.2017	MT024204	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	51.517	94.694	B6	B1	IMCB 72	Russia (Tyva Republic)	30.06.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	51.401	94.68	B6.2	B1	IMCB 75	Russia (Tyva Republic)	01.07.2017	MT024204	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	51.418	94.668	B14	B1	IMCB 77	Russia (Tyva Republic)	01.07.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	49.719	88.662	B6	B1	IMCB 88	Russia (Altai Republic)	01.08.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	50.031	88.608	B19.1	B1	IMCB 89	Russia (Altai Republic)	09.08.2017	MT024216	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	feather	+ +
<i>M. migrans</i>	50.029	88.618	B19.1	B1	IMCB 90	Russia (Altai Republic)	09.08.2017	MT024216	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	50.03	88.614	B14	B1	IMCB 91	Russia (Altai Republic)	05.08.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	feather	+ +
<i>M. migrans</i>	50.021	88.658	B19.1	B1	IMCB 92	Russia (Altai Republic)	31.07.2017	MT024216	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	50.025	88.641	B6.3	B1	IMCB 93	Russia (Altai Republic)	31.07.2017	MT024205	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	50.024	88.646	B6.1.1	B1	IMCB 94	Russia (Altai Republic)	31.07.2017	MT024203	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	50.032	88.604	B14	B1	IMCB 95	Russia (Altai Republic)	05.08.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +

Table A4. Continued

<i>M. migrans</i>	50.027	88.632	B14	B1	IMCB 96	Russia (Altai Republic)	31.07.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	50.023	88.65	B6.2	B1	IMCB 97	Russia (Altai Republic)	31.07.2017	MT024204	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	50.957	85.021	B6	B1	IMCB 99	Russia (Altai Republic)	22.07.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	E. Nikolenko	feather	+ +
<i>M. migrans</i>	50.027	88.632	B6	B1	IMCB 100	Russia (Altai Republic)	31.07.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	feather	+ +
<i>M. migrans</i>	50.026	88.637	B6	B1	IMCB 101	Russia (Altai Republic)	31.07.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	feather	+ +
<i>M. migrans</i>	50.028	88.628	B14	B1	IMCB 102	Russia (Altai Republic)	05.08.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	feather	+ +
<i>M. migrans</i>	50.795	85.92	B6	B1	IMCB 103	Russia (Altai Republic)	30.07.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	49.95	88.735	B19	B1	IMCB 106	Russia (Altai Republic)	05.08.2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	50.793	85.918	B14	B1	IMCB 107	Russia (Altai Republic)	30.07.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	50.948	84.751	B19	B1	IMCB 110	Russia (Altai Republic)	20.07.2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	E. Nikolenko	molted feather	+ +
<i>M. migrans</i>	50.948	84.751	B14	B1	IMCB 111	Russia (Altai Republic)	20.07.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	E. Nikolenko	molted feather	+ +
<i>M. migrans</i>	50.022	88.653	B19	B1	IMCB 112	Russia (Altai Republic)	31.07.2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	49.654	89.081	B19	B1	IMCB 113	Russia (Altai Republic)	05.08.2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	egg shell	+ +
<i>M. migrans</i>	50.077	88.727	B14	B1	IMCB 114	Russia (Altai Republic)	05.08.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	50.082	88.75	B6	B1	IMCB 117	Russia (Altai Republic)	17.06.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	pin feather	+ +
<i>M. migrans</i>	50.079	88.735	B14	B1	IMCB 119	Russia (Altai Republic)	17.06.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	pin feather	+ +
<i>M. migrans</i>	48.967	89.897	B19	B1	IMCB 120	Mongolia (Bayan-Ölgii)	14.06.2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	48.966	89.899	B19	B1	IMCB 122	Mongolia (Bayan-Ölgii)	14.06.2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	48.968	89.891	B19	B1	IMCB 123	Mongolia (Bayan-Ölgii)	14.06.2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	52.46	104.25	B14	B1	IMCB 212	Russia (Irkutsk Oblast)	26.08.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	V. & M. Alekseyenko	feather	+ +
<i>M. migrans</i>	51.94	104.733	B6	B1	IMCB 213	Russia (Irkutsk Oblast)	24.08.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	M. Alekseyenko	molted feather	+ +
<i>M. migrans</i>	51.94	104.733	B19.3	B1	IMCB 214	Russia (Irkutsk Oblast)	24.08.2017	MT024218	lineatus	Andreyenkova <i>et al.</i> 2021	M. Alekseyenko	molted feather	+ +
<i>M. migrans</i>	51.94	104.733	B6	B1	IMCB 215	Russia (Irkutsk Oblast)	24.08.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	M. Alekseyenko	molted feather	+ +
<i>M. migrans</i>	51.94	104.733	B6	B1	IMCB 216	Russia (Irkutsk Oblast)	24.08.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	M. Alekseyenko	molted feather	+ +
<i>M. migrans</i>	51.94	104.733	B6	B1	IMCB 217	Russia (Irkutsk Oblast)	24.08.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	M. Alekseyenko	molted feather	+ +
<i>M. migrans</i>	51.94	104.733	B19	B1	IMCB 218	Russia (Irkutsk Oblast)	24.08.2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	M. Alekseyenko	molted feather	+ +
<i>M. migrans</i>	51.94	104.733	B14	B1	IMCB 219	Russia (Irkutsk Oblast)	24.08.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	M. Alekseyenko	molted feather	+ +
<i>M. migrans</i>	51.94	104.733	B6	B1	IMCB 220	Russia (Irkutsk Oblast)	24.08.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	M. Alekseyenko	molted feather	+ +
<i>M. migrans</i>	51.94	104.733	B6	B1	IMCB 221	Russia (Irkutsk Oblast)	24.08.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	M. Alekseyenko	molted feather	+ +
<i>M. migrans</i>	51.94	104.733	B14	B1	IMCB 223	Russia (Irkutsk Oblast)	24.08.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	M. Alekseyenko	molted feather	+ +
<i>M. migrans</i>	51.94	104.733	B6	B1	IMCB 224	Russia (Irkutsk Oblast)	24.08.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	M. Alekseyenko	molted feather	+ +
<i>M. migrans</i>	51.94	104.733	B6	B1	IMCB 225	Russia (Irkutsk Oblast)	24.08.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	M. Alekseyenko	molted feather	+ +
<i>M. migrans</i>	51.94	104.733	B19	B1	IMCB 226	Russia (Irkutsk Oblast)	24.08.2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	M. Alekseyenko	molted feather	+ +
<i>M. migrans</i>	51.94	104.733	B14	B1	IMCB 227	Russia (Irkutsk Oblast)	24.08.2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	M. Alekseyenko	molted feather	+ +
<i>M. migrans</i>	49.555	90.481	B6	B1	IMCB 240	Mongolia (Bayan-Ölgii)	15.06.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+ +
<i>M. migrans</i>	50.048	88.268	B6	B1	IMCB 243	Russia (Altai Republic)	05.07.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+ +
<i>M. migrans</i>	51.21	94.979	B14	B1	IMCB 245	Russia (Tyva Republic)	31.05.2016	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	E. Shnayder	feather	+ +
<i>M. migrans</i>	50.258	85.7	B14	B1	IMCB 300	Russia (Altai Republic)	2017	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	E. Rakin	molted feather	+ +
<i>M. migrans</i>	50.258	85.7	B6	B1	IMCB 301	Russia (Altai Republic)	2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	E. Rakin	molted feather	+ +
<i>M. migrans</i>	50.258	85.7	B6	B1	IMCB 302	Russia (Altai Republic)	2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	E. Rakin	molted feather	+ +
<i>M. migrans</i>	50.258	85.7	B19	B1	IMCB 303	Russia (Altai Republic)	2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	E. Rakin	molted feather	+ +

Table A4. Continued

<i>M. migrans</i>	50.258	85.7	B6	B1	IMCB 304	Russia (Altai Republic)	2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	E. Rakin	molted feather	+	+
<i>M. migrans</i>	50.258	85.7	B6	B1	IMCB 305	Russia (Altai Republic)	2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	E. Rakin	molted feather	+	+
<i>M. migrans</i>	50.258	85.7	B19.1	B1	IMCB 306	Russia (Altai Republic)	2017	MT024216	lineatus	Andreyenkova <i>et al.</i> 2021	E. Rakin	molted feather	+	+
<i>M. migrans</i>	52.295	85.837	B14	B1	IMCB 321	Russia (Altai Krai)	15.05.2009	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	51.21	94.979	B6	B1	IMCB 323	Russia (Tyva Republic)	22.06.2011	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	51.211	94.978	B14	B1	IMCB 327	Russia (Tyva Republic)	22.06.2006	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	50.859	92.659	B19	B1	IMCB 330	Russia (Tyva Republic)	18.06.2008	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	47.978	90.546	B19	B1	IMCB 331	Mongolia (Bayan-Ölgii)	17.06.2016	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	49.719	88.662	B6	B1	IMCB 355	Russia (Altai Republic)	01.08.2017	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	51.007	85.054	B19	B1	IMCB 356	Russia (Altai Republic)	23.07.2017	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	I. Karyakin	egg shell	+	+
<i>M. migrans</i>	51.705	101.526	B14	B1	IMCB 589	Russia (Republic of Buryatia)	02.08.2018	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	I. Fefelov	molted feather	+	+
<i>M. migrans</i>	50.929	84.762	B14	B1	IMCB 600	Russia (Altai Republic)	10.09.2018	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+	+
<i>M. migrans</i>	50.929	84.762	B14	B1	IMCB 621	Russia (Altai Republic)	10.09.2018	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+	+
<i>M. migrans</i>	50.929	84.762	B14	B1	IMCB 622	Russia (Altai Republic)	10.09.2018	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+	+
<i>M. migrans</i>	50.929	84.762	B19	B1	IMCB 623	Russia (Altai Republic)	10.09.2018	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+	+
<i>M. migrans</i>	50.929	84.762	B14	B1	IMCB 624	Russia (Altai Republic)	10.09.2018	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+	+
<i>M. migrans</i>	35.088	128.909	B19	B1	IN1594	South Korea	04.01.2017	MG930481	lineatus	Jeon <i>et al.</i> 2018			+	+
<i>M. migrans</i>	44.405	105.354	B19	B1	IPMB 23840	Mongolia (South Gobi)	26.6.2002	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	44.417	105.317	B19.4	B1	IPMB 23841	Mongolia (South Gobi)	27.6.2002	MT024219	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	44.417	105.317	B14	B1	IPMB 23844	Mongolia (South Gobi)	27.6.2002	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	42.3	105.633	B19	B1	IPMB 23851	Mongolia (South Gobi)	27.6.2002	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	42.577	105.339	B19	B1	IPMB 23853	Mongolia (South Gobi)	3.7.2002	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	50.067	106.167	B6	B1	IPMB 23883	Mongolia (Selenge)	2000	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	50.067	106.167	B14	B1	IPMB 23885	Mongolia (Selenge)	2001	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	50.067	106.167	B6	B1	IPMB 23887	Mongolia (Selenge)	2001	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	50.067	106.167	B6	B1	IPMB 23889	Mongolia (Selenge)	2001	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	42.456	105.364	B6	B1	IPMB 23890	Mongolia (South Gobi)	20.07.2001	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	44.41	105.351	B19	B1	IPMB 23894	Mongolia (South Gobi)	26.6.2002	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	44.405	105.355	B14	B1	IPMB 23895	Mongolia (South Gobi)	26.6.2002	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	44.402	105.358	B14	B1	IPMB 23899	Mongolia (South Gobi)	18.7.2001	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	44.404	105.358	B19.4	B1	IPMB 23900	Mongolia (South Gobi)	18.7.2001	MT024219	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	44.417	105.317	B14	B1	IPMB 23902	Mongolia (South Gobi)	18.7.2001	MT024210	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	44.417	105.317	B19	B1	IPMB 23903	Mongolia (South Gobi)	18.7.2001	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	44.413	105.36	B19.1	B1	IPMB 23904	Mongolia (South Gobi)	18.7.2001	MT024216	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	44.405	105.354	B19.1	B1	IPMB 23905	Mongolia (South Gobi)	18.7.2001	MT024216	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	44.417	105.317	B19.1	B1	IPMB 23906	Mongolia (South Gobi)	18.7.2001	MT024216	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	36.37	138.63	B19	B1	IPMB 24813	Japan	2003	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	K. Nakajima	blood	+	+
<i>M. migrans</i>	36.37	138.63	B14.1	B1	IPMB 24814	Japan	2003	MT024211	lineatus	Andreyenkova <i>et al.</i> 2021	K. Nakajima	blood	+	+
<i>M. migrans</i>	36.37	138.63	B19	B1	IPMB 24869	Japan	2003	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	K. Nakajima		+	+
<i>M. migrans</i>	51.7	94.433	B6	B1	IPMB 25689	Russia (Tyva Republic)	2003	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+
<i>M. migrans</i>	51.7	94.433	B19	B1	IPMB 25690	Russia (Tyva Republic)	2003	MT024215	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+	+

