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Authors: Wink, Michael, El-Sayed, Abdel-Aziz, Sauer-Gürth, Hedi, and Gonzalez, Javier

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Molecular phylogeny of owls (Strigiformes) inferred from DNA sequences of the mitochondrial cytochrome *b* and the nuclear *RAG-1* gene

Michael Wink^{1,*}, Abdel-Aziz El-Sayed¹, Hedi Sauer-Gürth¹ & Javier Gonzalez¹



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For 97 owl taxa from 15 of the larger genera (some monotypic taxa are not represented) a molecular phylogeny was inferred from a combined dataset of nucleotide sequences of mitochondrial cytochrome *b* and nuclear *RAG-1* genes. The molecular phylogeny can be used to create a taxonomic framework, which agrees with cladistics. Strigiformes are divided into two families: Tytonidae and Strigidae. The Tytonidae are subdivided into the subfamilies Tytoninae (with *Tyto*) and Phodilinae (with *Phodilus*). The Strigidae cluster in three subfamilies: Striginae, Surniinae and Ninoxinae (with the genera *Ninox*, and possibly the monotypic *Uroglaux* and *Sceloglaux*). The Surniinae are subdivided in three tribes Surnini (with *Surnia*, *Glaucidium* and *Taenioglaux*), Athenini (with *Athene*) and Aegolini (with *Aegolius*). The Striginae are subdivided into six tribes: Bubonini (with *Bubo* including the former *Nyctea*, *Ketupa* and *Scotopelia*), Strigini (with *Strix* and *Jubula*), Pulsatrigini (with *Pulsatrix* and *Lophotrix*), Megascopini (with *Megascops* and *Psilosops*), Otini (with *Otus* and *Mimizuku*) and Asionini (with *Asio*, *Ptilopsis* and possibly the monotypic *Nesasio* and *Pseudoscops*).

Key words: Strigiformes, Strigidae, Tytonidae, cytochrome *b*, *RAG-1*, phylogeny, cladistics

¹Institute of Pharmacy and Molecular Biotechnology, University of Heidelberg, Im Neuenheimer Feld 364, 69120 Heidelberg, Germany;

*corresponding author (wink@uni-hd.de)

INTRODUCTION

The avian order Strigiformes represents a fascinating group of nocturnal raptor with a complex biology (Bock & McEvey 1969, Eck & Busse 1973, Mikkola 1983, Amadon & Bull 1988, Burton 1992, del Hoyo *et al.* 1999, König *et al.* 1999, König & Weick 2008). In order to occupy the ecological niche of a nocturnal raptor, owls had to evolve several adaptations. Besides specialized hunting strategies, owls developed a sophisticated acoustical communication system. Morphology is often cryptic and invariant in many owl species but the distinctive calls, which are inherited and not learned, are of considerable taxonomic value (Hekstra 1982, König 1991a,b, 1994a,b). If phylogenetic relationships were reconstructed on the basis of the morphological charac-

teristics alone, wrong conclusions might be drawn since some of these characteristics may be convergent traits that are not related to the underlying phylogeny.

The Strigiformes are subdivided into two families (Sibley & Monroe 1990, del Hoyo *et al.* 1999, Weick 2006): Tytonidae and Strigidae. Whereas the Tytonidae consist of two subfamilies and two genera (and no further substructure), the Strigidae have a much more complex structure being split in three subfamilies which are further subdivided in six tribes:

- subfamily Striginae with tribes Otini, Bubonini and Strigini,
- subfamily Asioninae,
- subfamily Surniinae with tribes Surnini, Aegolini and Ninoxini.

We have chosen the mitochondrial (mt) cytochrome *b* gene to study the finer details of speciation and phylogeny of owls (Wink & Heidrich 1999, 2000, Wink *et al.* 2004, 2008). We have enlarged our cytochrome *b* data base and have additionally sequenced the nuclear (nc) *RAG-1* gene for all groups that were critical in order to get better support for the deeper branches. Basically, the ncDNA data support the results obtained from mtDNA (Wink & Heidrich 1999, Wink *et al.* 2004, 2008). Our present dataset has a good coverage for most genera. The missing genera belong to monotypic ones, so that a general picture on the phylogeny of owls becomes possible with this analysis.

