Article

Old and Cosmopolite: Molecular Phylogeny of Tropical–Subtropical Kites (Aves: Elaninae) with Taxonomic Implications

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Abstract: Kites of the Elaninae group are small and medium-sized, mostly tropical raptors traditionally considered as an early diverged subfamily of the Accipitridae. We used nucleotide sequences of three genetic markers (mitochondrial *Cyt b* and *COI*, nuclear *RAG-1*) to reconstruct the phylogenetic relationships of the Elaninae, other kites, and representatives of different families of diurnal raptors. Our results confirm the basal position of Elaninae, separated the latest in Early Miocene, including *Chelictinia riocourii,* which was not sequenced before and belongs to this group. Not only DNA data but also cytological, morphological, and ecological data show the singularity of Elaninae. We suggest elevating this group to family level as Elanidae within the order Accipitriformes. It includes *Gampsonyx swainsonii* as a monotypic subfamily because of distinctive traits and DNA sequence data. Taxonomic implications for other macrogroups of Accipitriformes are discussed.

Keywords: kites; phylogeny; Elaninae; tropics; taxonomy; mtDNA; *RAG-1*

1. Introduction

Elaninae Blyth, 1850, are traditionally considered as one of raptor subfamilies of the family Accipitridae Viellot, 1816 [1–3]. They are small and medium-sized red-eyed kites and inhabit mostly semi-open and open tropical biomes in all continents [4,5] (Figure 1). Actually, this small group counts three genera, and two of them *Gampsonyx* (Vigors, 1825) and *Chelictinia* (Lesson, 1843) are monotypic. The small-tailed colorful Pearl Kite *Gampsonyx swainsonii* (Vigors, 1825), living in Central and South America, consists of three subspecies. The Scissor-tailed Kite *Chelictinia riocourii* (Temminck, 1821) is a monotypic species, small gray-white kite with a long forked tail from Central Africa. The genus *Elanus* (Savigny, 1809), includes tropical and subtropical white-gray-black kites of medium size with short tails quite similar to each other. This taxon consists of four species: Old World cosmopolite Black-winged Kite *E. caeruleus* (Desfontaines, 1789) with three [6,7] or four [8,9] subspecies recognized; American White-tailed Kite *E. leucurus* (Vieillot, 1818) with two subspecies; and Australian monotypic kites: Black-shouldered *E. axillaris* (Latham, 1801) and Letter-winged *E. scriptus* (Gould, 1842).
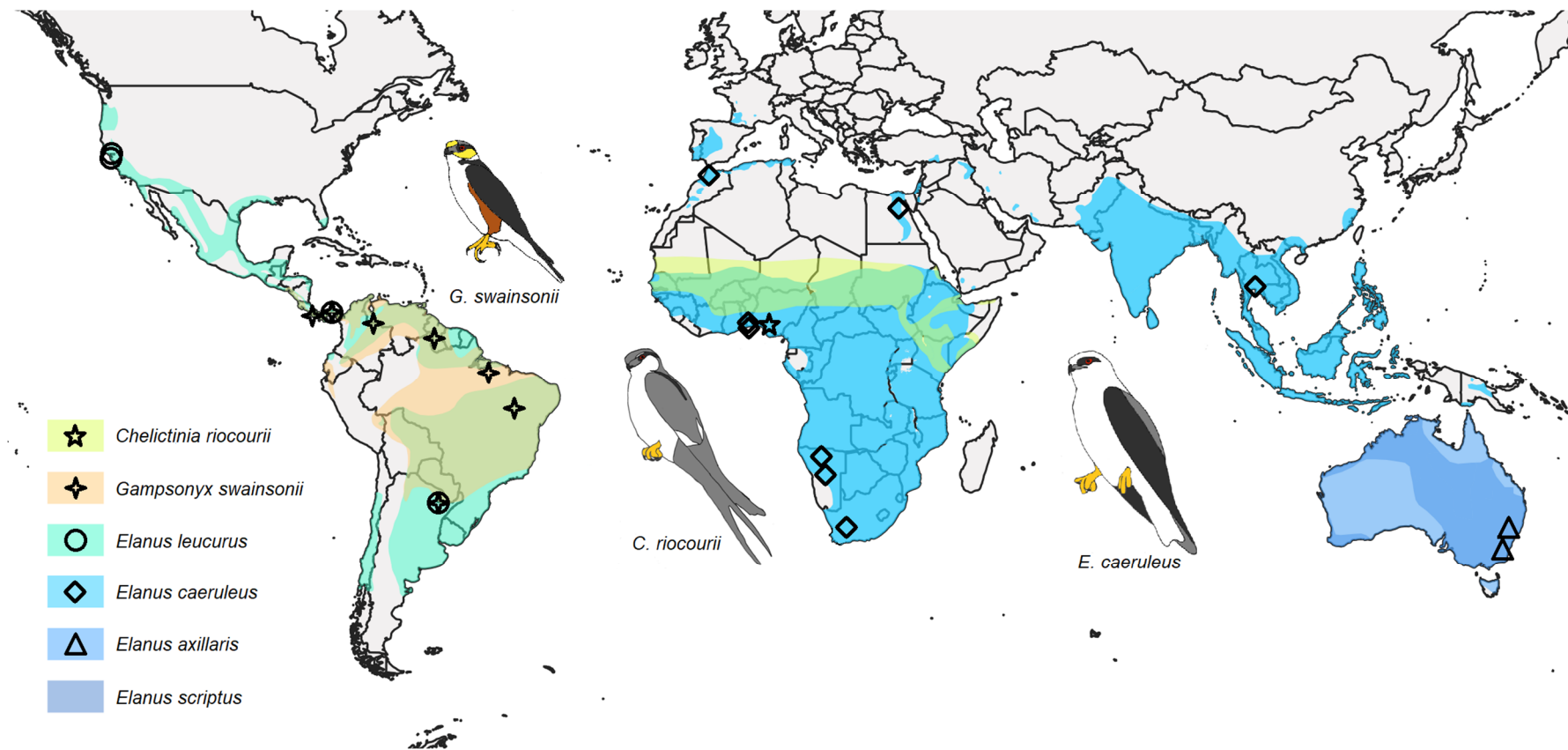
Figure 1. Sample locations (geometric symbols), range (from [10–15]), and schematic illustrations of Elanin kites genera representatives.