Table A4. Continued

<i>M. migrans</i>	51.7	94.433	B6	B1	IPMB 25691	Russia (Tyva Republic)	2003	MT024201	lineatus	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	35.025	135.864	B19	B1	UMMZ 96560	Japan	05.03.1936	AY994393	lineatus	Johnson <i>et al.</i> 2005			+ +
<i>M. migrans</i>			B19	B1		Japan		LC666826	lineatus	Nagai & Tokita in press			+ +
<i>M. migrans</i>			B19	B1		Japan		LC666827	lineatus	Nagai & Tokita in press			+ +
<i>M. migrans</i>			B19.5	B1		Japan		LC666828	lineatus	Nagai & Tokita in press			+ +
<i>M. migrans</i>			B19.6	B1		Japan		LC666829	lineatus	Nagai & Tokita in press			+ +
<i>M. migrans</i>			B19	B1		Japan		LC666830	lineatus	Nagai & Tokita in press			+ +
<i>M. migrans</i>			B19	B1		Japan		LC666831	lineatus	Nagai & Tokita in press			+ +
<i>M. migrans</i>	-16.192	142.833	B20	B2	ANWC B57592	Australia (Queensland)	24.07.2015	MT024220	affinis	Andreyenkova <i>et al.</i> 2021	CSIRO	liver	+ +
<i>M. migrans</i>	-16.617	145.333	B20	B2	ANWC B34111	Australia (Queensland)	04.08.2001	MT024220	affinis	Andreyenkova <i>et al.</i> 2021	CSIRO	liver	+ +
<i>M. migrans</i>	-8.995	148.519	B20	B2	ANWC B57670	Papua New Guinea	03.07.2016	MT024220	affinis	Andreyenkova <i>et al.</i> 2021	CSIRO	liver	+ +
<i>M. migrans</i>	-8.612	148.324	B20.4	B2	ANWC B57629	Papua New Guinea	30.06.2016	MT024226	affinis	Andreyenkova <i>et al.</i> 2021	CSIRO	liver	+ +
<i>M. migrans</i>	-16.45	141.583	B20	B2	ANWC B32210	Australia (Queensland)	05.06.1999	MT024220	affinis	Andreyenkova <i>et al.</i> 2021	CSIRO	liver	+ +
<i>M. migrans</i>	-19.264	146.695	B20.5	B2	ANWC B53862	Australia (Queensland)	01.02.2001	MT024227	affinis	Andreyenkova <i>et al.</i> 2021	CSIRO	liver	+ +
<i>M. migrans</i>	-17.267	145.483	B20	B2	ANWC B32576	Australia (Queensland)	01.01.2000	MT024220	affinis	Andreyenkova <i>et al.</i> 2021	CSIRO	liver	+ +
<i>M. migrans</i>	-16.932	145.744	B20	B2	ANWC B53853	Australia (Queensland)		MT024220	affinis	Andreyenkova <i>et al.</i> 2021	CSIRO	liver	+ +
<i>M. migrans</i>	-12.577	131.966	B20.5	B2	IMCB 603	Australia (Northern Territory)	16.04.2018	MT024227	affinis	Andreyenkova <i>et al.</i> 2021	W. Riddell	feather	+ +
<i>M. migrans</i>	-12.659	131.328	B20	B2	IMCB 604	Australia (Northern Territory)	30.03.2018	MT024220	affinis	Andreyenkova <i>et al.</i> 2021	W. Riddell	feather	+ +
<i>M. migrans</i>	-12.681	131.38	B20	B2	IMCB 605	Australia (Northern Territory)	29.04.2018	MT024220	affinis	Andreyenkova <i>et al.</i> 2021	W. Riddell	feather	+ +
<i>M. migrans</i>	-5.134	119.465	B20.10	B2	AMNH 532051	Indonesia	11.1895	AY994398	affinis	Johnson <i>et al.</i> 2005			+ +
<i>M. migrans</i>	-17.319	123.645	B20	B2	AMNH 532063	Australia (Western Australia)	09.05.1911	AY994396	affinis	Johnson <i>et al.</i> 2005			+ +
<i>M. migrans</i>	-17.669	141.096	B20	B2	AMNH 532081	Australia (Queensland)	03.05.1914	AY994395	affinis	Johnson <i>et al.</i> 2005			+ +
<i>M. migrans</i>	-5.964	144.803	B20	B2	AMNH 704655	Papua New Guinea	05.1952	AY994397	affinis	Johnson <i>et al.</i> 2005			+ +
<i>M. migrans</i>	-16.15	136.44	B20.6	B2	IPMB 23896	Australia (Northern Territory)		MT024228	affinis	Andreyenkova <i>et al.</i> 2021	J. Olsen	feather	+ +
<i>M. migrans</i>	-17.954	122.239	B20.7	B2	IPMB 25079	Australia (Western Australia)	.9.1997	MT024229	affinis	Andreyenkova <i>et al.</i> 2021	H. McArthur	muscle	+ +
<i>M. migrans</i>	-16.15	136.44	B20	B2	IPMB 29914	Australia (Northern Territory)		MT024220	affinis	Andreyenkova <i>et al.</i> 2021	J. Olsen	feather	+ +
<i>M. migrans</i>	-16.15	136.44	B20	B2	IPMB 29916	Australia (Northern Territory)		MT024220	affinis	Andreyenkova <i>et al.</i> 2021	J. Olsen	feather	+ +
<i>M. aegyptius</i>	10.006	8.288	F22	F2	3LF-2835	Nigeria	09.07.1905	MH536180	par./aeg.	Heneberg <i>et al.</i> unpubl.	P. Echi		+ +
<i>M. aegyptius</i>	10.006	8.288	F22	F2	3LF-4002	Nigeria	10.07.1905	MH536181	par./aeg.	Heneberg <i>et al.</i> unpubl.	P. Echi		+ +
<i>M. aegyptius</i>	0.264	6.568	F22.1	F2	AMNH 264858	Saõ Tomé and Príncipe	29.03.1928	AY994412	par./aeg.	Johnson <i>et al.</i> 2005			+ +
<i>M. aegyptius</i>	5.835	12.589	F22	F2	AMNH 388140	Cameroon	22.04.1905	AY994408	par./aeg.	Johnson <i>et al.</i> 2005			+ +
<i>M. aegyptius</i>	14.772	-16.976	F22	F2	AMNH 531965	Senegal	30.04.1908	AY994411	par./aeg.	Johnson <i>et al.</i> 2005			+ +
<i>M. aegyptius</i>	9.025	7.739	F22	F2	AMNH 531971	Nigeria	22.12.1919	AY994409	par./aeg.	Johnson <i>et al.</i> 2005			+ +
<i>M. aegyptius</i>	15.211	45.928	F22.2	F2	AMNH 532038	Yemen	13.08.1913	AY994405	par./aeg.	Johnson <i>et al.</i> 2005			+ +
<i>M. aegyptius</i>	2.703	34.083	F22	F2	AMNH 789260	Uganda	04.02.1956	AY994406	par./aeg.	Johnson <i>et al.</i> 2005			+ +
<i>M. aegyptius</i>	8.096	-5.616	F22	F2	IPMB 25546	Ivory Coast	29.01.2004	MT024234	par./aeg.	Andreyenkova <i>et al.</i> 2021	G. Rondeau & J. Scheider	blood	+ +
<i>M. aegyptius</i>	8.096	-5.616	F22	F2	IPMB 25547	Ivory Coast	29.01.2004	MT024234	par./aeg.	Andreyenkova <i>et al.</i> 2021	G. Rondeau & J. Scheider	blood	+ +
<i>M. aegyptius</i>	8.096	-5.616	F22	F2	IPMB 25548	Ivory Coast	29.01.2004	MT024234	par./aeg.	Andreyenkova <i>et al.</i> 2021	G. Rondeau & J. Scheider	blood	+ +
<i>M. aegyptius</i>	8.096	-5.616	F22 ¹	F2	IPMB 25550	Ivory Coast	29.01.2004		par./aeg.	Andreyenkova <i>et al.</i> 2021	G. Rondeau & J. Scheider	blood	+
<i>M. aegyptius</i>	8.096	-5.616	F22 ¹	F2	IPMB 25552	Ivory Coast	29.01.2004		par./aeg.	Andreyenkova <i>et al.</i> 2021	G. Rondeau & J. Scheider	blood	+
<i>M. aegyptius</i>	8.096	-5.616	F22 ¹	F2	IPMB 25553	Ivory Coast	29.01.2004		par./aeg.	Andreyenkova <i>et al.</i> 2021	G. Rondeau & J. Scheider	blood	+

Table A4. Continued

<i>M. aegyptius</i>	8.096	-5.616	F22 ¹	F2	IPMB 25554	Ivory Coast	29.01.2004		par./aeg.	Andreyenkova <i>et al.</i> 2021	G. Rondeau & J. Scheider	blood	+
<i>M. migrans</i>	48.767	16.667	A4	A	CT781	Czechia	01.07.2016	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	48.483	22.067	A4	A	D5609	Slovakia	01.07.2016	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	48.8	16.583	A11	A	CT1923	Czechia	22.07.2017	MT024208	migrans	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	41.65	25.917	A13G	A	KITE28	Bulgaria	21.06.2017	MT024209	migrans	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	48.767	16.867	A4.2.1	A	CT775	Czechia	02.07.2016	MT024197	migrans	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	49.667	12.817	A4.2	A	C155543	Czechia	26.06.2016	MT024196	migrans	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	49.1	14.7	A4	A	C159265	Czechia	22.06.2016	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	48.783	17.067	A3	A	CT1926	Czechia	11.07.2017	MT024189	migrans	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	48.95	16.533	A4	A	CT1925	Czechia	11.07.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	48.767	16.867	A4.2.1	A	CT1922	Czechia	03.07.2017	MT024197	migrans	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	48.483	21.917	A4	A	D6164	Slovakia	24.06.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	48.367	21.833	A5	A	D6163	Slovakia	24.06.2017	MT024199	migrans	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	49.873	24.496	A3.4	A	L9147	Ukraine	30.06.2018	MK140572 ²	migrans	Literák <i>et al.</i> 2019		pin feather	+ +
<i>M. migrans</i>	42.046	11.977	A4	A	IMCB 581	Italy (Lazio)	29.06.2018	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	G. Dell'Omo	blood	+ +
<i>M. migrans</i>	41.903	12.496	A3	A	IMCB 583	Italy (Lazio)	01.06.2018	MT024189	migrans	Andreyenkova <i>et al.</i> 2021	G. Dell'Omo	feather	+ +
<i>M. migrans</i>	41.903	12.496	A3	A	IMCB 584	Italy (Lazio)	01.06.2018	MT024189	migrans	Andreyenkova <i>et al.</i> 2021	G. Dell'Omo	feather	+ +
<i>M. migrans</i>	41.874	12.457	A5	A	IMCB 627	Italy (Lazio)	29.06.2018	MT024199	migrans	Andreyenkova <i>et al.</i> 2021	G. Dell'Omo	blood	+ +
<i>M. migrans</i>	41.762	12.442	A5	A	IMCB 628	Italy (Lazio)	26.06.2017	MT024199	migrans	Andreyenkova <i>et al.</i> 2021	G. Dell'Omo	blood	+ +
<i>M. migrans</i>	41.757	12.457	A3.3	A	IMCB 629	Italy (Lazio)	26.06.2017	MT024192	migrans	Andreyenkova <i>et al.</i> 2021	G. Dell'Omo	blood	+ +
<i>M. migrans</i>	48.65	16.91	A3 ¹	A	1177	Czechia	summer 2014	KU670079	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.68	16.98	A10 ¹	A	1179	Czechia	summer 2014	KU670086	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.95	16.6	A3.3 ¹	A	1985	Czechia	summer 2014	KU670079	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.95	16.6	A4.2.1 ¹	A	1989	Czechia	summer 2014	KU670080	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.73	16.88	A4 ¹	A	1992	Czechia	summer 2014	KU670080	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.82	16.8	A4 ¹	A	1993	Czechia	summer 2014	KU670080	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.83	16.77	A11 ¹	A	1996	Czechia	summer 2014	KU670087	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.72	16.88	A11 ¹	A	1999	Czechia	summer 2014	KU670087	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.68	16.92	A3 ¹	A	2000	Czechia	summer 2014	KU670079	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.65	16.93	A4 ¹	A	2001	Czechia	summer 2014	KU670080	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.68	16.97	A4 ¹	A	2003	Czechia	summer 2014	KU670080	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	51.05	11.18	A4 ¹	A	2046	Germany (Thuringia)	summer 2014	KU670080	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.93	16.62	A4 ¹	A	2065	Czechia	summer 2014	KU670080	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.95	16.62	A4 ¹	A	2066	Czechia	summer 2014	KU670080	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.98	16.57	A5 ¹	A	2069	Czechia	summer 2014	KU670081	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.95	16.57	A5 ¹	A	2070	Czechia	summer 2014	KU670081	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.98	16.65	A3 ¹	A	2071	Czechia	summer 2014	KU670079	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	48.68	16.92	A3 ¹	A	2072	Czechia	summer 2014	KU670079	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	49.1	14.7	A4 ¹	A	2073	Czechia	summer 2014	KU670080	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	49.07	14.72	A4 ¹	A	2075	Czechia	summer 2014	KU670080	migrans	Heneberg <i>et al.</i> 2016			+
<i>M. migrans</i>	49.07	14.72	A4 ¹	A	2076	Czechia	summer 2014	KU670080	migrans	Heneberg <i>et al.</i> 2016			+