METHODS

The cytochrome *b* and *RAG-1* genes were amplified by PCR (primer sequences in Groth & Barrowclough 1999, Wink 2000). First, sequences were obtained by using AlfExpress (Amersham Pharmacia Biotech) or ABI 3100 (Applied Biosystems). Since 2003, sequences were determined using the DYEnamic ET Terminator Cycle Sequencing Kit (Amersham Pharmacia Biotech). Sephadex™ G-50 columns (Amersham Biosciences) and MultiScreen filter plates (Millipore Corporation) were used for sequencing purification products. Sequences were analyzed by capillary electrophoresis using a MegaBACE™ 1000 sequencer (Molecular Dynamics Inc., Amersham Pharmacia). Sequences of 900–1000 base pairs (bp) for cytochrome *b* and 953 bp for *RAG-1* have been deposited in GenBank (Appendix 1).

The sequences were aligned by BioEdit version 7.0.5 (Hall 2004). Basic statistics, variable and parsimony informative sites, and *p*-distances were calculated with MEGA version 4.0 (Tamura *et al.* 2007). Molecular phylogenies were constructed using maximum likelihood (ML) in PAUP* v. 4.0b10a (Swofford 2002) and Bayesian inference (BI) in MPI-MrBayes version 3.1.2. (Ronquist & Huelsenbeck 2003, Altekar *et al.* 2004). Phylogenetic analyses were performed for both genes separately and concatenated (*cytb* + *RAG-1*) as well. We explored the model of sequence evolution that fits the data best with Modeltest version 3.7 (Posada & Crandall 1998). The best model was then used with the ML analyses. Robustness of nodes was assessed by 1000 bootstrap replicates using the program GARLI version 0.951 (Zwickl 2006). For BI analyses, two independent runs of 8 000 000 generations each were performed along with four Markov chains. The evolutionary model selected for BI analysis was the GTR + Γ + I. Trees were sampled every 500 genera-

tions and the first 4000 samples were discarded as 'burn-in'. Two partitions (*cytb* and *RAG-1*) were considered in BI analysis in the combined dataset.

For most species we have determined the cytochrome *b* at least from two individuals, so that the sequences used in this analysis are unequivocal and reliable (Heidrich 1998, Wink & Heidrich 1999, Wink *et al.* 2008). When a significant haplotype differentiation was absent the molecular analysis were conducted with a single sequence (*cytb* + *RAG-1*) per taxon.

Three outgroup species were selected to root the owl tree: Mountain Owllet-nightjar *Aegotheles albertisi*, the Greater White-fronted Goose *Anser albifrons* and the chicken *Gallus gallus*. The sequences for these taxa were available from GenBank.

RESULTS AND DISCUSSION

ML and BI trees were inferred from a combined dataset (*cytb* + *RAG-1*) of 97 sequences (Fig. 1), which resolves even the deeper nodes. Most of the clades are supported by high bootstrap and posterior probability values allowing a re-evaluation of the traditional owl systematics in terms of families, subfamilies, tribes and genera.

Relationships within the family Tytonidae

The genetic data support the view of a monophyletic family Tytonidae which consists of two monophyletic subfamilies: Tytoninae and Phodilinae (Fig. 1).

Although several taxa in the *Tyto* complex have been recognized as distinct species already (Sibley & Monroe 1990, König *et al.* 1999, Weick 2006, König & Weick 2008), several others within *T. alba*, *T. delicatula*, *T. novaehollandiae*, *T. longimembris*, *T. tenebricosa* and *T. furcata* are considered to be subspecies. Some of them, especially some island taxa, may apparently represent distinct and endemic species. According to König & Weick (2008) and Weick (2006) 25 species are recognized.