When the Elaninae subfamily was described to distinguish from other diurnal birds of prey, Blyth [1] included inside *Elanus*, *Chelictinia*, and *Gampsonyx* genera, but he considered the last as part of *Elanus*. However, Ridgway [16] used for these raptors the name "group Elani" inside of the subfamily Buteoninae (Vigors, 1825), with genera *Elanus*, *Gampsonyx*, and further [17] *Elanoides* (Vieillot, 1818). After an osteological examination, Shufeldt [18] moved Elaninae inside in the family Milvidae (Vigors, 1825). The last suggestion was not supported by later taxonomists. Pycraft [19] placed Elaninae in Buteonidae (synonym of Accipitridae) and added *Macheiramphus* (Bonaparte, 1850). Later, its position was questioned and this genus is conditionally placed among Perninae (Blyth, 1850) [3]. Peters [2] added in this subfamily *Chelictinia* and placed *Gampsonyx* in Falconidae (Leach, 1820). Friedmann [20] moved it back to Elaninae.

The modern constitution of this group was proposed by Jollie [21–23] based on the morphology of the bones, muscles, and plumage. He considered "elanins" as *Elanus*, *Gampsonyx*, and *Chelictinia* within the subfamily of Milvinae (Vigors, 1825), or as a separate subfamily which might be doubtfully enlarged with *Ictinia* (Vieillot, 1816), *Harpagus* (Vigors, 1824), and *Macheiramphus* [23]. Stresemann and Amadon in the second edition of the first volume of Peters's "Check-list of birds of the world" placed *Elanus*, *Gampsonyx*, and *Chelictinia* as the majority of diurnal raptors genera to the large Accipitrinae subfamily [24]. Wolters [25], on the other hand, proposed multiple subfamilies in the Accipitridae; among them, Elaninae with *Elanus* and *Chelictinia* and monotypic Gampsonychinae (Wolters, 1975). Because Wolters did not provide a diagnosis for this taxon and other new taxa, they must be considered as *nomina nuda* and are not valid according to the International Code of Zoological Nomenclature (Article 13). Amadon and Bull [26] added *Macheiramphus* to Elaninae again. Recently, the name of Elaninae as a subfamily of Accipitridae with three genera—*Elanus*, *Gampsonyx*, and *Chelictinia*—was used after an analysis of mitochondrial sequences by Lerner and Mindell [3], which is close to the first classification proposed by Blyth a century and a half ago.

Before the molecular era, Elaninae, like other kites, were considered by their morphology as an old and primitive group of the Accipitridae [4,23,27]. In the family tree of Accipitridae, the Elaninae are found as the most ancient branch, and their position is basal to other subfamilies, including different kite genera after trees based on mitochondrial *Cyt b* [28,29], combined mitochondrial and nuclear *Cyt b+RAG-1* [30], *Cyt b+ND2+BF-I7* [3], and *Cyt b+RAG-1+GAPDH+LDH+AK+c-myc+c-mos* [31] sequences. Moreover, because of their distant position to the "main" Accipitridae, we proposed to treat this group as a separate family Elanidae [28,29], and even the suggestion of the order Elaniformes was raised [32]. Further research on raptor molecular phylogeny confirmed that *Macheirhamphus* as well as *Elanoides,* which were formerly placed in Elaninae, are distant from *Elanus*. However, *Gampsonyx* appears to be closer to *Elanus* [3,31,33].

The aim of this study is to analyze the molecular phylogeny of the Elanin kite group and its position in the order Accipitriformes (Vieillot, 1816), using nucleotide sequences of the mitochondrial cytochrome *b* (*Cyt b*) and cytochrome oxidase 1 (*COI*) genes, and the nuclear recombination-activating gene 1 (*RAG-1*). Results are discussed in relation to their taxonomy, morphology, ecology, and geographic distribution.

2. Materials and Methods

2.1. Laboratory Procedures

Samples from 17 wild individuals of *Elanus caeruleus*, *E. axillaris*, *E. leucurus*, and *Chelictinia riocourii* deposited in the specimen collection of the Institute of Pharmacy and Molecular Biotechnology (IPMB) were investigated (Table 1, Figure 1), GenBank accession numbers MT800519–MT800541, MT897851–MT897865. The DNA was extracted from tissue, feather, and blood samples and isolated using standard proteinase K (Merck, Darmstadt) and a phenol/chloroform protocol [34]. The loci were amplified using specific primers (Table 2).

Table 1. Samples of Elanin kites used in the phylogenetic analysis.

Taxon	Origin	Source	IPMB Number/GenBank Accession Number/BOLD Process ID		
			Cyt b	*COI*	*RAG-1*
Elanus caeruleus caeruleus	Egypt	This study	IPMB373/MT800519	IPMB373/MT800534	IPMB373/MT897851
Elanus caeruleus caeruleus	Morocco	This study	IPMB4251/MT800520	IPMB4251/MT800535	IPMB4251/MT897852
Elanus caeruleus caeruleus	South Africa, Cape Province	This study	IPMB9965/MT800521	IPMB9965/MT800536	IPMB9965/MT897853
Elanus caeruleus caeruleus	South Africa, Cape Province	This study	IPMB9966/MT800522	IPMB9966/MT800537	IPMB9966/MT897854
Elanus caeruleus caeruleus	South Africa, Cape Province	This study	IPMB9967/MT800523	-	IPMB9967/MT897855
Elanus caeruleus caeruleus	Namibia, Okaukuejo	This study	IPMB20593/MT800524	-	IPMB20593/MT897856
Elanus caeruleus caeruleus	Namibia, Windhoek	This study	IPMB47115/MT800525	-	IPMB47115/MT897857
Elanus caeruleus caeruleus	Namibia, Windhoek	This study	IPMB47116/MT800526	IPMB47116/MT800538	IPMB47116/MT897858
Elanus caeruleus caeruleus	Namibia, Windhoek	This study	IPMB47117/MT800527	-	IPMB47117/MT897859
Elanus caeruleus caeruleus	Namibia, Windhoek	This study	IPMB47118/MT800528	-	IPMB47118/MT897860
Elanus caeruleus caeruleus	Namibia, Windhoek	This study	IPMB47119/MT800529	-	-
Elanus caeruleus caeruleus	Benin, Cotonou	This study	IPMB58999/MT800530	-	IPMB58999/MT897861
Elanus caeruleus caeruleus	Benin, Bohicon	This study	IPMB75231/MT800531	IPMB75231/MT800539	IPMB75231/MT897862
Elanus caeruleus vociferus	Thailand	Boonyaprakob and Kasorndorkbua, unpubl.	-	MK932886	-
Elanus caeruleus ssp.	unknown	[33]	-	-	EF078724
Elanus leucurus leucurus	Argentina, San Cayetano (Corrientes)	[35]	-	FJ027543/KBARG184-07	-
Elanus leucurus majusculus	USA	[3]	AY987233	-	-
Elanus leucurus majusculus	Panama, Pacora	Smithsonian Tropical Res. Inst., unpubl.	-	BSENC001-06	-
Elanus leucurus majusculus	Panama, Pacora	Smithsonian Tropical Res. Inst., unpubl.	-	BSPAC008-14	-
Elanus leucurus majusculus	USA, Rodeo (California)	[36]	-	DQ432907/CDMVZ014-05	-
Elanus leucurus majusculus	USA, Berkeley	[36]	-	DQ432908/CDMVZ015-05	-
Elanus axillaris	Australia, Birriwa vicinity	This study	-	-	IPMB8050/MT897863
Elanus axillaris	Australia, Canberra	This study	-	-	IPMB29917/MT897864
Elanus axillaris	Australia, Canberra	This study	IPMB29920/MT800532	IPMB29920/MT800540	-
Gampsonyx swainsonii swainsonii	Argentina, San Cayetano (Corrientes)	Mus. Argent. Cienc. Nat. Rivadavia, unpubl.	-	FJ027613/KBAR776-06	-
Gampsonyx swainsonii swainsonii	Brazil, Serra das Confusoes	[37]	-	JN801680/LGEMA021-07	-
Gampsonyx swainsonii swainsonii	Brazil, Tailândia	[37]	-	LGEMA404-08	-
Gampsonyx swainsonii leonae	Guyana, Saddle Mountain vicinity	[38]	-	JQ174910/USNMI208-11	-