Table A4. Continued

<i>M. migrans</i>	51.883	11.317	A3	A	IPMB 23859	Germany (Saxony-Anhalt)	6.6.2002	MT024189	migrans	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	52.517	11.317	A4	A	IPMB 23861	Germany (Saxony-Anhalt)	9.6.2002	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	51.883	11.317	A4	A	IPMB 23864	Germany (Saxony-Anhalt)	10.6.2002	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	51.883	11.317	A4	A	IPMB 23865	Germany (Saxony-Anhalt)	10.6.2002	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	51.883	11.317	A4	A	IPMB 23866	Germany (Saxony-Anhalt)	10.6.2002	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	51.883	11.317	A3	A	IPMB 23868	Germany (Saxony-Anhalt)	10.6.2002	MT024189	migrans	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	51.8	11.05	A4	A	IPMB 23869	Germany (Saxony-Anhalt)	12.6.2002	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	51.917	11.05	A10	A	IPMB 23871	Germany (Saxony-Anhalt)	14.6.2002	MT024207	migrans	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	51.917	11.05	A10	A	IPMB 23872	Germany (Saxony-Anhalt)	14.6.2002	MT024207	migrans	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	51.85	11.25	A4	A	IPMB 23874	Germany (Saxony-Anhalt)	14.6.2002	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	51.817	11.2	A4	A	IPMB 23876	Germany (Saxony-Anhalt)	19.6.2002	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	51.883	11.317	A3.5	A	IPMB 23878	Germany (Saxony-Anhalt)	21.6.2002	MT024193	migrans	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	51.883	11.317	A5	A	IPMB 23879	Germany (Saxony-Anhalt)	21.6.2002	MT024199	migrans	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	51.883	11.317	A4	A	IPMB 23880	Germany (Saxony-Anhalt)	21.6.2002	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	M. Stubbe	blood	+ +
<i>M. migrans</i>	48.1	8.933	A5	A	IPMB 25227	Germany (Baden-Württemberg)	2003	MT024199	migrans	Andreyenkova <i>et al.</i> 2021	E. Thielscher	feather	+ +
<i>M. migrans</i>	50.744	4.657	A4.2	A	IPMB 28271	Belgium		MT024196	migrans	Andreyenkova <i>et al.</i> 2021	Merlin Zoo	blood	+ +
<i>M. migrans</i>	47.65	11.35	A3	A	IPMB 41494	Germany (Bavaria)	27.6.2006	MT024189	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	tissue	+ +
<i>M. migrans</i>	47.85	12.00	A3	A	IPMB 41558	Germany (Bavaria)	12.8.2006	MT024189	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	feather	+ +
<i>M. migrans</i>	52.417	13.25	A4	A	IPMB 47601	Germany (Berlin)	2008	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	H. Dannecker	blood	+ +
<i>M. migrans</i>	47.85	12.117	A3	A	IPMB 47636	Germany (Bavaria)	2008	MT024189	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	tissue	+ +
<i>M. migrans</i>	47.65	11.367	A4.2	A	IPMB 62437	Germany (Bavaria)	2011	MT024196	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	tissue	+ +
<i>M. migrans</i>	47.783	11.2	A4	A	IPMB 62450	Germany (Bavaria)	2011	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	tissue	+ +
<i>M. migrans</i>	47.667	11.3	A13G	A	IPMB 79340	Germany (Bavaria)	17.6.2014	MT024209	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	tissue	+ +
<i>M. migrans</i>	47.767	12.00	A4	A	IPMB 91881	Germany (Bavaria)	10.6.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	feather	+ +
<i>M. migrans</i>	50.155	11.564	A4.2	A	IPMB 9927	Germany (Bavaria)		MT024196	migrans	Andreyenkova <i>et al.</i> 2021	C. Fentzloff	blood	+ +
<i>M. migrans</i>	43.533	4.5	A4	A	IPMB 9929	France	1999	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	E. Hennig		+ +
<i>M. migrans</i>	50.3	14.333	A15.1	A	C155855	Czechia	26.07.2017	MT024213	migrans	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	48.7	17.00	A15	A	2004	Czechia	summer 2014	MT024212 ³	migrans	Heneberg <i>et al.</i> 2016			+ +
<i>M. migrans</i>	47.9	11.417	A15	A	IPMB 41497	Germany (Bavaria)	16.6.2006	MT024212	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	tissue	+ +
<i>M. migrans</i>	47.9	11.417	A15	A	IPMB 44722	Germany (Bavaria)	.6.2007	MT024212	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	tissue	+ +
<i>M. migrans</i>	48.75	17.03	B14 ¹	B1	2005	Czechia	summer 2014	KU670090	migrans	Heneberg <i>et al.</i> 2016			+ +
<i>M. migrans</i>	51.33	14.2	B6 ¹	B1	2149	Germany (Saxony)	summer 2014	KU670082	migrans	Heneberg <i>et al.</i> 2016			+ +
<i>M. migrans</i>	51.32	14.28	B6 ¹	B1	2163	Germany (Saxony)	summer 2014	KU670082	migrans	Heneberg <i>et al.</i> 2016			+ +
<i>M. migrans</i>	8.748	76.697	B20.2	B2	IMCB 372	India (Kerala)	19.11.2017	MT024222	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	8.382	76.986	B20	B2	IMCB 380	India (Kerala)	22.11.2017	MT024220	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	8.385	76.982	B20	B2	IMCB 408	India (Kerala)	06.04.2018	MT024220	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	8.385	76.982	B20.8	B2	IMCB 414	India (Kerala)	06.04.2018	MT024230	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	8.385	76.982	B20	B2	IMCB 415	India (Kerala)	06.04.2018	MT024220	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	8.385	76.982	B20	B2	IMCB 416	India (Kerala)	06.04.2018	MT024220	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	8.382	76.986	B20	B2	IMCB 438	India (Kerala)	06.04.2018	MT024220	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	8.382	76.986	B20	B2	IMCB 439	India (Kerala)	06.04.2018	MT024220	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +

Table A4. Continued

<i>M. migrans</i>	54.839	83.08	A3.1	A	IMCB 134	Russia (Novosibirsk Oblast)	20.07.2017	MT024190	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. Andreyenkov	feather	+ +
<i>M. migrans</i>	54.896	83.161	A3	A	IMCB 139	Russia (Novosibirsk Oblast)	25.04.2017	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. Andreyenkov	feather	+ +
<i>M. migrans</i>	54.892	83.158	A5	A	IMCB 143	Russia (Novosibirsk Oblast)	24.07.2017	MT024199	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	48.711	71.635	A3	A	IMCB 151	Kazakhstan (Karaganda)	27.09.2017	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+ +
<i>M. migrans</i>	48.711	71.635	A4	A	IMCB 153	Kazakhstan (Karaganda)	27.09.2017	MT024194	mig./lin.	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+ +
<i>M. migrans</i>	48.711	71.635	A3	A	IMCB 156	Kazakhstan (Karaganda)	27.09.2017	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+ +
<i>M. migrans</i>	48.711	71.635	A5	A	IMCB 158	Kazakhstan (Karaganda)	27.09.2017	MT024199	mig./lin.	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+ +
<i>M. migrans</i>	48.711	71.635	A3	A	IMCB 179	Kazakhstan (Karaganda)	27.09.2017	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+ +
<i>M. migrans</i>	54.879	73.425	A5	A	IMCB 229	Russia (Omsk Oblast)	18.09.2017	MT024199	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Voronin	molted feather	+ +
<i>M. migrans</i>	54.879	73.425	A3	A	IMCB 230	Russia (Omsk Oblast)	18.09.2017	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Voronin	molted feather	+ +
<i>M. migrans</i>	54.879	73.425	A3	A	IMCB 234	Russia (Omsk Oblast)	18.09.2017	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Voronin	molted feather	+ +
<i>M. migrans</i>	54.879	73.425	A4.1	A	IMCB 237	Russia (Omsk Oblast)	18.09.2017	MT024195	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Voronin	molted feather	+ +
<i>M. migrans</i>	47.993	80.408	A3	A	IMCB 247	Kazakhstan (East Kazakhstan)	14.09.2017	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+ +
<i>M. migrans</i>	47.993	80.408	A4	A	IMCB 252	Kazakhstan (East Kazakhstan)	14.09.2017	MT024194	mig./lin.	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+ +
<i>M. migrans</i>	47.993	80.408	A10	A	IMCB 255	Kazakhstan (East Kazakhstan)	14.09.2017	MT024207	mig./lin.	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+ +
<i>M. migrans</i>	47.993	80.408	A4	A	IMCB 261	Kazakhstan (East Kazakhstan)	14.09.2017	MT024194	mig./lin.	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+ +
<i>M. migrans</i>	43.545	76.783	A3	A	IMCB 270	Kazakhstan (Almaty)	03.09.2017	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	V. Fedorenko	molted feather	+ +
<i>M. migrans</i>	43.545	76.783	A5	A	IMCB 274	Kazakhstan (Almaty)	03.09.2017	MT024199	mig./lin.	Andreyenkova <i>et al.</i> 2021	V. Fedorenko	molted feather	+ +
<i>M. migrans</i>	43.545	76.783	A3	A	IMCB 276	Kazakhstan (Almaty)	03.09.2017	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	V. Fedorenko	molted feather	+ +
<i>M. migrans</i>	43.545	76.783	A3	A	IMCB 290	Kazakhstan (Almaty)	27.08.2017	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	V. Fedorenko	molted feather	+ +
<i>M. migrans</i>	43.545	76.783	A3	A	IMCB 292	Kazakhstan (Almaty)	27.08.2017	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	V. Fedorenko	molted feather	+ +
<i>M. migrans</i>	43.545	76.783	A4	A	IMCB 293	Kazakhstan (Almaty)	27.08.2017	MT024194	mig./lin.	Andreyenkova <i>et al.</i> 2021	V. Fedorenko	molted feather	+ +
<i>M. migrans</i>	53.092	82.534	A4	A	IMCB 325	Russia (Altai Kray)	26.07.2015	MT024194	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	52.633	81.611	A4	A	IMCB 332	Russia (Altai Kray)	04.08.2015	MT024194	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	53.936	80.628	A3	A	IMCB 335	Russia (Altai Kray)	27.08.2017	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	feather	+ +
<i>M. migrans</i>	54.015	80.904	A3	A	IMCB 336	Russia (Altai Kray)	30.08.2017	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	feather	+ +
<i>M. migrans</i>	53.822	81.261	A5	A	IMCB 338	Russia (Altai Kray)	30.08.2017	MT024199	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	53.822	81.261	A10	A	IMCB 339	Russia (Altai Kray)	30.08.2017	MT024207	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	54.1	81.029	A4	A	IMCB 341	Russia (Altai Kray)	11.08.2017	MT024194	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	53.949	80.766	A4	A	IMCB 342	Russia (Altai Kray)	26.08.2017	MT024194	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	feather	+ +
<i>M. migrans</i>	53.949	80.766	A4	A	IMCB 345	Russia (Altai Kray)	26.08.2017	MT024194	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	feather	+ +
<i>M. migrans</i>	53.822	81.261	A4	A	IMCB 351	Russia (Altai Kray)	30.08.2017	MT024194	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	53.822	81.261	A4	A	IMCB 352	Russia (Altai Kray)	30.08.2017	MT024194	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	53.822	81.261	A5	A	IMCB 353	Russia (Altai Kray)	30.08.2017	MT024199	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	54.65	83.353	A5	A	IMCB 555	Russia (Novosibirsk Oblast)	23.08.2017	MT024199	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	52.548	85.419	A3	A	C835583	Russia (Altai Kray)	07.07.2018	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	52.514	85.362	A3	A	C835587	Russia (Altai Kray)	08.07.2018	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	52.457	85.168	A3	A	C835590	Russia (Altai Kray)	09.07.2018	MT024189	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	52.457	85.168	A4	A	C835594	Russia (Altai Kray)	10.07.2018	MT024194	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	56.039	92.992	A4	A	IMCB 585	Russia (Krasnoyarsk Kray)	07.10.2017	MT024194	mig./lin.	Andreyenkova <i>et al.</i> 2021	T. Veselova	molted feather	+ +
<i>M. migrans</i>	56	92.9	A10	A	IPMB 41286	Russia (Krasnoyarsk Kray)	2006	MT024207	mig./lin.	Andreyenkova <i>et al.</i> 2021	E. Ekimov	tissue	+ +

Table A4. Continued

<i>M. migrans</i>	54.892	83.158	B6	B1	IMCB 1	Russia (Novosibirsk Oblast)	04.06.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	feather	+ +
<i>M. migrans</i>	54.892	83.158	B14	B1	IMCB 2	Russia (Novosibirsk Oblast)	18.07.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	54.892	83.158	B14	B1	IMCB 3	Russia (Novosibirsk Oblast)	18.07.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	54.662	82.889	B14	B1	IMCB 4	Russia (Novosibirsk Oblast)	09.07.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	54.892	83.158	B14	B1	IMCB 6	Russia (Novosibirsk Oblast)	09.07.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	54.892	83.158	B6	B1	IMCB 7	Russia (Novosibirsk Oblast)	09.07.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	54.892	83.158	B6	B1	IMCB 10	Russia (Novosibirsk Oblast)	09.07.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	54.892	83.158	B6	B1	IMCB 11	Russia (Novosibirsk Oblast)	09.07.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	54.892	83.158	B14	B1	IMCB 12	Russia (Novosibirsk Oblast)	09.07.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	54.358	83.066	B14	B1	IMCB 14	Russia (Novosibirsk Oblast)	11.07.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	54.358	83.066	B19.1	B1	IMCB 17	Russia (Novosibirsk Oblast)	11.07.2017	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	54.847	83.001	B19.1	B1	IMCB 26	Russia (Novosibirsk Oblast)	19.08.2017	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	54.847	83.001	B6	B1	IMCB 27	Russia (Novosibirsk Oblast)	19.08.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	54.847	83.001	B14	B1	IMCB 28	Russia (Novosibirsk Oblast)	19.08.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	54.847	83.001	B6	B1	IMCB 29	Russia (Novosibirsk Oblast)	19.08.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	54.847	83.001	B6	B1	IMCB 30	Russia (Novosibirsk Oblast)	19.08.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	55.049	83.066	B19.1	B1	IMCB 35	Russia (Novosibirsk Oblast)	06.09.2017	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	55.049	83.066	B6	B1	IMCB 37	Russia (Novosibirsk Oblast)	06.09.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	55.049	83.066	B14	B1	IMCB 42	Russia (Novosibirsk Oblast)	06.09.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	55.049	83.066	B19.1	B1	IMCB 43	Russia (Novosibirsk Oblast)	06.09.2017	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+ +
<i>M. migrans</i>	54.524	90.234	B19	B1	IMCB 49	Russia (Republic of Khakassia)	04.07.2017	MT024215	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	54.863	83.029	B19.1	B1	IMCB 78	Russia (Novosibirsk Oblast)	18.07.2017	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	D. Shtol	pin feather	+ +
<i>M. migrans</i>	54.881	83.033	B6	B1	IMCB 80	Russia (Novosibirsk Oblast)	18.07.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	D. Shtol	pin feather	+ +
<i>M. migrans</i>	54.858	83.031	B6	B1	IMCB 81	Russia (Novosibirsk Oblast)	18.07.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	D. Shtol	pin feather	+ +
<i>M. migrans</i>	54.871	83.027	B14	B1	IMCB 82	Russia (Novosibirsk Oblast)	18.07.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	D. Shtol	pin feather	+ +
<i>M. migrans</i>	54.302	81.766	B19.1	B1	IMCB 83	Russia (Novosibirsk Oblast)	11.07.2017	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	54.294	81.742	B19.1	B1	IMCB 84	Russia (Novosibirsk Oblast)	11.07.2017	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	54.949	83.046	B19	B1	IMCB 85	Russia (Novosibirsk Oblast)	13.07.2017	MT024215	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	54.662	82.892	B14	B1	IMCB 86	Russia (Novosibirsk Oblast)	09.07.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	54.302	81.766	B19.2	B1	IMCB 87	Russia (Novosibirsk Oblast)	11.07.2017	MT024217	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	pin feather	+ +
<i>M. migrans</i>	54.947	83.045	B19.1	B1	IMCB 104	Russia (Novosibirsk Oblast)	13.07.2017	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. Andreyenkov	molted feather	+ +
<i>M. migrans</i>	54.658	82.884	B19.1	B1	IMCB 105	Russia (Novosibirsk Oblast)	16.07.2017	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. Andreyenkov	molted feather	+ +
<i>M. migrans</i>	54.047	83.401	B19	B1	IMCB 108	Russia (Novosibirsk Oblast)	29.07.2017	MT024215	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	feather	+ +
<i>M. migrans</i>	52.274	81.442	B14	B1	IMCB 116	Russia (Altai Kray)	18.05.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	egg shell	+ +
<i>M. migrans</i>	53.326	92.178	B6	B1	IMCB 118	Russia (Krasnoyarsk Kray)	05.06.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	muscle	+ +
<i>M. migrans</i>	52.192	81.294	B14	B1	IMCB 121	Russia (Altai Kray)	18.05.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+ +
<i>M. migrans</i>	52.192	81.294	B19	B1	IMCB 124	Russia (Altai Kray)	18.05.2017	MT024215	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	feather	+ +
<i>M. migrans</i>	54.839	83.08	B6	B1	IMCB 125	Russia (Novosibirsk Oblast)	20.07.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. Andreyenkov	feather	+ +
<i>M. migrans</i>	54.839	83.08	B19	B1	IMCB 126	Russia (Novosibirsk Oblast)	20.07.2017	MT024215	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. Andreyenkov	feather	+ +
<i>M. migrans</i>	54.839	83.08	B14	B1	IMCB 127	Russia (Novosibirsk Oblast)	20.07.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. Andreyenkov	feather	+ +
<i>M. migrans</i>	54.839	83.08	B14	B1	IMCB 128	Russia (Novosibirsk Oblast)	20.07.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. Andreyenkov	feather	+ +