The Australian region is settled by two different lineages of the genus *Tyto*: (1) *T. novaehollandiae*, *T. castanops*, *T. multipuncta*, *T. longimembris* and *T. tenebricosa* and (2) *T. delicatula* (including the more derived *T. d. sumbaensis* – from Sumba Islands – which probably merits species status).

The Eurasian Barn Owl *Tyto alba* has been divided into several subspecies, of which a number have already been converted into true and distinct species. Whereas the subspecies *T. alba* and *T. guttata* can hardly be distinguished genetically, *T. erlangeri* (from the eastern Mediterranean) and *T. affinis* (from Africa)

form distinct but not highly diverged lineages within the *T. alba* complex. *Tyto soumagnei* from Madagascar is a sister to *T. alba* and *T. furcata*, which together share ancestry with the *T. delicatula* group from Australasia (Wink et al. 2008).

Relationships within the subfamily Striginae

Within the Striginae in its traditional circumscription, three tribes are recognised (Weick 2006): Strigini (with *Strix*, *Jubula*, *Lophostrix* and *Pulsatrix*), Bubonini (with the genera *Bubo*, *Nyctea*, *Ketupa* and *Scotopelia*) and Otini (with the genera *Otus*, *Megascops*, *Macabra*, *Pyrroglaux*, *Gymnoglaux*, *Psiloscoops*, *Ptilopsis* and *Mimizuku*).

TRIBE STRIGINI

Presently, 18 species are recognised in the genus *Strix* (Weick 2006). Tawny and Wood Owls (genus *Strix*) always form a monophyletic clade (94% bootstrap support, see Fig. 1) and cluster as a sister group to the *Bubo* complex (tribe Bubonini) with a 73% of bootstrap proportion.

The New World species *S. rufipes* and *S. varia* form a monophyletic clade and cluster as a sister to the Old World species, which diverged from a common ancestor 5–6 Myr ago (Wink & Heidrich 1999). Future studies, which should include several of the numerous New World species, will show whether this assumption holds true for all New World species.

Three species are recognized in the Central and South American genus *Pulsatrix*, of which we have studied *P. perspicillata* and *P. koenigswaldiana*. The phylogenetic position of *Pulsatrix* cannot be resolved with certainty even with the concatenated dataset (*cytb* + *RAG-1*): in ML analyses (Fig. 1) it clusters between *Strix* and *Megascops*, but nodes are not supported by high bootstrap values. It is therefore questionable whether *Pulsatrix* is a true member of the tribe Strigini.

Lophostrix and *Jubula* are both monotypic genera: *Jubula lettii* occurs in West and Central Africa while *Lophostrix cristata* in Central and South America. Only a short DNA sequence of *cytb* has been submitted to GenBank, which corresponds to *L. cristata*. A preliminary DNA analysis would place it as a sister to *Pulsatrix* (Wink et al. 2008). Whether both taxa belong to the tribe Strigini cannot be answered with certainty at present. It is more likely that *Lophostrix* and *Pulsatrix* form their own tribe, the Pulsatrigini.

TRIBE BUBONINI

Members of the tribe Bubonini form a monophyletic clade in all the phylogenetic reconstructions (with 99–100% of bootstrap support). About 19 species are

recognised in the genus *Bubo* (Weick 2006). *Bubo ascalaphus*, which occurs in North West Africa and the Near East, has been treated as a distinct species (Sibley & Monroe 1990). In our analysis, *B. bubo* and *B. ascalaphus* differ by an uncorrected *p*-distance of 3.5%. Also *B. b. interpositus*, which is morphologically distinct from *B. bubo* and thrives in the desert from Israel, is also genetically distinct (*p*-distance of 2.8%, Wink & Heidrich 1999); it clusters as a sister to *Bubo ascalaphus*. Since a sequence divergence of more than 2% is indicative of species level, it could be justified to treat both taxa, *Bubo ascalaphus* and *Bubo interpositus*, as distinct species or at least *B. interpositus* as a subspecies of *B. ascalaphus*.