Table 1. *Cont.*

Taxon	Origin	Source	IPMB Number/GenBank Accession Number/BOLD Process ID		
			Cyt b	*COI*	*RAG-1*
Gampsonyx swainsonii leonae	Guyana, Saddle Mountain vicinity	[38]	-	JQ174911/USNMK306-11	-
Gampsonyx swainsonii leonae	Panama, Pacora	Smithsonian Tropical Res. Inst., unpubl.	-	BSPBA002-07	-
Gampsonyx swainsonii leonae	Panama, Puerto Armuelles	Smithsonian Tropical Res. Inst., unpubl.	-	BSPBA005-07	-
Gampsonyx swainsonii leonae	Colombia, Caño Agua Verde (Arauca) vicinity	Inst. Invest. Recurs. Biol. von Humboldt, unpubl.	-	IAVHB082-13	-
Gampsonyx swainsonii leonae	unknown	[33]	-	-	EF078725
Chelictinia riocourii	Nigeria, Agbor	This study	IPMB47157/MT800533	IPMB47157/MT800541	IPMB47157/MT897865

Table 2. Primers used in this study.

Gene	Primer	Sequence (5'-3')	Reference
Cyt b	L14764	F-TGRTACAAAAAAATAGGMCCMGAAGG	[39]
	MT-c2	F-TGAGGACAAATATCATTCTGAGG	[40,41]
	Mt-Fr	R-CTAAGAAGGGTGGAGTCTTCAGTTTTTGGTTTACAAGAC	[39], modified
	Mt-E	R-GCAAATAGGAAGTATCATTCTGG	[41]
COI	Passer F1	F-CCAACCACAAAGACATCGGAACC	[42]
	Passer R1	R-GTAAACTTCTGGGTGACCAAAGAATC	[42]
RAG-1	R17	F-CCCTCCTGCTGGTATCCTTGCTT	[43]
	R51	R-GACCCTCTTTCTGCTATGAGGGGGC	[44]

PCR amplifications were carried out in 50 μL reaction volumes containing PCR buffer, 100 μM dNTPs, 0.2 units of Taq DNA polymerase (Bioron, Ludwigshafen), 200 ng of DNA, and 5 pmol of primers. PCR conditions were set as follows for *Cyt b/COI/RAG-1*, respectively: 95/95/94 °C initialization for 5 min; 95/95/94 °C denaturation for 45 s, 54/50/54 °C for annealing temperature for 1 min, and 72 °C for extension for 1.5/2/2 min, running in 38 cycles. A final elongation step was conducted at 72 °C for 10 min.

The PCR product was purified by precipitation in 4 M NH_4Ac and absolute ethanol (1:1:10), centrifuged at 13,000 rpm for a period of 30 min, followed by centrifugation with 70% ethanol using the same settings and later dissolved in 25 μL of sterile H_2O. 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 carried out on ABI 3730 automated capillary sequencer (Applied Biosystems, Carlsbad, CA, USA) with the ABI Prism Big Dye Terminator Cycle Sequencing Ready Reaction Kit 3.1 (executed by STARSEQ GmbH, Mainz, Germany).

2.2. Phylogenetic Analysis

Mitochondrial DNA sequences were controlled in order to exclude the possibility of stop codons, indicating that these sequences did not come from nuclear copies. Alignments were created in BioEdit 7.2.6 [45], nucleotide sequences were aligned using the MUSCLE algorithm [46].

We analyzed 1039 aligned base pairs (bp) of *Cyt b*, 604 bp of *COI*, and 878 bp of *RAG-1* genes of Elaninae. Some sequences remained unsuccessful. A total of 17 sequences from GenBank and Barcode of Life Data System (BOLD) databases were added in the analysis, thus, we examined all taxa of Elaninae except *E. scriptus* (Table 1, Figure 1). Maximum Likelihood and Neighbor-Joining trees for each locus and average pairwise p-distances were calculated with MEGA 6.06 [47]. Relative branch support was evaluated with 1000 bootstrap replicates for the Maximum Likelihood and 10,000 for Neighbor-Joining trees.

For phylogenetic analysis, we added Bat Hawk *Macheiramphus alcinus* (Bonaparte, 1850), and Swallow-tailed Kite *Elanoides forficatus* (Linnaeus, 1758) sequences [3,33,36], formerly belonging to the same group with *Elanus*; one species per genera, for which we found sequences from all three genes, considered actually or in the past as a kite [2,3,7,48]: *Ictinia*, *Milvus* (Lacépède, 1799), *Haliastur* (Selby, 1840), *Rostrhamus* (Lesson, 1830), *Pandion* Savigny, 1809, sequences [3,33,35,37,49–52]; sequences from three genes of representatives from different subfamilies, one species for each, of Accipitridae [53–58], and other diurnal raptors as Secretarybird [59] and a falcon [60] from complete mitogenomes deposited in GenBank, nuclear IPMB (GenBank accession numbers MT897866–MT897875), and GenBank sequences as outgroup.