Table A4. Continued

<i>M. migrans</i>	43.545	76.783	B6	B1	IMCB 296	Kazakhstan (Almaty)	27.08.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	V. Fedorenko	molted feather	+	+
<i>M. migrans</i>	43.545	76.783	B6	B1	IMCB 297	Kazakhstan (Almaty)	27.08.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	V. Fedorenko	molted feather	+	+
<i>M. migrans</i>	43.545	76.783	B6	B1	IMCB 298	Kazakhstan (Almaty)	27.08.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	V. Fedorenko	molted feather	+	+
<i>M. migrans</i>	43.545	76.783	B6	B1	IMCB 299	Kazakhstan (Almaty)	27.08.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	V. Fedorenko	molted feather	+	+
<i>M. migrans</i>	54.358	83.066	B14	B1	IMCB 317	Russia (Novosibirsk Oblast)	11.07.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+	+
<i>M. migrans</i>	54.358	83.066	B6	B1	IMCB 318	Russia (Novosibirsk Oblast)	11.07.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+	+
<i>M. migrans</i>	54.358	83.066	B6	B1	IMCB 319	Russia (Novosibirsk Oblast)	11.07.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+	+
<i>M. migrans</i>	53.072	82.368	B14	B1	IMCB 322	Russia (Altai Kray)	27.07.2015	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	52.712	81.666	B14	B1	IMCB 324	Russia (Altai Kray)	31.07.2015	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	feather	+	+
<i>M. migrans</i>	53.093	82.53	B14	B1	IMCB 326	Russia (Altai Kray)	26.07.2015	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	52.606	81.517	B6	B1	IMCB 328	Russia (Altai Kray)	03.08.2015	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	52.593	81.509	B14	B1	IMCB 329	Russia (Altai Kray)	03.08.2015	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	52.882	81.074	B6	B1	IMCB 333	Russia (Altai Kray)	18.07.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	feather	+	+
<i>M. migrans</i>	53.822	81.261	B6	B1	IMCB 337	Russia (Altai Kray)	30.08.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	54.099	81.018	B14	B1	IMCB 340	Russia (Altai Kray)	11.08.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	54.097	81.471	B6	B1	IMCB 343	Russia (Novosibirsk Oblast)	12.08.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	54.058	81.058	B14	B1	IMCB 344	Russia (Altai Kray)	10.08.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	53.949	80.766	B14	B1	IMCB 346	Russia (Altai Kray)	26.08.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	feather	+	+
<i>M. migrans</i>	53.822	81.261	B14	B1	IMCB 347	Russia (Altai Kray)	30.08.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	53.822	81.261	B19.1	B1	IMCB 348	Russia (Altai Kray)	30.08.2017	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	53.822	81.261	B19.1	B1	IMCB 349	Russia (Altai Kray)	30.08.2017	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	53.822	81.261	B19	B1	IMCB 350	Russia (Altai Kray)	30.08.2017	MT024215	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	53.822	81.261	B19	B1	IMCB 354	Russia (Altai Kray)	30.08.2017	MT024215	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	54.65	83.353	B14	B1	IMCB 384	Russia (Novosibirsk Oblast)	23.08.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+	+
<i>M. migrans</i>	54.65	83.353	B6	B1	IMCB 385	Russia (Novosibirsk Oblast)	23.08.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+	+
<i>M. migrans</i>	54.65	83.353	B6	B1	IMCB 386	Russia (Novosibirsk Oblast)	23.08.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+	+
<i>M. migrans</i>	54.65	83.353	B19.1	B1	IMCB 387	Russia (Novosibirsk Oblast)	23.08.2017	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+	+
<i>M. migrans</i>	54.65	83.353	B6	B1	IMCB 554	Russia (Novosibirsk Oblast)	23.08.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+	+
<i>M. migrans</i>	54.65	83.353	B6	B1	IMCB 556	Russia (Novosibirsk Oblast)	23.08.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+	+
<i>M. migrans</i>	54.65	83.353	B14	B1	IMCB 557	Russia (Novosibirsk Oblast)	23.08.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+	+
<i>M. migrans</i>	54.892	83.158	B14	B1	IMCB 558	Russia (Novosibirsk Oblast)	18.07.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+	+
<i>M. migrans</i>	54.892	83.158	B19.1	B1	IMCB 559	Russia (Novosibirsk Oblast)	18.07.2017	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+	+
<i>M. migrans</i>	54.892	83.158	B6	B1	IMCB 560	Russia (Novosibirsk Oblast)	18.07.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+	+
<i>M. migrans</i>	54.892	83.158	B14	B1	IMCB 561	Russia (Novosibirsk Oblast)	18.07.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. & N. Andreyenkova	molted feather	+	+
<i>M. migrans</i>	52.528	85.529	B19	B1	C835581	Russia (Altai Kray)	06.07.2018	MT024215	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+	+
<i>M. migrans</i>	52.57	85.504	B6.1	B1	C835582	Russia (Altai Kray)	07.07.2018	MT024202	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+	+
<i>M. migrans</i>	52.591	85.254	B14	B1	C835584	Russia (Altai Kray)	07.07.2018	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+	+
<i>M. migrans</i>	52.514	85.362	B14	B1	C835586	Russia (Altai Kray)	08.07.2018	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+	+
<i>M. migrans</i>	52.514	85.362	B6	B1	C835588	Russia (Altai Kray)	08.07.2018	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+	+
<i>M. migrans</i>	52.469	85.252	B19.1	B1	C835589	Russia (Altai Kray)	09.07.2018	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+	+
<i>M. migrans</i>	52.457	85.168	B6	B1	C835592	Russia (Altai Kray)	09.07.2018	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+	+

Table A4. Continued

<i>M. migrans</i>	52.528	85.529	B6	B1	D1	Russia (Altai Kray)	07.07.2018	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	52.533	85.487	B14	B1	C553828	Russia (Altai Kray)	07.07.2018	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Literák	pin feather	+ +
<i>M. migrans</i>	56.039	92.992	B6	B1	IMCB 586	Russia (Krasnoyarsk Kray)	13.10.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	T. Veselova	molted feather	+ +
<i>M. migrans</i>	54.766	83.218	B14	B1	IMCB 620	Russia (Novosibirsk Oblast)	17.07.2018	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	O. Andreyenkov	feather	+ +
<i>M. migrans</i>	56.483	84.983	B6	B1	IPMB 92466	Russia (Tomsk Oblast)	18.7.2017	MT024201	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Starikov	blood	+ +
<i>M. migrans</i>	55.367	86.067	B14	B1	IPMB 92467	Russia (Kemerovo Oblast)	18.7.2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Starikov	blood	+ +
<i>M. migrans</i>	56.795	60.553	B19	B1	IPMB 92540	Russia (Sverdlovsk Oblast)	03.08.2017	MT024215	mig./lin.	Andreyenkova <i>et al.</i> 2021	I. Starikov	blood	+ +
<i>M. migrans</i>	55.367	86.067	B14	B1	IPMB 92657	Russia (Kemerovo Oblast)	spring 2017	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	N. Ivleva & collaborators	feather	+ +
<i>M. migrans</i>	55.367	86.067	B19.1	B1	IPMB 92663	Russia (Kemerovo Oblast)	8.9.2016	MT024216	mig./lin.	Andreyenkova <i>et al.</i> 2021	N. Ivleva & collaborators	feather	+ +
<i>M. migrans</i>	55.367	86.067	B14	B1	IPMB 92664	Russia (Kemerovo Oblast)	26.6.2016	MT024210	mig./lin.	Andreyenkova <i>et al.</i> 2021	N. Ivleva & collaborators	feather	+ +
<i>M. migrans</i>	48.711	71.635	B20.1	B2	IMCB 160	Kazakhstan (Karaganda)	27.09.2017	MT024221	mig./lin.	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+ +
<i>M. migrans</i>	30.283	71.933	A3.1	A	IPMB 24893	Pakistan	7.8.2002	MT024190	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.217	71.417	A4	A	IPMB 24907	Pakistan	20.8.2002	MT024194	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.95	70.933	B19.1	B1	IPMB 24880	Pakistan	11.11.2002	MT024216	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.95	70.933	B19	B1	IPMB 24883	Pakistan	5.11.2002	MT024215	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.95	70.933	B19	B1	IPMB 24884	Pakistan	11.11.2002	MT024215	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.283	71.933	B6	B1	IPMB 24887	Pakistan	5.8.2002	MT024201	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.283	71.933	B14	B1	IPMB 24888	Pakistan	8.8.2002	MT024210	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.283	71.933	B6	B1	IPMB 24889	Pakistan	5.8.2002	MT024201	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.283	71.933	B14	B1	IPMB 24890	Pakistan	6.8.2002	MT024210	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.283	71.933	B19.1	B1	IPMB 24891	Pakistan	6.8.2002	MT024216	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.283	71.933	B14	B1	IPMB 24892	Pakistan	4.8.2002	MT024210	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.283	71.933	B14	B1	IPMB 24894	Pakistan	4.8.2002	MT024210	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.283	71.933	B19.1	B1	IPMB 24899	Pakistan	3.8.2002	MT024216	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.95	70.933	B19	B1	IPMB 24902	Pakistan	4.11.2002	MT024215	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.95	70.933	B19	B1	IPMB 24905	Pakistan	12.11.2002	MT024215	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.217	71.417	B19	B1	IPMB 24926	Pakistan	11.8.2002	MT024215	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	24.961	68.035	B19	B1	UMMZ 78382	Pakistan	28.02.1934	AY994391	mig./lin./gov.	Johnson <i>et al.</i> 2005			+ +
<i>M. migrans</i>	30.95	70.933	B20	B2	IPMB 24877	Pakistan	9.11.2002	MT024220	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.95	70.933	B20	B2	IPMB 24882	Pakistan	10.11.2002	MT024220	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.95	70.933	B20	B2	IPMB 24885	Pakistan	6.11.2002	MT024220	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.95	70.933	B20	B2	IPMB 24886	Pakistan	5.11.2002	MT024220	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.217	71.417	B20	B2	IPMB 24895	Pakistan	17.8.2002	MT024220	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.217	71.417	B20	B2	IPMB 24896	Pakistan	14.8.2002	MT024220	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.217	71.417	B20	B2	IPMB 24898	Pakistan	20.8.2002	MT024220	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.217	71.417	B20	B2	IPMB 24900	Pakistan	19.8.2002	MT024220	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.95	70.933	B20	B2	IPMB 24903	Pakistan	4.11.2002	MT024220	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.283	71.933	B20	B2	IPMB 24909	Pakistan	24.7.2002	MT024220	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	liver	+ +
<i>M. migrans</i>	30.283	71.933	B20	B2	IPMB 24921	Pakistan	26.7.2002	MT024220	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	liver	+ +
<i>M. migrans</i>	30.217	71.417	B20	B2	IPMB 24923	Pakistan	21.8.2002	MT024220	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.217	71.417	B20	B2	IPMB 24924	Pakistan	22.8.2002	MT024220	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +

Table A4. Continued

<i>M. migrans</i>	30.283	71.933	B20	B2	IPMB 24925	Pakistan	2.8.2002	MT024220	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.95	70.933	B20.3	B2	IPMB 24881	Pakistan	7.11.2002	MT024223	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.95	70.933	B20.3	B2	IPMB 24901	Pakistan	2.11.2002	MT024223	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.95	70.933	B20.3	B2	IPMB 24904	Pakistan	2.11.2002	MT024223	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	muscle	+ +
<i>M. migrans</i>	30.95	70.933	B20.3	B2	IPMB 24919	Pakistan	25.7.2002	MT024223	mig./lin./gov.	Andreyenkova <i>et al.</i> 2021	A. Khan	liver	+ +
<i>M. aegyptius</i>	-12.321	49.33	F21	F1	AMNH 532032	Madagascar	23.11.1916	AY994413	parasitus	Johnson <i>et al.</i> 2005			+ +
<i>M. aegyptius</i>	-27.471	26.639	F21	F1	CRH 8	South Africa	05.2003	AY994415	parasitus	Johnson <i>et al.</i> 2005			+ +
<i>M. aegyptius</i>	-29.018	24.205	F21 ¹	F1	IPMB 9924	South Africa			parasitus	Andreyenkova <i>et al.</i> 2021	W. Bednarek	blood	+
<i>M. aegyptius</i>	-29.018	24.205	F21	F1	IPMB 9925	South Africa		MT024233	parasitus	Andreyenkova <i>et al.</i> 2021	W. Bednarek	blood	+ +
<i>M. aegyptius</i>	-29.018	24.205	F21	F1	IPMB 9926	South Africa		MT024233	parasitus	Andreyenkova <i>et al.</i> 2021	W. Bednarek	blood	+ +
<i>M. aegyptius</i>	-29.018	24.205	F21	F1	WOB 10	South Africa	05.2003	AY994414	parasitus	Johnson <i>et al.</i> 2005			+ +
<i>M. migrans</i>	54.168	48.241	A4	A	IMCB 181	Russia (Ulyanovsk Oblast)	14.08.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	M. Korol'kov	molted feather	+ +
<i>M. migrans</i>	54.168	48.241	A4	A	IMCB 182	Russia (Ulyanovsk Oblast)	14.08.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	M. Korol'kov	molted feather	+ +
<i>M. migrans</i>	55.674	52.571	A4	A	IMCB 183	Russia (Republic of Tatarstan)	11.08.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	A3	A	IMCB 184	Russia (Republic of Tatarstan)	09.08.2017	MT024189	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.633	51.186	A4	A	IMCB 185	Russia (Republic of Tatarstan)	24.08.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	feather	+ +
<i>M. migrans</i>	55.541	51.761	A5	A	IMCB 188	Russia (Republic of Tatarstan)	09.08.2017	MT024199	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	A3	A	IMCB 189	Russia (Republic of Tatarstan)	09.08.2017	MT024189	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	A3	A	IMCB 190	Russia (Republic of Tatarstan)	09.08.2017	MT024189	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	A4	A	IMCB 193	Russia (Republic of Tatarstan)	09.08.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	A4	A	IMCB 197	Russia (Republic of Tatarstan)	09.08.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	A4	A	IMCB 200	Russia (Republic of Tatarstan)	09.08.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	A4	A	IMCB 202	Russia (Republic of Tatarstan)	09.08.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	A4	A	IMCB 203	Russia (Republic of Tatarstan)	09.08.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	A5.1	A	IMCB 204	Russia (Republic of Tatarstan)	09.08.2017	MT024200	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	A3.2	A	IMCB 207	Russia (Republic of Tatarstan)	09.08.2017	MT024191	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	A4	A	IMCB 210	Russia (Republic of Tatarstan)	09.08.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	A4	A	IMCB 211	Russia (Republic of Tatarstan)	09.08.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	53.231	45.203	A4	A	IMCB 307	Russia (Omsk Oblast)	14.08.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	G. Sadykov	molted feather	+ +
<i>M. migrans</i>	53.231	45.203	A4	A	IMCB 310	Russia (Omsk Oblast)	14.08.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	G. Sadykov	molted feather	+ +
<i>M. migrans</i>	53.231	45.203	A4	A	IMCB 312	Russia (Omsk Oblast)	14.08.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	G. Sadykov	molted feather	+ +
<i>M. migrans</i>	55.433	37.75	A4	A	IPMB 92523	Russia (Moscow Oblast)	6.8.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	I. Starikov	blood	+ +
<i>M. migrans</i>	54.933	48.833	A4	A	IPMB 92527	Russia (Republic of Tatarstan)	1.8.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	I. Starikov	blood	+ +
<i>M. migrans</i>	54.233	48.55	A4	A	IPMB 92528	Russia (Ulyanovsk Oblast)	1.8.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	I. Starikov	blood	+ +
<i>M. migrans</i>	54.317	48.417	A3	A	IPMB 92530	Russia (Ulyanovsk Oblast)	1.8.2017	MT024189	migrans	Andreyenkova <i>et al.</i> 2021	I. Starikov	blood	+ +
<i>M. migrans</i>	54.233	48.533	A4	A	IPMB 92771	Russia (Ulyanovsk Oblast)	5.2017	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	G. Pilyugina & I. Starikov	tissue	+ +
<i>M. migrans</i>	54.168	48.241	B19.1	B1	IMCB 180	Russia (Ulyanovsk Oblast)	14.08.2017	MT024216	migrans	Andreyenkova <i>et al.</i> 2021	M. Korol'kov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	B6	B1	IMCB 186	Russia (Republic of Tatarstan)	09.08.2017	MT024201	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	B6	B1	IMCB 187	Russia (Republic of Tatarstan)	09.08.2017	MT024201	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	B6	B1	IMCB 191	Russia (Republic of Tatarstan)	09.08.2017	MT024201	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +
<i>M. migrans</i>	55.541	51.761	B14	B1	IMCB 192	Russia (Republic of Tatarstan)	09.08.2017	MT024210	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+ +

Table A4. Continued

<i>M. migrans</i>	55.541	51.761	B6	B1	IMCB 194	Russia (Republic of Tatarstan)	09.08.2017	MT024201	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+	+
<i>M. migrans</i>	55.541	51.761	B14	B1	IMCB 195	Russia (Republic of Tatarstan)	09.08.2017	MT024210	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+	+
<i>M. migrans</i>	55.541	51.761	B6	B1	IMCB 196	Russia (Republic of Tatarstan)	09.08.2017	MT024201	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+	+
<i>M. migrans</i>	55.541	51.761	B14	B1	IMCB 198	Russia (Republic of Tatarstan)	09.08.2017	MT024210	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+	+
<i>M. migrans</i>	55.541	51.761	B6	B1	IMCB 199	Russia (Republic of Tatarstan)	09.08.2017	MT024201	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+	+
<i>M. migrans</i>	55.541	51.761	B6.4	B1	IMCB 201	Russia (Republic of Tatarstan)	09.08.2017	MT024206	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+	+
<i>M. migrans</i>	55.541	51.761	B6	B1	IMCB 205	Russia (Republic of Tatarstan)	09.08.2017	MT024201	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+	+
<i>M. migrans</i>	55.541	51.761	B6	B1	IMCB 206	Russia (Republic of Tatarstan)	09.08.2017	MT024201	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+	+
<i>M. migrans</i>	55.541	51.761	B6	B1	IMCB 208	Russia (Republic of Tatarstan)	09.08.2017	MT024201	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+	+
<i>M. migrans</i>	55.541	51.761	B14	B1	IMCB 209	Russia (Republic of Tatarstan)	09.08.2017	MT024210	migrans	Andreyenkova <i>et al.</i> 2021	R. Bekmansurov	molted feather	+	+
<i>M. migrans</i>	53.231	45.203	B6	B1	IMCB 308	Russia (Omsk Oblast)	14.08.2017	MT024201	migrans	Andreyenkova <i>et al.</i> 2021	G. Sadykov	molted feather	+	+
<i>M. migrans</i>	53.231	45.203	B6	B1	IMCB 311	Russia (Omsk Oblast)	14.08.2017	MT024201	migrans	Andreyenkova <i>et al.</i> 2021	G. Sadykov	molted feather	+	+
<i>M. migrans</i>	53.231	45.203	B6	B1	IMCB 313	Russia (Omsk Oblast)	14.08.2017	MT024201	migrans	Andreyenkova <i>et al.</i> 2021	G. Sadykov	molted feather	+	+
<i>M. migrans</i>	53.231	45.203	B6	B1	IMCB 314	Russia (Omsk Oblast)	14.08.2017	MT024201	migrans	Andreyenkova <i>et al.</i> 2021	G. Sadykov	molted feather	+	+
<i>M. migrans</i>	54.217	49.583	B19	B1	IPMB 92529	Russia (Ulyanovsk Oblast)	1.8.2017	MT024215	migrans	Andreyenkova <i>et al.</i> 2021	I. Starikov	blood	+	+
<i>M. migrans</i>	56.296	43.893	B19.1	B1	IPMB 93822	Russia (Nizhny Novgorod Oblast)	29.12.2017	MT024216	migrans	Andreyenkova <i>et al.</i> 2021	I. Starikov	blood	+	+
<i>M. migrans</i>	8.096	-5.616	A4 ¹	A	IPMB 25551	Ivory Coast	29.01.2004		parasitus	Andreyenkova <i>et al.</i> 2021	G. Rondeau & J. Scheider	blood		+
<i>M. migrans</i>	33.681	-5.369	A4	A	AMNH 289860	Morocco	22.04.1929	AY994400	migrans	Johnson <i>et al.</i> 2005			+	+
<i>M. migrans</i>	31.778	65.857	A5	A	AMNH 464875	Afghanistan	18.10.1937	AY994402	mig./lin./gov.	Johnson <i>et al.</i> 2005			+	+
<i>M. migrans</i>	35.333	6.267	A17	A	AMNH 531936	Algeria	12.05.1909	AY994399	migrans	Johnson <i>et al.</i> 2005			+	+
<i>M. migrans</i>	41.6	41.583	A4	A	IPMB 67054	Georgia	8.10.2012	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	feather	+	+
<i>M. migrans</i>	41.6	41.583	A4	A	IPMB 67057	Georgia	4.10.2012	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	feather	+	+
<i>M. migrans</i>	41.6	41.583	A4	A	IPMB 77284	Georgia	28.9.2013	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	tissue	+	+
<i>M. migrans</i>	41.6	41.583	A4	A	IPMB 77286	Georgia	7.10.2013	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	tissue	+	+
<i>M. migrans</i>	41.6	41.583	A3	A	IPMB 77292	Georgia	12.10.2013	MT024189	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	tissue	+	+
<i>M. migrans</i>	41.6	41.583	A4	A	IPMB 86807	Georgia	15.9.2015	MT024194	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	feather	+	+
<i>M. migrans</i>	15.687	-23.03	A4	A	NBPC F00022	Cape Verde	08.2002	AY994429	migrans	Johnson <i>et al.</i> 2005			+	+
<i>M. migrans</i>	15.687	-23.03	A17	A	NBPC F00050	Cape Verde	08.2002	AY994430	migrans	Johnson <i>et al.</i> 2005			+	+
<i>M. migrans</i>	15.687	-23.03	A4	A	NBPC F00053	Cape Verde	08.2002	AY994431	migrans	Johnson <i>et al.</i> 2005			+	+
<i>M. migrans</i>	15.687	-23.03	A4	A	NBPC F00056	Cape Verde	08.2002	AY994432	migrans	Johnson <i>et al.</i> 2005			+	+
<i>M. migrans</i>	15.687	-23.03	A5	A	NBPC F00059	Cape Verde	08.2002	AY994433	migrans	Johnson <i>et al.</i> 2005			+	+
<i>M. migrans</i>	30.017	31.217	A16	A	UMMZ 150962	Egypt	03.1953	AY994403	aegyptius	Johnson <i>et al.</i> 2005			+	+
<i>M. migrans</i>	41.6	41.583	A15.2	A	IPMB 86808	Georgia	18.9.2015	MT024214	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	feather	+	+
<i>M. migrans</i>	41.6	41.583	A15.2	A	IPMB 86809	Georgia	18.9.2015	MT024214	migrans	Andreyenkova <i>et al.</i> 2021	D. Ristow	feather	+	+
<i>M. migrans</i>	15.684	73.71	B19	B1	IMCB 24	India (Goa)	03.02.2017	MT024215	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.672	73.711	B19	B1	IMCB 382	India (Goa)	15.01.2017	MT024215	govinda	Andreyenkova <i>et al.</i> 2021	E. Shnayder	molted feather	+	+
<i>M. migrans</i>	15.042	74.0	B19	B1	IMCB 419	India (Goa)	30.03.2018	MT024215	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.042	74.0	B19	B1	IMCB 420	India (Goa)	30.03.2018	MT024215	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.042	74.0	B19	B1	IMCB 422	India (Goa)	30.03.2018	MT024215	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.042	74.0	B6	B1	IMCB 423	India (Goa)	30.03.2018	MT024201	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.042	74.0	B14	B1	IMCB 424	India (Goa)	30.03.2018	MT024210	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+

Table A4. End

<i>M. migrans</i>	15.042	74.0	B14	B1 ¹	IMCB 425	India (Goa)	30.03.2018	MT024210	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.042	74.0	B18.1	B1 ¹	IMCB 426	India (Goa)	30.03.2018	MT024232	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.042	74.0	B19	B1 ¹	IMCB 427	India (Goa)	30.03.2018	MT024215	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.042	74.0	B6	B1 ¹	IMCB 428	India (Goa)	30.03.2018	MT024201	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.042	74.0	B6	B1 ¹	IMCB 430	India (Goa)	30.03.2018	MT024201	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B14	B1 ¹	IMCB 487	India (Goa)	03.04.2018	MT024210	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B6	B1 ¹	IMCB 500	India (Goa)	03.04.2018	MT024201	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B19	B1 ¹	IMCB 501	India (Goa)	03.04.2018	MT024215	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B6.1.1	B1 ¹	IMCB 504	India (Goa)	03.04.2018	MT024203	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B19.1	B1 ¹	IMCB 508	India (Goa)	03.04.2018	MT024216	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B19.1	B1 ¹	IMCB 509	India (Goa)	03.04.2018	MT024216	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B6	B1 ¹	IMCB 510	India (Goa)	03.04.2018	MT024201	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B19	B1 ¹	IMCB 512	India (Goa)	03.04.2018	MT024215	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B6	B1 ¹	IMCB 514	India (Goa)	03.04.2018	MT024201	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.67	73.71	B14	B1 ¹	IMCB 587	India (Goa)	28.01.2018	MT024210	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B19.1	B1 ¹	IMCB 609	India (Goa)	03.04.2018	MT024216	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B14	B1 ¹	IMCB 611	India (Goa)	03.04.2018	MT024210	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B14	B1 ¹	IMCB 612	India (Goa)	03.04.2018	MT024210	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B19.1	B1 ¹	IMCB 613	India (Goa)	03.04.2018	MT024216	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B14	B1 ¹	IMCB 614	India (Goa)	03.04.2018	MT024210	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B14	B1 ¹	IMCB 615	India (Goa)	03.04.2018	MT024210	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	15.041	73.99	B14	B1 ¹	IMCB 616	India (Goa)	03.04.2018	MT024210	govinda	Andreyenkova <i>et al.</i> 2021	I. Karyakin	molted feather	+	+
<i>M. migrans</i>	28.633	77.22	B19	B1 ¹	IMCB 618	India (Delhi)	11.12.2017	MT024215	govinda	Andreyenkova <i>et al.</i> 2021	T. Petrova	molted feather	+	+
<i>M. migrans</i>	28.633	77.22	B14	B1 ¹	IMCB 619	India (Delhi)	11.12.2017	MT024210	govinda	Andreyenkova <i>et al.</i> 2021	T. Petrova	molted feather	+	+
<i>M. migrans</i>	26.126	91.539	B19	B1 ¹	UMMZ 140425	India (Assam)	18.12.1951	AY994392	govinda	Johnson <i>et al.</i> 2005			+	+
<i>M. migrans</i>	23.389	74.227	B18	B1 ¹	UMMZ 78383	India (Rajasthan)	06.03.1933	AY994394	govinda	Johnson <i>et al.</i> 2005			+	+
<i>M. milvus</i>					AMNH 261698	Sweden	29.03.1905	AY994419		Johnson <i>et al.</i> 2005				+
<i>M. milvus</i>					AMNH 531852	Hungary	24.03.1905	AY994420		Johnson <i>et al.</i> 2005				+
<i>M. milvus</i>					AMNH 531856	Italy	04.1900	AY994417		Johnson <i>et al.</i> 2005				+
<i>M. milvus</i>					NBPC G00177	Germany	10.2003	AY994421		Johnson <i>et al.</i> 2005				+
<i>M. milvus</i>					UMMZ 155642	Spain	03.12.1957	AY994416		Johnson <i>et al.</i> 2005				+

¹ - sequences that are shorter than 699 bp, used only to determine the haplogroup

² - a Black x Red Kites hybrid that had a Black Kite mitochondrion as its mother was a Black Kite

³ - previously partially published KU670091, the complete sequence of 699-bp fragment courtesy of P. Heneberg

Table A5. Variable sites of Cyt *b* sequences of Black and Yellow-Billed kites.