The Snowy Owl (*Bubo scandiacus*, formerly *Nyctea scandiaca*) shares definite common ancestry with the genus *Bubo* (Fig. 1), especially with the New World species *B. virginianus*. The separation from a common ancestor took place more than 4 Myr ago (Wink & Heidrich 1999). *Nyctea* represents a monotypic genus but unambiguously clusters within the *Bubo* complex, which would make the genus *Bubo* paraphyletic. Since paraphyletic taxa should be avoided in systematics, the taxonomic consequences would be to lump *Nyctea* with *Bubo* and call the species *Bubo scandiacus*. This change has been accepted already by most authorities, except Weick (2006).

A similar paraphyly as in *Nyctea* can be seen in *Ketupa*, of which three species (*K. zeylonensis*, *K. flavipes* and *K. ketupu*) have been described from Southeast Asia. *Ketupa zeylonensis* and *K. ketupu* cluster as close relatives to the Asian *Bubo* species, such as *B. nipalensis* (Fig. 1). Also the general appearance of *Ketupa* is similar to that of *Bubo*; because of genetic relationships (*p*-distance of 9–10%) we agree with Amadon & Bull (1988) to merge *Ketupa* in *Bubo*. Also this change has been accepted by now by most authorities (König & Weick 2008).

Three species have been described in African Fishing Owls of the genus *Scotopelia*. So far, we could only compare the *cytb* sequence of a single individual from *S. peli* with other members of the tribe Bubonini. According to this analysis (Wink et al. 2008), *Scotopelia* unequivocally clusters together with *Bubo vossleri*, *B. nipalensis* and *B. sumatranus* (Wink et al. 2008). Such a position would make the genus *Bubo* paraphyletic. In order to overcome the problem, the simplest way would be to merge *Scotopelia* in *Bubo*, as suggested for *Nyctea* and *Ketupa*.

TRIBE OTINI

The combined dataset (*cytb* + *RAG-1*) unambiguously

shows that members of the tribe Otini cluster in at least three different monophyletic lineages, indicating that the genus *Otus* and the tribe Otini are paraphyletic or polyphyletic in their former circumscriptions (Wink & Heidrich 1999); a systematic revision of the genus *Otus* and the tribe Otini was a logical consequence.

The Screech Owls of the New World represent a distinct group, which is separated from Old World mem-

bers of *Otus* by genetic distances of 12–16% (equivalent to 6–8 Myr, Wink & Heidrich 1999). Within the Screech Owl complex, which has its radiation centre in South and Central America, several species have been recognized on account of different acoustic repertoires (König 1994a). Sequence data could corroborate these findings (Heidrich *et al.* 1995a), stressing the importance of vocalization for speciation and taxonomy.