Bayesian concatenated mitochondrial and nuclear gene trees were calculated using BEAUti 1.8.0 [61]. For finding the best evolution model, jModelTest 2.1.10 was applied [62,63] with the Akaike information criterion [64], which showed a GTR+I+Γ model for *Cyt b* and *COI* complete datasets, TrN+Γ for the *RAG-1* dataset, TPM1uf+Γ for *Cyt b*, and TIM2+I+Γ for separate *COI* kite datasets. Because the three last (and many other) models are not available in the BEAST/BEAUti package, they were changed to the most similar by Δ of corrected AIC, and finally GTR+I [65,66], GTR+Γ, and GTR+I+Γ [65,67,68] were chosen for *RAG-1*, separate kites *Cyt b*, and all other datasets, respectively. 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 [69], and 1.8% for *COI* [70], the estimated rate with lognormal prior distribution of the substitution rate for nuclear alignment. We chose the strict clock model, Yule speciation process [71,72], for the Markov chain Monte Carlo method to measure the length of the chain set with 10 million runs, sampling every 1000th run. Phylogenetic trees were performed in BEAST 1.8.0 [61], log files were checked for convergence of runs in Tracer 1.7.1 [73], and the trees with

the best likelihood were summarized using TreeAnnotator 1.8.0 [61], and the first 10% of trees were discarded as burn-in. Completed phylogenetic trees were arranged and visualized in FigTree 1.4.3.

3. Results

The numbers of parsimony-informative and variable uninformative sites for Elanin kites were 91 and 118 bp of a total 1039 bp for *Cyt b*, 114 and 31 bp of 604 bp for *COI*, and 5 and 16 bp of 878 bp for *RAG-1* gene loci, respectively. Sequence divergences using pairwise distances are relatively high and consist up to 2.2% for *COI* between subspecies, 8.7–10.9% for *Cyt b* and 8.8–9.6% for *COI* between species of the genus *Elanus*, and 11.4–13.0% for *Cyt b* and 11.9–15.2% for *COI* between genera of the group (Table 3).

As can be seen from Figure 2, the families Sagittaridae (Finsch and Hartlaub, 1870), and Pandionidae (Sclater and Salvin, 1873), represent the basal branches 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 mitochondrial gene sequences (Figure 2a) as well as for the nuclear *RAG-1* gene (Figure 2b). As expected, other kites demonstrate polyphyly of this artificial group, forming clades together with different subfamily representatives, except *Elanoides*, which clusters with other non-Elaninae Accipitridae, with the genus being basal to the non-Elanin clade (Figure 2). Phylogenetic trees, which were constructed with ML and NJ, provide mostly identical topologies for separate mitochondrial and nuclear datasets (Figures S1–S3).

According to the molecular clock model used in Bayesian analysis, we can estimate the separation of Elaninae from other diurnal raptors at Early Miocene, 21.3 Mya (with 95% interval of highest posterior density 24.9–17.6 Mya; Figure 3). The divergence within the group between *Elanus* and two other genera passed 16.7–15.3 Mya (95% HPD = 20.1–12.7 Mya for both nodes), and the speciation inside *Elanus* occurred in Late Miocene 8.6–7.5 Mya (95% HPD = 10.2–6.1 Mya for both nodes).

Chelictinia riocourii, which was never sequenced before, unequivocally, belongs to the Elaninae kite clade. The position of *Gampsonyx swainsonii* is more distant to the two other Elaninae genera. The separate position of *Elanus axillaris* in the genus as revealed by mitochondrial sequences is not confirmed by nuclear *RAG-1* sequences. There are several different haplotypes inside *Elanus caeruleus* belonging to nominative subspecies supported by mitochondrial and nuclear data (Figure 2).

Table 3. Pairwise p-distance values for taxa of Elaninae, Accipitridae, and other diurnal raptors used in the phylogenetic analysis, based on *Cyt b* (below diagonal) and *COI* (above diagonal).