	1 1 1 1 1 1 1 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 3																																						
Sequence/Position	9	7	6	8	4	7	2	7	8	9	6	8	6	9	1	1	8	6	9	0	9	5	2	4	9	3	1	9	2	1	6	9	4						
M._migrans_A3	G	C	G	T	A	C	G	A	T	C	A	C	G	C	A	T	G	C	A	C	G	A	T	A	G	G	G	C	T	G	A	C	G						
M._migrans_A3.1					
M._migrans_A3.2					
M._migrans_A3.3					
M._migrans_A3.4					
M._migrans_A3.5					
M._migrans_A4					
M._migrans_A4.1	C					
M._migrans_A4.2				
M._migrans_A4.2.1	.	.	A				
M._migrans_A4.3	A	T				
M._migrans_A5			
M._migrans_A5.1			
M._migrans_A10			
M._migrans_A11			
M._migrans_A13			
M._migrans_A15	.	.	A	A	.	C	.	T	.	A			
M._migrans_A15.1	.	.	A	C	.	T	.	A			
M._migrans_A15.2	.	.	A	C	.	T	.	A			
M._migrans_A16	T	G			
M._migrans_A17		
M._migrans_B6	.	.	.	G	.	.	.	C	.	.	.	A	T	.	.	C			
M._migrans_B6.1	.	.	.	G	.	.	.	C	.	.	.	A	T	.	.	C			
M._migrans_B6.1.1	.	.	.	G	.	.	.	C	.	.	.	A	T	.	.	C	A			
M._migrans_B6.2	.	.	.	G	.	.	.	C	.	.	.	A	T	.	.	C			
M._migrans_B6.3	.	.	.	G	.	.	.	C	.	.	.	A	T	.	.	C			
M._migrans_B6.4	.	.	.	G	.	.	.	C	.	.	.	A	T	.	.	C	A			
M._migrans_B14	.	.	.	G	.	.	.	C	.	.	.	A	T			
M._migrans_B14.1	.	.	.	G	.	.	.	C	.	.	.	A	T			
M._migrans_B18	.	.	.	G	.	.	.	C	.	.	.	A	T	G			
M._migrans_B18.1	.	.	.	G	.	.	.	C	.	.	.	A	T	.	.	.	G			
M._migrans_B19	.	.	.	G	.	.	.	C	.	.	.	A	T			
M._migrans_B19.1	.	.	.	G	.	.	.	C	.	.	.	A	T	.	T			
M._migrans_B19.2	.	.	.	G	.	.	.	C	.	.	.	A	T			
M._migrans_B19.3	.	.	.	G	.	.	.	C	.	.	.	A	T			
M._migrans_B19.4	.	.	.	G	.	.	.	C	.	.	.	A	T			
M._migrans_B19.5	.	.	.	G	.	.	.	C	.	.	.	A	T			
M._migrans_B19.6	.	.	.	G	.	.	.	C	.	.	.	A	T			
M._migrans_B20	.	.	.	G	.	.	.	C	.	.	.	A	T	C	.		
M._migrans_B20.1	.	.	.	G	.	.	.	C	.	.	.	A	T	A	C	.			
M._migrans_B20.2	.	.	.	G	.	.	.	C	.	.	.	A	T	C	.		
M._migrans_B20.3	.	.	.	G	.	.	.	C	.	.	.	A	T	C	.		
M._migrans_B20.3.1.1	T	.	.	G	.	.	.	C	.	.	.	A	T	C	.			
M._migrans_B20.3.2	.	.	.	G	.	.	.	C	.	.	.	A	T	C	A		
M._migrans_B20.4	.	.	.	G	.	A	C	A	T	C	.		
M._migrans_B20.5	.	.	.	G	.	.	.	C	.	.	.	A	T	A	C	.		
M._migrans_B20.6	.	.	.	G	.	.	.	C	.	.	.	A	T	C	.	
M._migrans_B20.7	.	.	.	G	.	.	.	C	.	G	.	A	T	C	.	
M._migrans_B20.8	.	.	.	G	.	.	.	C	.	.	.	A	T	.	A	C	.	
M._migrans_B20.9	C	.	.	.	A	T	C	.	
M._migrans_B20.10	A	.	.	G	T	.	.	C	.	.	.	A	T	C	.		
M._aegyptius_F21	C	.	.	T	A	.	T	.	.	.	T	A		
M._aegyptius_F22	C	T	.	T	A	T	.	C	.	T	T	.	
M._aegyptius_F22.1	.	.	C	C	T	.	T	A	T	.	C	.	T	T	.	
M._aegyptius_F22.2	C	T	.	T	A	T	.	C	.	T	T	.

Table A5. Continued

	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	6	6
	2	3	4	5	6	9	9	9	9	0	2	3	3	5	6	6	9	1	1	3	4	8	8	9	9	9	9	9
Sequence/Position	5	7	7	8	7	4	7	8	9	6	8	0	9	1	0	3	2	1	4	8	8	0	6	3	5	8	8	
M._migrans_A3	T	C	G	T	T	A	T	A	T	A	T	A	A	G	G	A	A	A	T	A	G	G	A	C	A	C	C	
M._migrans_A3.1	G
M._migrans_A3.2	C
M._migrans_A3.3	C
M._migrans_A3.4	G	.	.
M._migrans_A3.5	A
M._migrans_A4
M._migrans_A4.1
M._migrans_A4.2	G
M._migrans_A4.2.1	G
M._migrans_A4.3
M._migrans_A5
M._migrans_A5.1
M._migrans_A10	A
M._migrans_A11
M._migrans_A13	G
M._migrans_A15	A
M._migrans_A15.1	T	.	.
M._migrans_A15.2
M._migrans_A16
M._migrans_A17
M._migrans_B6	T	.
M._migrans_B6.1	C	T	.	.
M._migrans_B6.1.1	C	T	.	.
M._migrans_B6.2	A	T	.	.
M._migrans_B6.3	G	T	.	.	.
M._migrans_B6.4	T	.	.	.
M._migrans_B14
M._migrans_B14.1	G
M._migrans_B18	G
M._migrans_B18.1	.	A	G
M._migrans_B19	G
M._migrans_B19.1	G
M._migrans_B19.2	C	G
M._migrans_B19.3	G	A
M._migrans_B19.4	.	.	.	C	G
M._migrans_B19.5	C	.	.	G
M._migrans_B19.6	G	G
M._migrans_B20	G
M._migrans_B20.1	G	A
M._migrans_B20.2	.	A	G
M._migrans_B20.3	G	G
M._migrans_B20.3.1.1	G	G	G
M._migrans_B20.3.2	G	G
M._migrans_B20.4	G
M._migrans_B20.5	G
M._migrans_B20.6	.	.	C	G
M._migrans_B20.7	G
M._migrans_B20.8	G
M._migrans_B20.9	G
M._migrans_B20.10	G
M._aegyptius_F21	G	A
M._aegyptius_F22	T	.	.	.	C	G	A	A	G
M._aegyptius_F22.1	T	.	.	.	C	G	A	A	G
M._aegyptius_F22.2	T	.	.	.	C	G	A	A	G	G	G	G

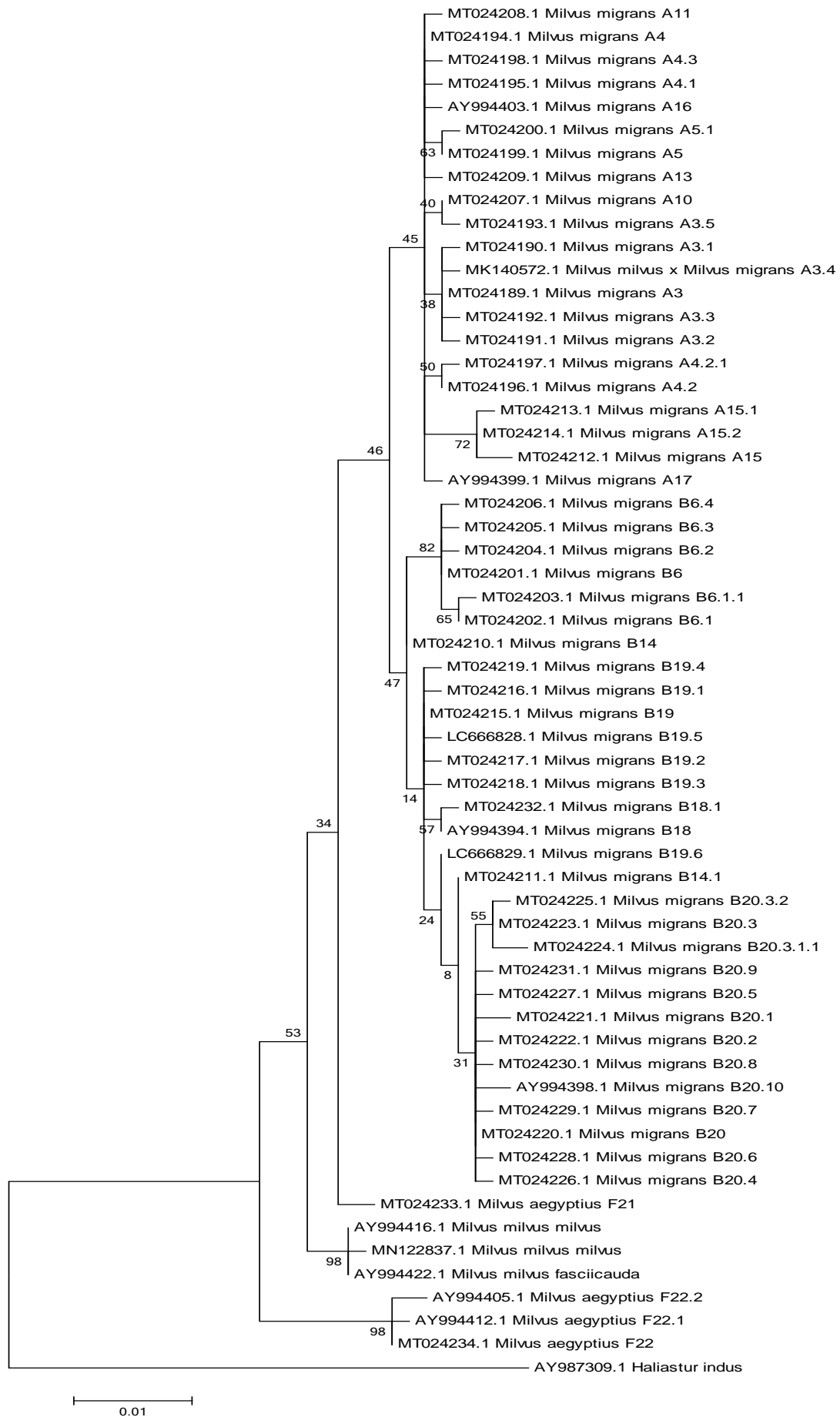


Figure A10. Maximum likelihood tree of Black and Yellow-Billed kites *Cyt b* sequences.