| №	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1	*Elanus caeruleus caeruleus*		-	0.109	-	0.103	0.130	-	-	0.167	0.153	0.159	0.169	0.151	0.155	0.167	0.157	0.164	0.153	0.163	0.170	0.162	0.162	0.177
2	*Elanus caeruleus vociferus*	0.022		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	*Elanus axillaris*	0.090	0.088		-	0.087	0.114	-	-	0.143	0.146	0.149	0.147	0.138	0.147	0.145	0.150	0.162	0.138	0.145	0.149	0.146	0.153	0.161
4	*Elanus leucurus leucurus*	0.092	0.096	0.096		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	*Elanus leucurus majusculus*	0.092	0.096	0.096	0.000		0.127	-	-	0.162	0.158	0.154	0.154	0.150	0.150	0.164	0.156	0.160	0.143	0.160	0.164	0.149	0.161	0.176
6	*Chelictinia riocourii*	0.133	0.131	0.123	0.141	0.141		-	-	0.131	0.142	0.134	0.147	0.139	0.141	0.146	0.148	0.150	0.137	0.131	0.153	0.146	0.145	0.162
7	*Gampsonyx swainsonii leonae*	0.137	0.136	0.151	0.119	0.119	0.128		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	*Gampsonyx swainsonii swainsonii*	0.138	0.137	0.152	0.121	0.121	0.129	0.000		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	*Elanoides forficatus*	0.163	0.164	0.159	0.164	0.164	0.149	0.153	0.154		0.145	0.137	0.134	0.127	0.136	0.144	0.137	0.138	0.141	0.138	0.140	0.157	0.158	0.159
10	*Ictinia plumbea*	0.156	0.161	0.157	0.157	0.157	0.137	0.141	0.141	0.142		0.073	0.103	0.091	0.075	0.116	0.115	0.105	0.114	0.131	0.130	0.146	0.158	0.167
11	*Rostrhamus sociabilis*	0.150	0.149	0.152	0.162	0.162	0.132	0.139	0.139	0.146	0.109		0.103	0.095	0.080	0.113	0.123	0.106	0.118	0.130	0.133	0.142	0.161	0.174
12	*Haliastur indus*	0.153	0.161	0.156	0.161	0.161	0.154	0.159	0.159	0.137	0.124	0.114		0.075	0.100	0.124	0.121	0.113	0.117	0.132	0.144	0.157	0.168	0.174
13	*Milvus migrans*	0.158	0.164	0.151	0.169	0.169	0.166	0.163	0.162	0.144	0.108	0.111	0.076		0.093	0.111	0.116	0.108	0.114	0.130	0.121	0.150	0.154	0.158
14	*Buteo buteo*	0.160	0.159	0.151	0.147	0.147	0.127	0.139	0.139	0.139	0.089	0.098	0.113	0.106		0.113	0.119	0.109	0.121	0.130	0.133	0.146	0.160	0.176
15	*Accipiter nisus*	0.138	0.151	0.144	0.167	0.167	0.152	0.154	0.156	0.154	0.123	0.121	0.127	0.123	0.136		0.123	0.133	0.138	0.134	0.137	0.161	0.174	0.177
16	*Circus cyaneus*	0.155	0.156	0.144	0.164	0.164	0.146	0.159	0.159	0.156	0.119	0.126	0.127	0.113	0.119	0.108		0.131	0.134	0.138	0.135	0.162	0.167	0.172
17	*Haliaeetus albicilla*	0.148	0.149	0.136	0.154	0.154	0.129	0.143	0.142	0.137	0.096	0.104	0.096	0.096	0.096	0.108	0.099		0.131	0.149	0.141	0.149	0.171	0.177
18	*Aquila chrysaetos*	0.143	0.151	0.137	0.166	0.166	0.129	0.151	0.151	0.144	0.116	0.134	0.123	0.127	0.126	0.109	0.123	0.109		0.130	0.126	0.155	0.160	0.165
19	*Spilornis cheela*	0.150	0.151	0.146	0.152	0.152	0.137	0.141	0.141	0.154	0.141	0.142	0.132	0.136	0.124	0.149	0.144	0.129	0.134		0.132	0.149	0.156	0.166
20	*Aegypius monachus*	0.148	0.156	0.154	0.162	0.162	0.149	0.151	0.151	0.154	0.129	0.134	0.119	0.126	0.126	0.141	0.118	0.123	0.137	0.132		0.166	0.163	0.168
21	*Pandion haliaetus*	0.145	0.144	0.154	0.157	0.157	0.121	0.148	0.149	0.139	0.139	0.156	0.147	0.149	0.141	0.142	0.149	0.132	0.136	0.142	0.161		0.150	0.179
22	*Sagittarius serpentarius*	0.166	0.171	0.164	0.169	0.169	0.146	0.156	0.156	0.161	0.166	0.157	0.146	0.164	0.156	0.171	0.175	0.159	0.159	0.169	0.152	0.151		0.173
23	*Falco peregrinus*	0.171	0.175	0.172	0.184	0.184	0.164	0.161	0.161	0.184	0.161	0.157	0.175	0.182	0.166	0.171	0.179	0.172	0.156	0.182	0.179	0.169	0.171	
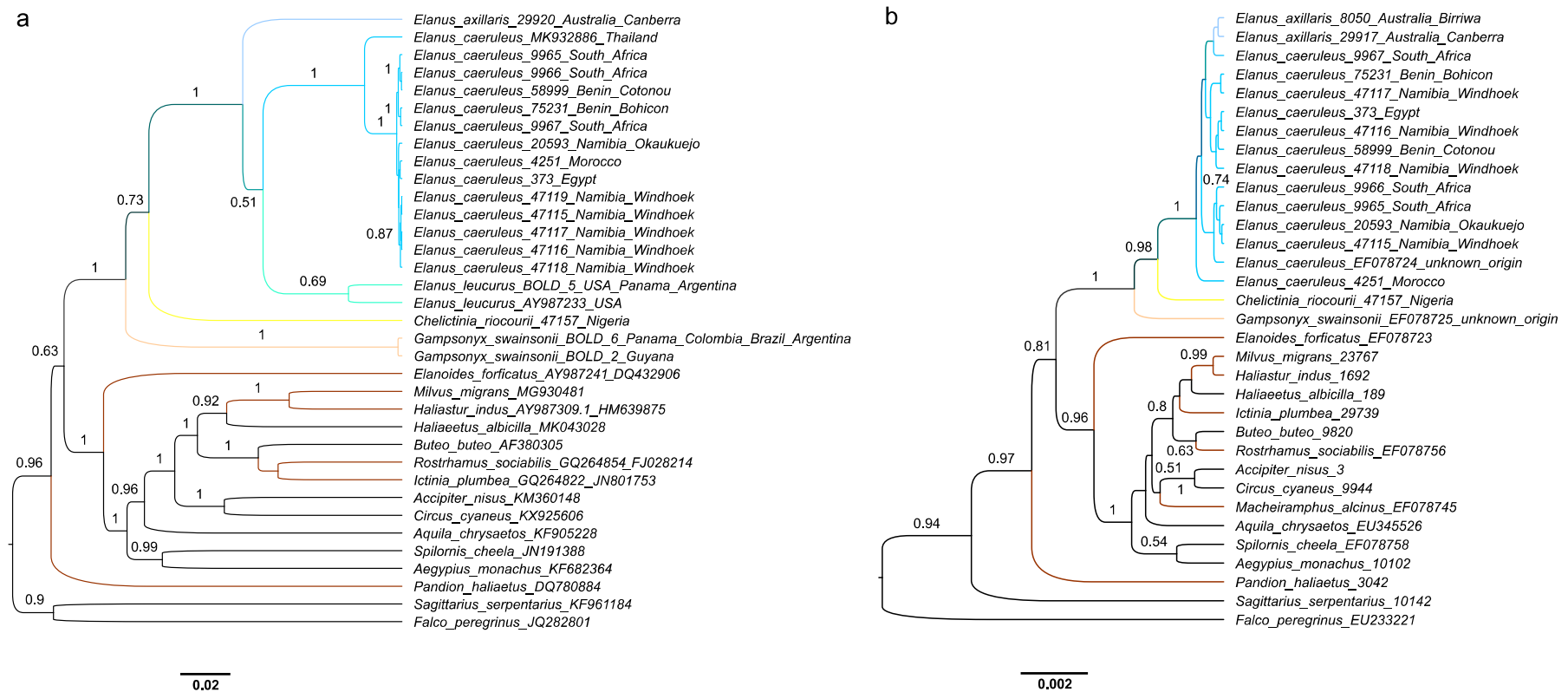
Figure 2. Phylogenetic relationships between taxa of Elaninae (in colors), other kites (in brown), and diurnal raptors based on Bayesian Inference of concatenated mitochondrial dataset *Cyt b+COI* (**a**) and nuclear dataset *RAG-1* (**b**). Posterior probabilities (>0.5) are indicated on the branches, last line represents number of substitutions per site.
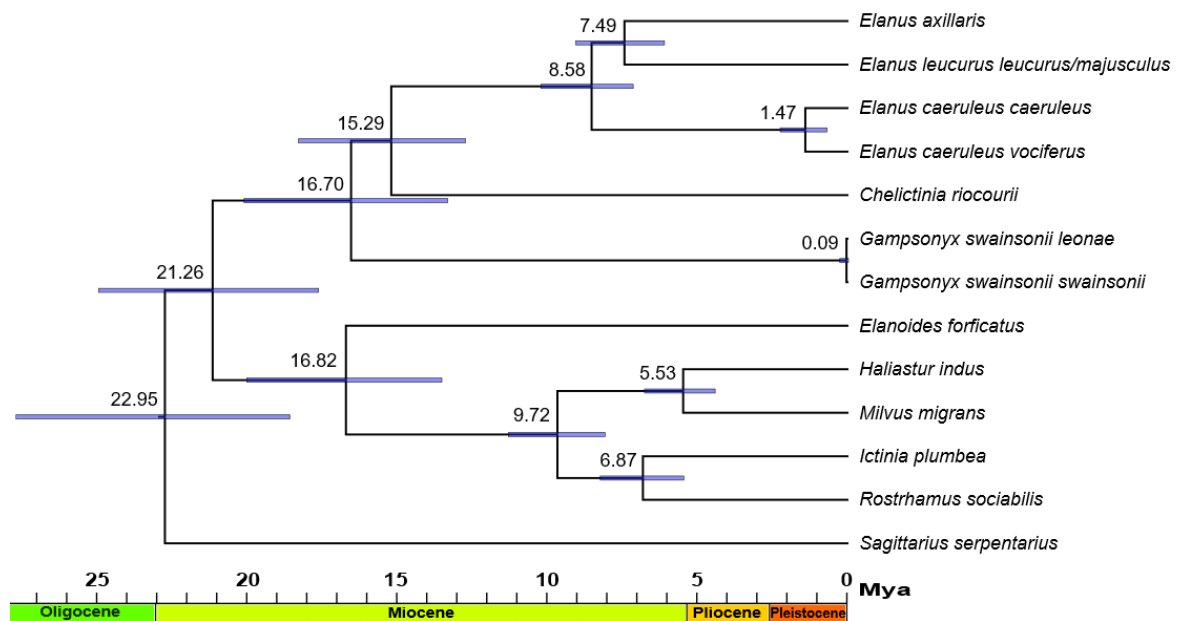
Figure 3. Phylogeny of elanins and other selected kites based on Bayesian Inference of the concatenated mitochondrial dataset. The secretarybird is an outgroup, node ages in million years ago are indicated on the branches. Node bars show the 95% highest posterior density of nodal age estimates.