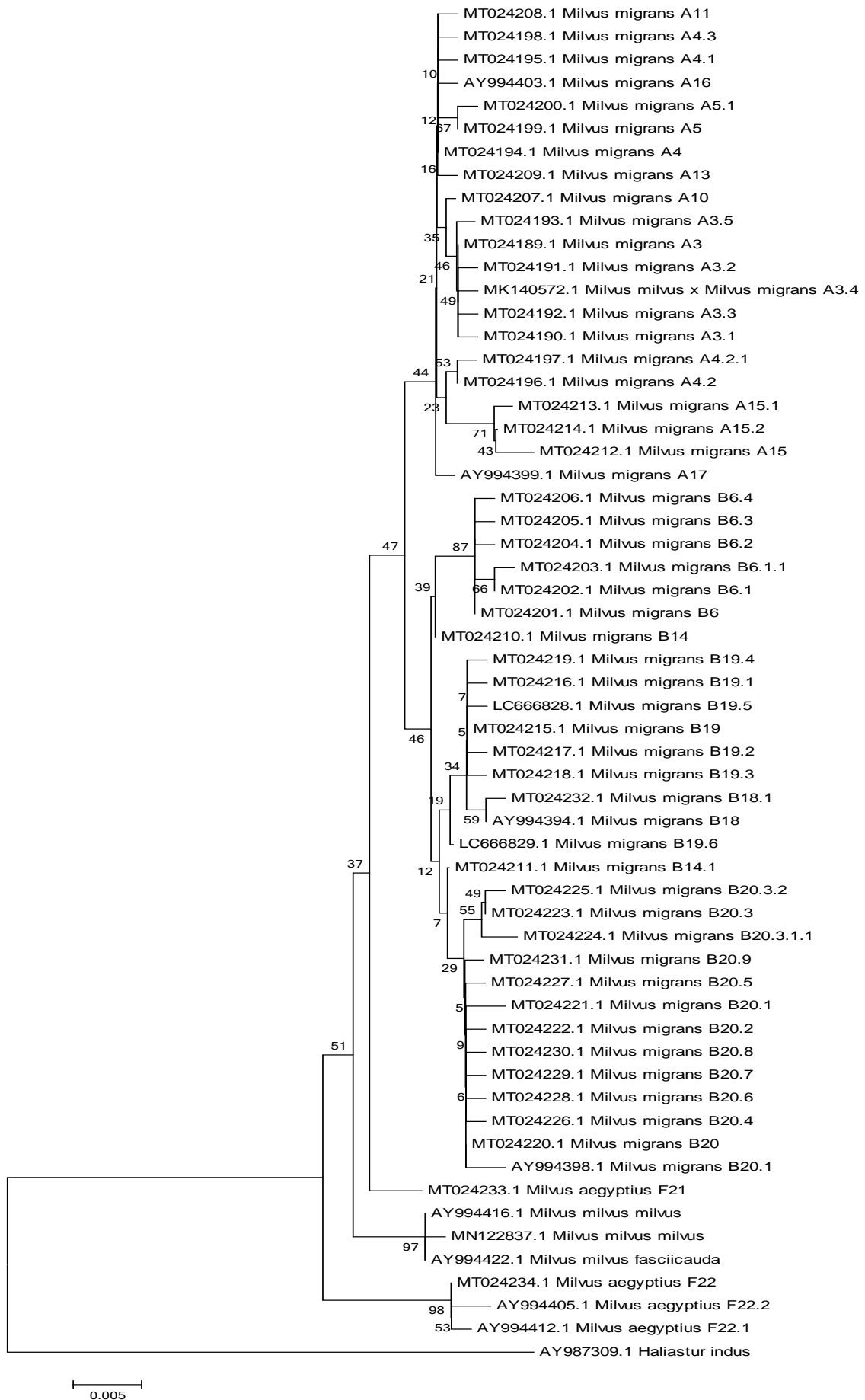


Figure A11. Neighbor-joining tree of Black and Yellow-Billed kites *Cyt b* sequences.

Table A6. Variable sites of COI sequences of the Little Owl. Here and below Arabic numbers represent the number of specimens per haplotype if more than one, Roman numbers show unique haplotypes with same number of specimens.

	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	3	3	3	3	3	3									
	1	2	2	7	9	9	0	1	2	2	4	6	7	8	9	0	1	1	2	4	7	8	9	0	0	0	0	1	3		
Sequence/Position	2	0	1	9	7	5	8	4	7	2	6	3	4	9	5	7	9	5	7	1	6	2	7	6	0	2	6	8	1	2	
Athene_noctua_noctua_84	T	T	G	C	C	G	A	T	G	G	A	G	A	C	C	T	G	T	C	T	C	A	G	C	C	G	T	A	C	A	
Athene_noctua_noctua_2
Athene_noctua_noctua_I
Athene_noctua_noctua_II
Athene_noctua_noctua_3
Athene_noctua_noctua_III	A
Athene_noctua_noctua_30
Athene_noctua_sarda_8
Athene_noctua_sarda_2	C
Athene_noctua_lilith_I	.	.	A
Athene_noctua_lilith_4
Athene_noctua_lilith_II
Athene_noctua_lilith_5	C	.	G
Athene_noctua_indigena_41
Athene_noctua_indigena_8
Athene_noctua_indigena_I
Athene_noctua_indigena_2_I
Athene_noctua_indigena_II	.	.	A
Athene_noctua_indigena_11	G
Athene_noctua_indigena_2_II
Athene_noctua_saharae_I	A	C
Athene_noctua_saharae_II	A	C
Athene_noctua_saharae_III	A	C
Athene_noctua_glaux	A	C
Athene_noctua_plumipes	C	.	.	T	T	.	C	.	A	.	A	G	.	.	C	.	T	.	.	A	.	T	A	
Athene_noctua_vidalii_4	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_vidalii_I	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_vidalii_3	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_vidalii_2_I	G	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_vidalii_II	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_vidalii_93	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_vidalii_2_II	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_vidalii_III	.	.	A	T	.	G	.	A	A	C	A	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_vidalii_IV	.	.	A	T	.	G	.	A	T	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_vidalii_V	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	G	T	T	.	.	.	
Athene_noctua_vidalii_VI	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	T	A	.	.	T	T	.	.	
Athene_noctua_vidalii_VII	.	G	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_vidalii_5	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	C	.	T	T	.	.	.	
Athene_noctua_ssp_I	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	C	.	T	T	.	.	.	
Athene_noctua_ssp_II	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_ssp_III	.	G	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_ssp_17	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_ssp_3
Athene_noctua_ssp_IV
Athene_noctua_ssp_V
Athene_noctua_ssp_10	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_ssp_11	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_ssp_2	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	
Athene_noctua_ssp_VI
Athene_noctua_ssp_VII
Athene_noctua_ssp_VIII
Athene_noctua_ssp_IX
Athene_noctua_ssp_X
Athene_noctua_ssp_XI	.	.	A	T	.	G	.	A	A	C	.	.	.	T	T	.	T	A	.	.	T	T	.	.	.	

Table A6. Continued

Sequence/Position	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5
	3	5	7	8	8	8	8	1	1	2	3	4	5	6	7	7	7	8	8	8	9	0	1	1	2	2	3	4	4	
	8	4	7	0	2	6	9	0	6	8	7	9	6	7	0	3	9	0	2	6	7	6	5	9	0	7	0	2	8	
Athene_noctua_noctua_84	T	G	C	C	C	A	C	A	A	C	A	C	C	C	T	C	C	C	G	G	G	A	T	G	C	C	A	A	A	
Athene_noctua_noctua_2	C
Athene_noctua_noctua_I	T
Athene_noctua_noctua_II	.	.	.	T
Athene_noctua_noctua_3
Athene_noctua_noctua_III
Athene_noctua_noctua_30
Athene_noctua_sarda_8
Athene_noctua_sarda_2
Athene_noctua_lilith_I
Athene_noctua_lilith_4
Athene_noctua_lilith_II	.	.	A	T
Athene_noctua_lilith_5
Athene_noctua_indigena_41
Athene_noctua_indigena_8	G	.	.	.
Athene_noctua_indigena_I
Athene_noctua_indigena_2_I	.	A	C
Athene_noctua_indigena_II
Athene_noctua_indigena_11
Athene_noctua_indigena_2_II	C
Athene_noctua_saharae_I	A	G	.	.
Athene_noctua_saharae_II	G	.	.
Athene_noctua_saharae_III	G	.	G	.	.	.
Athene_noctua_glauca	G	.	.
Athene_noctua_plumipes	G	T	.	.	T	.	T	G	T	A	.	.	C	.	.	A	G	G	
Athene_noctua_vidalii_4	C	.	.	T	.	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_vidalii_I	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	.	.	T	.	G	G	.	.	.	
Athene_noctua_vidalii_3	C	.	.	T	G	T	G	G	T	G	T	.	C	T	A	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_vidalii_2_I	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_vidalii_II	C	.	.	T	G	T	G	G	T	G	T	.	G	C	T	G	.	A	.	.	C	G	G	.	.	
Athene_noctua_vidalii_93	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_vidalii_2_II	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	A	.	.	C	G	G	.	.	
Athene_noctua_vidalii_III	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_vidalii_IV	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_vidalii_V	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_vidalii_VI	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_vidalii_VII	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_vidalii_5	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_ssp_I	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_ssp_II	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	.	.	T	.	G	G	.	.	.	
Athene_noctua_ssp_III	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_ssp_17	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_ssp_3
Athene_noctua_ssp_IV
Athene_noctua_ssp_V
Athene_noctua_ssp_10	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_ssp_11	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_ssp_2	C	.	.	T	G	T	G	G	T	G	T	.	C	T	A	.	A	.	.	C	G	G	.	.	.	
Athene_noctua_ssp_VI	G
Athene_noctua_ssp_VII
Athene_noctua_ssp_VIII
Athene_noctua_ssp_IX	C
Athene_noctua_ssp_X
Athene_noctua_ssp_XI	C	.	.	T	G	T	G	G	T	G	T	.	C	T	G	.	A	.	.	C	C	C	.	.	.	G	G	.	.	.

Table A7. Variable sites of *Cyt b* sequences of the Little Owl.

Sequence/Position	2	4	5	6	6	8	8	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3			
MN122880_Denmark	T	T	T	C	G	C	C	G	A	G	C	C	C	T	G	A	C	A	C	A	A	C	T	C	G	G	A	C	G	G	A	C	G	A	T	G	C	A	T	C	A	T	G	A			
2879_Greece	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.		
3678_Israel	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.		
3681_Israel	.	.	C	T	A	.	T	A	C	A	T	.	T	T	C	.	C	T	.	G	.	T	.	.	A	.	.	A	T	G	.	.	.	
3684_Israel	.	.	C	T	A	.	T	A	C	A	T	.	T	T	C	.	C	T	.	G	.	T	.	.	A	.	.	A	T	G	.	.	.	
6073_Germany_BW	
6087_Israel	.	.	C	T	A	.	T	A	C	A	T	.	T	T	C	.	C	T	.	G	.	T	.	.	A	.	.	A	T	G	.	.	.	
6088_Israel	.	.	C	T	A	.	T	A	C	A	T	.	T	T	C	.	C	T	.	G	.	T	.	.	A	.	.	A	T	G	.	.	.	
6184_Austria
6185_Austria
6307_Turkey	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.		
6932_Greece	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.		
8227_captive	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.		
20879_Cyprus	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.			
20883_Cyprus	.	.	C	.	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.			
23811_Mongolia	.	C	C	T	A	T	T	.	C	A	.	.	T	.	C	A	C	T	G	G	.	T	.	T	A	T	A	A	T	G	C	A	T	G	.		
23812_Mongolia	C	C	C	T	A	.	T	.	C	A	.	.	T	.	C	A	C	T	G	G	.	T	C	T	A	T	A	A	T	G	C	A	T	G	.		
23813_Mongolia	.	C	C	T	A	T	T	.	C	A	.	.	T	.	C	A	C	T	G	G	.	T	.	T	A	T	A	A	T	G	C	A	T		
23814_Mongolia	.	C	C	T	A	T	T	.	C	A	.	.	T	.	C	A	C	T	G	G	.	T	.	T	A	T	A	A	T	G	C	A	T		
23815_Mongolia	.	C	C	T	A	T	T	.	C	A	.	.	T	.	C	A	C	T	G	G	.	T	.	T	A	T	A	A	T	G	C	A	T		
23816_Mongolia	.	C	C	T	A	T	T	.	C	A	.	.	T	.	C	A	C	T	G	G	.	T	.	T	A	T	A	A	T	G	C	A	T		
28167_United_Kingdom	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.			
28169_United_Kingdom	
32994_Tunisia	.	.	C	T	A	.	T	.	C	A	T	T	T	.	C	.	C	T	.	G	.	T	.	.	A	T	.	A	T	G	.	.	.			
37797_Switzerland	
37799_Switzerland	
37800_Switzerland	
37801_Switzerland	
37803_Switzerland	
37804_Switzerland	
37805_Switzerland	
44754_Mali	.	.	C	T	A	.	T	.	C	A	T	.	T	.	C	.	C	T	.	G	.	T	.	.	A	T	.	A	T	G	.	.	.			
49372_Turkey	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.				
49373_Turkey	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.				
62442_Turkey	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.				
79008_Germany_NRW	
92461_Russia_Belgorod	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.				
92463_Russia_Volgograd	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.				
92495_Russia_Altai_Kray	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.				
93941_Germany_NRW		
93954_Germany_NRW		
97064_Hungary	
97071_Hungary		
97074_Hungary		
KAN776_Russia_Stavropol	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.					
KAN777_Russia_Stavropol	.	.	C	T	A	.	T	.	C	A	T	.	T	T	C	.	C	T	.	G	G	.	.	.	A	.	.	A	.	G	T	G	.	.	.					
KAN778_Russia_Stavropol	.	.	C	T	A																																										