4. Discussion

4.1. Morphological Features of Elanin Kites

Among evolutionary features, which distinguish elanins from other diurnal raptors, several morphological traits are found. Some of them are absent in other Accipitridae. Firstly, it has a primitive structure of the skull resembling birds of prey embryos [74]: the palate remains completely schizognathous [18]. This feature was later found in several Accipitridae genera [19,21], but are most strongly separated in Elaninae skull maxillopalatine processes [20,21]; the boundary of the *foramen olfactorii* is ossifying [74]; very low basicranial angle for *Elanus* and curved falcon-type form of the orbital process for *Gampsonyx* were also notified [22]. Features of limb bones: *manus* is longer than *humerus*, the inner spur of *hypotarsus* starts from the inner board of the shaft [19], distant positions of metatarsal scars (like Osprey) with a specific form of the middle trochlea, pillar-like medial process of calcaneal tuberosity, and "elanin subtype" of the tarsus in general as result of specialization for easy flexing of the toes. [22]. Other osteological traits are an absence of *hypocleidium* in furcula, specific form of coracoids—high position of coracoid foramen on procoracoid process and short sternocoracoid process, large depth of the keel and constitution of the sternum like Osprey, and the first cervical rib fused with the vertebra for *Elanus* [18,22,23].

Elanin kites equally have myological peculiarities. Among those related with limbs: the 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*, very weak *peroneus longus*, completely separated heads of the *pars perforatus digiti III*, as well as only medial and no lateral head of the *pars perforatus digiti IV* [23]. Other unique muscle types: *ceratoglossus* arise to the medial insertion of the massive *transverses hyoideus* like cathartids, Secretarybird, and in part Osprey; lack of *pars mandibularis*; muscles of innominate bones reach forward beneath the anterior plates of the ilia, and the *caudilio-femoralis* arising strongly forward by a tendon from the ventral point of the pygostyle. For *Gampsonyx*, the *pars metapatagialis* of *latissimus dorsi* is related with ribs not only three and four but equally five and six by aponeurosis like falcons [23].

Other unique morphological features of Elaninae are absent grooves on the claws [20]; almost complete absence of plumules on the crown for *Gampsonyx* [21], most distinct coloration parts among all Accipitriformes and absence of the median black throat stripe; weakly developed tympanic box in syrinx; and a simple gut: open duodenum, undeveloped ileum with absent supracecal loop [23]. The peculiarities which appear apparently independently during the evolution of elanins and other Accipitriformes should be added: lack of feathers in back patagium, also for the Hooded Vulture *Necrosyrtes* Gloger, 1841 [21]; perforated-type pelvis and reducing of zygomatic process like *Macheirhamphus* [22,23]; reducing of the insertion upon the third bronchial ring as for *Buteo* (Lacépède, 1799), hawks [23].

In recent study [75], *Elanus*, the well-investigated genus of this group is characterized unlike other diurnal birds of prey by owl-like features as a result of convergent evolution: zygodactylism (like Osprey), large frontally-placed eyes, vibrissae around the beck, velvet structure of upper parts of primary and secondary feathers as an adaptation for silent flight, and the producing of pellets with undigested bones as result of low stomach acidity [75]. The *Elanus* representatives are more or less nocturnal, the most night-active species is *Elanus scriptus*, which dispose an asymmetrical position of ear openings like several owls, which helps them to detect prey by sound [75]. Moreover, elanin eggs are intensively pigmented as falconid, and elements of their vocalization resemble the Barn Owl *Tyto* (Billberg, 1828)—screech, and falcons—chatter, maternal crock [32].