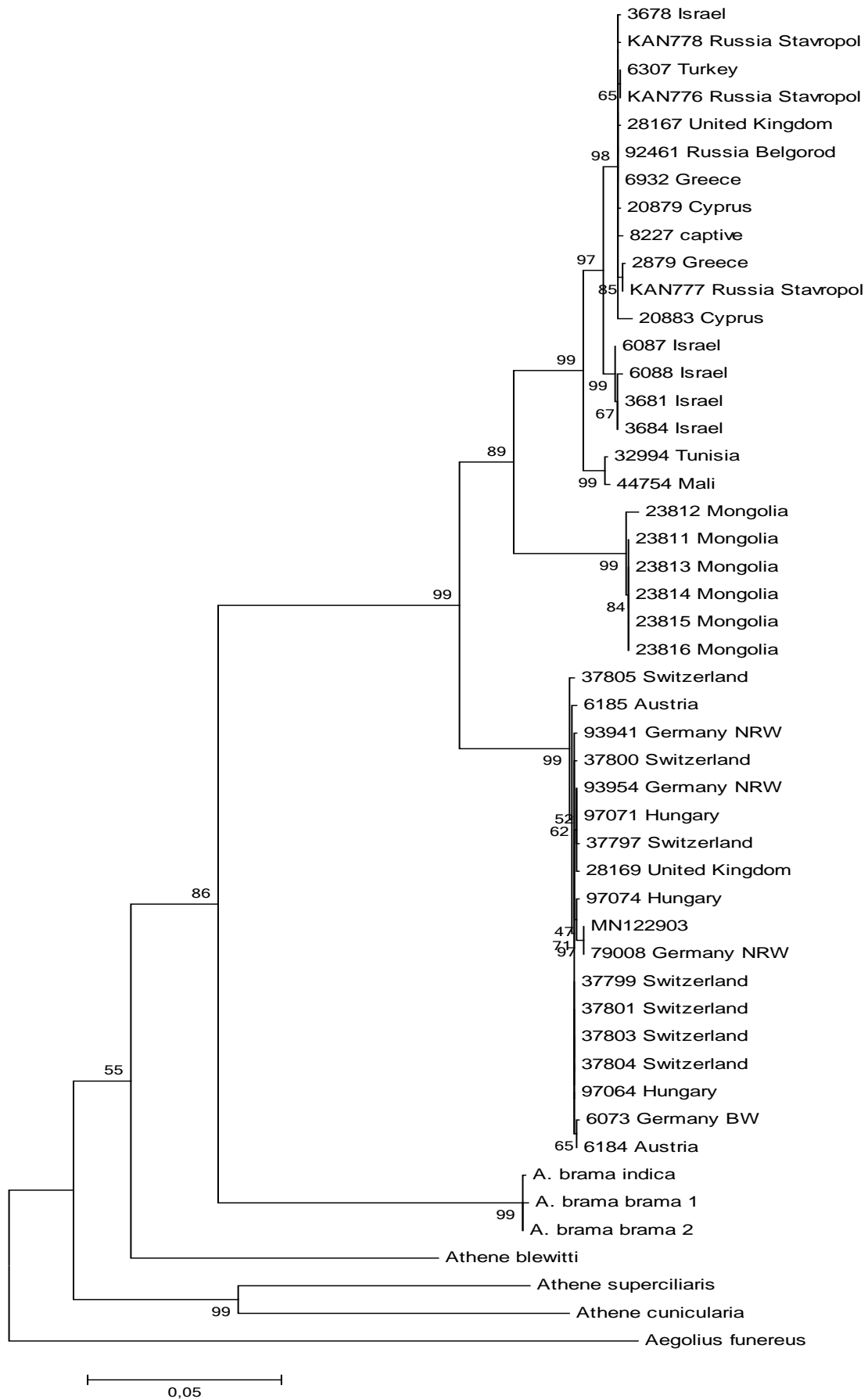


Figure A12. Maximum likelihood tree of mitochondrial (COI+Cyt *b*) sequences of Little owls.

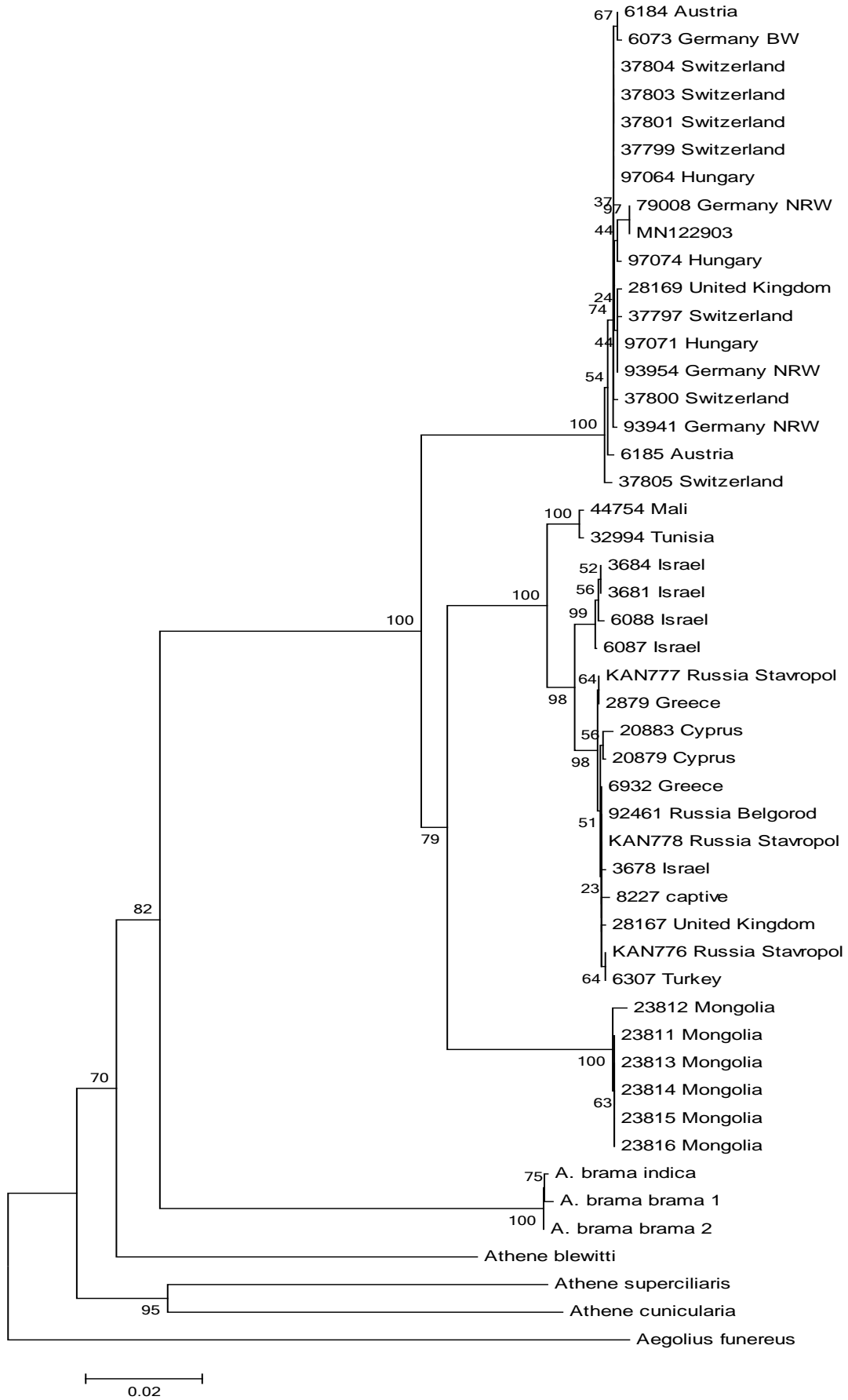


Figure A13. Neighbor-joining tree of mitochondrial (COI+Cyt *b*) sequences of Little owls.

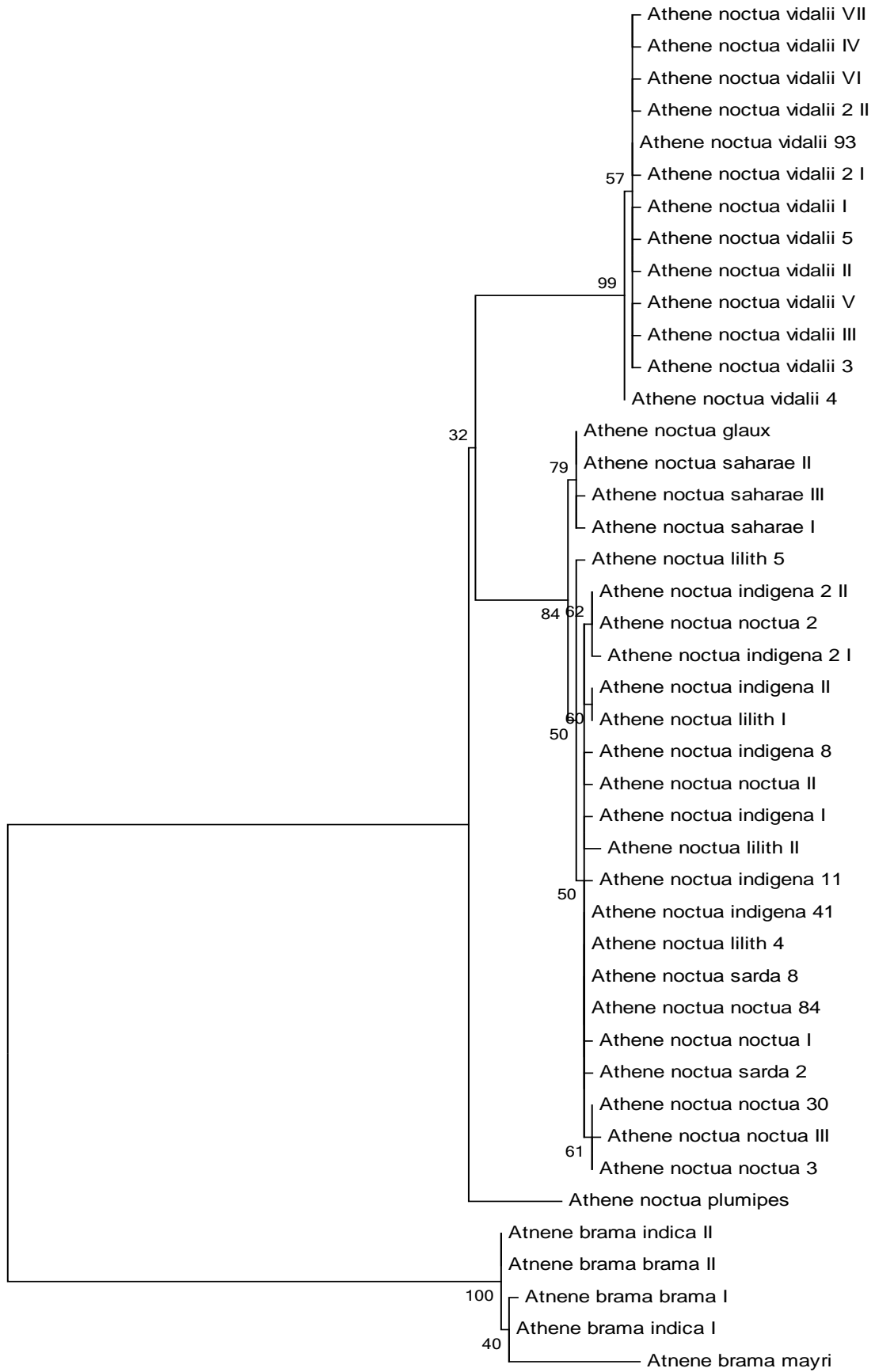
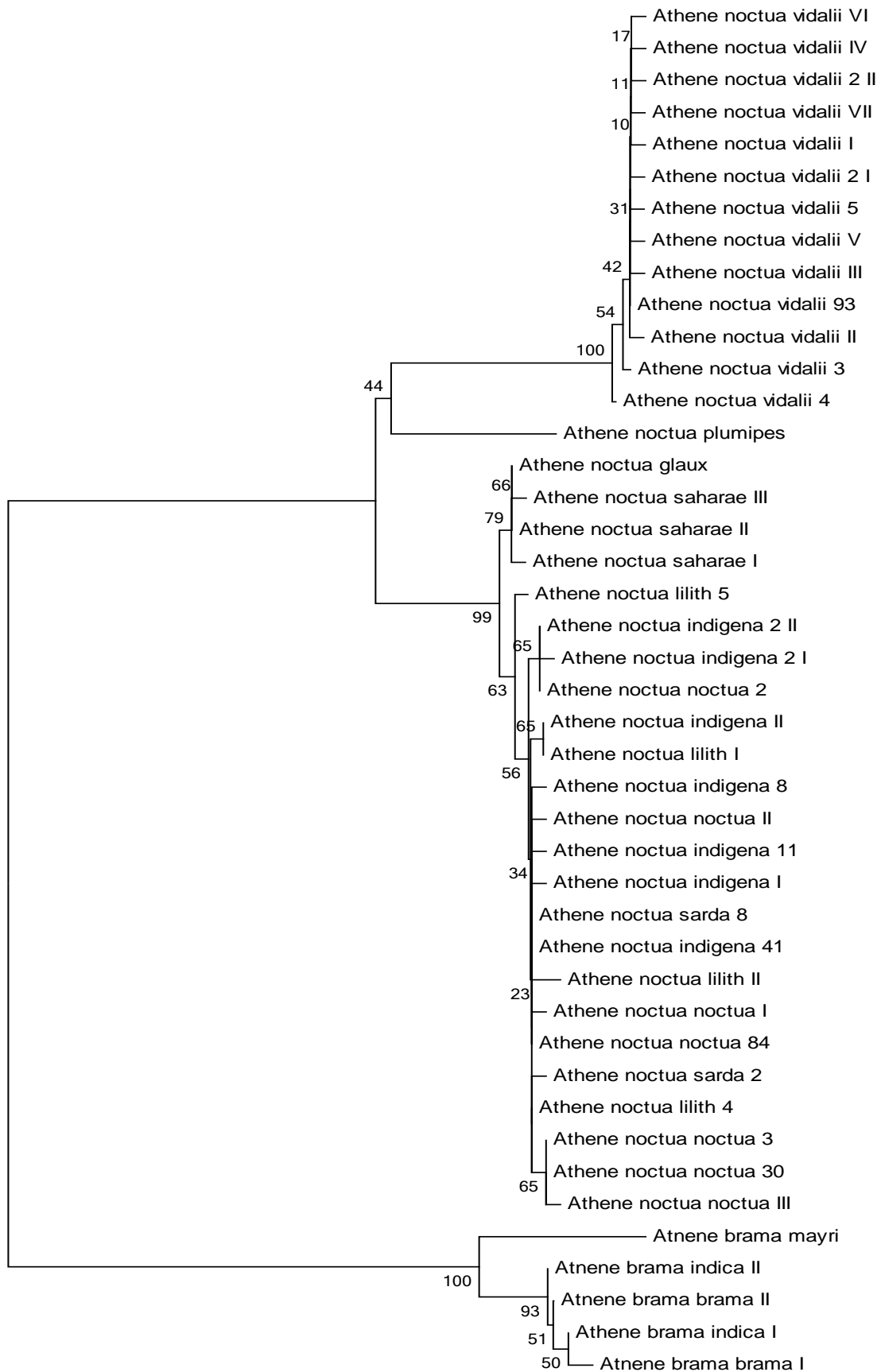


Figure A14. Maximum likelihood tree of COI sequences of Little owls taxa.



0.01

Figure A15. Neighbor-joining tree of COI sequences of Little owls taxa.