4.2. Cytogenetics of Elanus caeruleus

The study of the Black-winged Kite reveals its remarkable cytogenetic structure not observed in other Accipitridae [76]. Diurnal raptors have karyotype organized by medium-sized chromosomes with few numbers of small chromosomes, instead of macro- and dot-chromosome karyotypes of other birds. *Elanus caeruleus* show an even more specific organization with only one pair of microchromosomes. At the same time, nucleolus organizer regions of the Black-winged Kite are located on two chromosome pairs instead of one which is atypical for Accipitridae [77]. Finally, a comparison of its chromosome banding pattern with other raptor taxa demonstrates that high rearrangement and sex chromosomes of *E. caeruleus* are almost equal in size in contrast even to most other birds. All these particularities are considered as a result of chromosome evolution [76].

The specimens from India which should belong to *E. c. vociferus* (Latham, 1790) have been ascribed a diploid number of 66 chromosomes [78], while samples from Morocco and South Africa, which should be part of nominative subspecies that contain 68 [76] and 64 [79] chromosomes, respectively. However, the differences in the number of chromosomes between the latter two studies may be also erroneous in distinguishing and reporting microchromosomes [76]. This explanation seems more probable than the existence of populations in Southern Europe and Maghreb, which are significantly distinct in genetics and cytology from populations in the main range. Further research on the topic is necessary.

4.3. Phylogenetics, Distribution, and Ecology of Elanins

The molecular clock estimates of elanins based on our mitochondrial DNA data do not correspond to calculations on the appearance of different Accipitridae based on the calibration of three previously described raptor fossils, Osprey and two *Buteo* hawks [80], Snake Eagle and two vultures [81], both assuming a split for Elaninae of circa 34 Mya. The consistence between molecular and morphological data issued from fossils is usually not very high, and the retention index between phylogenetic trees [82] of two types of information for birds is 0.6–0.7 [83]. At the same time, our data are not far from previous estimations of the node *Elanus*/*Gampsonyx* with an age of ~20.5 Mya (95% HPD = 29.4–14.4 Mya) by Nagy and Tökölyi [80] and 16.7 Mya (95% HPD = 20.1–13.3 Mya) by this study (Figure 3). We did not find any data on Elaninae fossils, and the fossilization is often not usual for tropical biomes, but its existence eventually could highlight the origin of this group.

The position of *Chelictinia riocourii* has until recently been considered as provisional in absence of molecular data [7], and, traditionally, the Scissor-tailed Kite is placed in Elaninae [2]. Our study can thus confirm this assumption. The 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 *Cyt b* as well as for *COI* (Table 3) genes.

The phylogenetic position of subspecies of *Elanus* spp., including currently accepted and three formerly valid subspecies of *E. caeruleus* [84], cannot be determined with our dataset because of the lack of sufficient data. Several *Cyt b* and *RAG-1* haplotypes of the African subspecies of the Black-winged Kite *E. c. caeruleus* (Desfontaines, 1789) were found across the entire continent (Figure 2a, Figures S1 and S2). This may be explained by the nomadic active movements as subadults, and adults across their wide range may exceed 1000 km [85], and the dispersal of nestlings (probably together with adult movements) even 3000 km [86]. The suggestion of Negro et al. [75] appears relevant, stating that the relatively nocturnal *Elanus* feeding on small rodents may occupy the niche which is mostly used by nomadic owls in the Northern Hemisphere. The difference between haplotypes of *E. c. caeruleus*, even for the more variable *Cyt b* gene, is low and the same haplotype appears in Egypt and South Africa. At the same time, two subspecies of *E. leucurus* show identical haplotypes for the accessible sequences of *COI* (Table 3). These subspecies are distinguished by small but significant size differences of wing, tail, and culmen [87,88], and their range is disrupted by the Amazonian basin [5], thus, the validity of these subspecies is not in doubt. However, we observed no distinction by the DNA-barcoding marker, but it apparently may be found with high-variable parts of the mitogenome as control region.

The Pearl Kite, the smallest Neotropical raptor, is morphologically and ecologically distinct from other elanins, being the smallest and most sedentary kite of this group (Table 4), and phylogenetically, this is the most distant taxon (Figures 2 and 3, Figures S2 and S3). These facts could suggest that the origin of Elaninae might be the Neotropic realm, and their migration trait probably appeared after a divergence of *Gampsonyx* from the common ancestor. The neotropical ancestor distribution for Elaninae is also estimated by Nagy and Tökölyi [77]. When the Pearl Kite was described, Vigors [89] notified its remarkable appearance to be close to falcons and hawks, but placed it together with hawks cause of the form of its bill and size of the wings. Later, this genus was placed to Falconidae by different authors [2,90–92] and back to Accipitridae [20,93–95] families. Three subspecies were described: nominative *G. s. swainsonii* (Vigors, 1825), *G. s. leonae* (Chubb, 1918), and *G. s. magnus* (Chubb, 1918). According to the geographic origin of the samples, our dataset should have molecular data for the two first subspecies. However, he difference in *COI* haplotypes between them is low or absent, and only birds from Guyana, which belong to the *leonae* race differ by one substitution (Table 2, Figures 2a and 3). The range of these subspecies adjoin each other, and *swainsonii* and *leonae* differ slightly only by their plumage colors: gray upper surface darker, straw-color instead of the orange-beige of forehead and sides; and the *magnus* race, which has no rufous on its flanks and is also separated geographically, differing by wing, and tail measurements [5,96,97]. We cannot reject that a clinal variation may exist for this species with a wide range, thus, inviting detailed morphological and genetic studies on Pearl Kite subspecies in the future.

Table 4. Characteristics of elanin genera.

	Elanus	*Chelictinia*	*Gampsonyx*
Length (cm)	29–43	33–38	20–28
Wing (cm)	249–328	225–254	141–178
Wingspan (cm)	77–102	68–76	45–55
Tail (cm)	110–186	170–216	82–108
Tarsus (mm)	32–40	28–33	28–32
Weight (g)	160–427	100–140	94–140
Plumage color	gray, black, and white	gray, black, and white	black, white, rufous, yellow
Eyes color	red; orange-rufous (*E. leucurus*)	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 (*E. caeruleus*); coastal dunes (*E. axillaris*)	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 (*E. axillaris*)	migratory, nomadic	sedentary or locally nomadic
Feeding	small mammals, also small birds, reptiles and amphibians, large insects; occasionally dead fish (*E. caeruleus*)	insects, arachnids, lizards, also small snakes, sometimes rodents	lizards, large insects, spiders, also snakes, rodents
Social behavior	solitary or in pair; colonial (*E. scriptus*)	colonial or in pair	solitary or in pair
Nest place	trees; occasionally bush (*E. caeruleus*) 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
Number of eggs	3–5 (2–6)	4	3–4 (2–4)
Egg measurements	37–46 × 29–36	34–38 × 27–31	30 × 24

Note: data from [4,5,15,97–102].

Among the ecological features of elanins, parasites specific for these birds are worth mentioning separately. Clay [103] named the species group *elani* of *Degeeriella* (Neumann, 1906), a genus of Mallophaga (Nitzch, 1818), common for all genera of Elaninae, *Elanoides*, and *Aviceda*, that each of chewing lice species correspond to its own kite genus. It seems interesting to follow the cophylogeny of these lice and their hosts, like it was shown for other ectoparasites of different bird groups [104–107].

4.4. Taxonomic Implications for Elanins and Other Accipitrids

The South Asian subspecies of the Black-winged Kite *Elanus caeruleus vociferus* from India was described as full species [108]. The p-distance between African and the Thai *E. caeruleus COI* sequences (Table 2) is even higher than between several species of one genus in Accipitridae [109–113]. Their split occurred at 1.5 ± 0.8 Mya (Figure 3). We suppose that *E. c. vociferus* may be restored as species. This also may be confirmed by different karyotypes of this subspecies that we mentioned above. Nonetheless, this issue cannot be resolved without additional material gathered from different subspecies of *E. caeruleus*. Additionally, *vociferus* differs morphologically from other Black-winged Kites by well-defined black

tips of underwing coverts [114]. It is curious that this race is not even recognized as a subspecies by Brown and Amadon [4] followed by Ferguson-Lees and Christie [5], merging it with *caeruleus* because of their close morphology, and Mees [115] leaves the validity of *vociferus* to be discussed. Currently, *E. c. vociferus* is present in all main bird checklists [6,7,14].

At the same time, the position of *Elanus axillaris* sequences is contradictory. It is separate from large species *E. caeruleus* on the mitochondrial tree (Figure 2a), but both sequences of this species form clade with the Black-winged Kite (Figure 2b), though its support is very low (the posterior probabilities do not exceed 0.1). Apparently, the resolution of nuclear sequences *RAG-1* is not sufficient to separate these species. Nonetheless, the tentative separation in mitochondrial but not in nuclear sequences may offer support to the suggestions of Debus [32] that the Australian *E. axillaris* is a recent species, split from *E. caeruleus* of the Old World. *E. axillaris* as well as the American *E. leucurus* were merged by some authors with the "main" species of the group as subspecies [84,114,116,117], which was not supported by other researchers [4,20,24,118–120]. Clark and Banks [88] found conclusive evidence for the validity of these three species based on morphometric differences between them. Currently, the Black-shouldered and White-tailed Kites are mentioned as full species in the checklists [6,7,14]. All three species are considered as allospecies, forming superspecies *Elanus* [*caeruleus*] [24,88,118]. The presence of *E. axillaris* in *E. caeruleus* clade may mean that the Black-shouldered Kite is not homogeneous, despite the fact that there are no morphological differences inside of the species. We recognize the current taxonomic status of the *Elanus* species with the remark that the final composition of this genus may be changed when data from more mitochondrial and nuclear markers or even whole genomes for each species and subspecies will be available.

Based on the synthesis of phylogenetic, cytogenetic, morphological, and ecological data, we recommend elevating Elaninae to Elanidae (Blyth, 1850) stat. nov. (LSID urn:lsid:zoobank.org: act:4E7580BA-7338-48F4-9100-B3A85F760B3C) conserving internal subfamily Elaninae and distinguishing inside a monotypic subfamily Gampsonychinae once proposed by Wolters as invalid taxon [25]. We provide the description of the new subfamily below.

The change of status of elanins invites to look at neighboring taxa: A large group of hawk-like diurnal birds of prey Accipitridae together with the families Elanidae and Pandionidae could be considered as suborder Accipitres (Linnaeus, 1758), proposed by Coues and Prentiss [121], whose composition was changed by several taxonomists [4,122–125] in new frames.

If we consider Cathartiformes as separate order [14], phylogenetically, the most distant taxon of the order Accipitriformes is a morphologically distinct primarily terrestrial large predator and sub-Saharan African endemic the Secretarybird *Sagittarius serpentarius* (Miller, 1779). The time of his separation from the main branch is relatively close to other Accipitriformes by our calculations (Figure 3) but more distant by the measures using fossil calibrations [80,81], and the Secretarybird branch is well-supported by different analyses (Figure 2), [3,33]. Thus, it confirm a monotypic suborder Serpentarii Seebohm, 1890. Other taxonomic ranks as infraorder Sagittarii (Seebohm, 1890) proposed by Cracraft [126] or Wetmore's superfamily Sagittariioidea (Finsch and Hartlaub, 1870) [127] seem less appropriate. Firstly, this taxon is phylogenetically (Figure 2) [3,31,33] and morphologically [21–23] more distant from other taxa of Accipitriformes and should not have the same taxonomic rank as those. Furthermore, Cracraft grouped the Secretarybird in suborder Accipitres together with infraorder Falconii, which consisted of all other diurnal raptors except New World vultures, and Wetmore considered all other diurnal birds of prey as second superfamily Falconoidea. Today, after the separation of former order Falconiformes in two [7] or even three [14] orders, these classifications are apparently outdated.

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 dorsi* 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.

5. Conclusions

The examination of the molecular phylogeny of Elanin kites based on mitochondrial and nuclear markers confirms their position as sister taxa to other Accipitridae, and together with morphological, cytogenetic, and ecological data, lead to separating them in the family Elanidae. At the same time, the peculiarities of the Pearl Kite allow us to distinguish it as a monotypic subfamily Gampsonychinae, which forms Elanidae with a second subfamily Elaninae consisting of genera *Elanus* and *Chelictinia*. An accumulation of genetic data will permit us to clarify the phylogeny on a species–subspecies level of elanins in perspective. Phylogenetic relationships between Elanidae, Accipitridae, and Pandionidae from one side and the distant Secretarybird from the other allow us to classify them in two suborders of Accipitriformes.

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