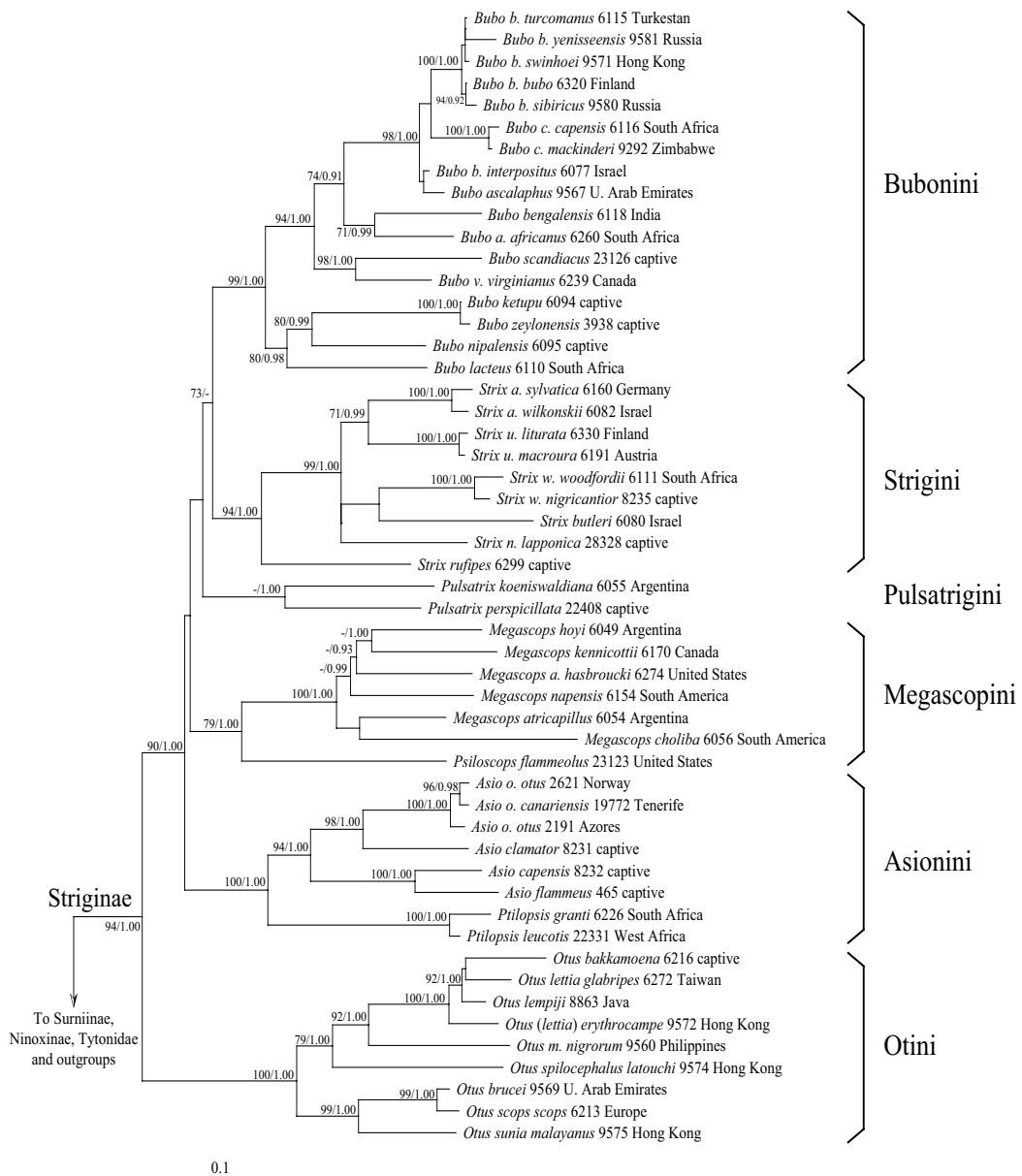


Figure 1. ML bootstrap phylogram of the generic relationships in owls based on a combined dataset of *cytb* and *RAG-1* sequences. ML bootstrap values/BI posterior probability values indicated for each node. The tree is separated in two parts in order to make it readable.

The American taxa have been either placed in the genus *Megascops* (with 25 species) or *Psilosops*. The Flammulated Owl *Otus flammeolus* differs in vocalisation and genetics (Fig. 1) from *Megascops*, therefore a monotypic genus *Psilosops* (Coues 1899), which clusters as a sister group to *Megascops*, appears to be adequate (Penhallurick 2002, Weick 2006, König & Weick 2008). *Megascops albogularis* has been placed in the subgenus *Macabra* (Weick 2006); however, the phylogenetic data do not support such a monotypic subgenus (Wink et al., 2008).

Several Old World Scops Owls (44 species) have been described (overview in Sibley & Monroe 1990, Weick 2006) of which 10 have been included here as representatives for this group. As can be seen from Fig. 1 these Scops Owls fall into a common clade, which is very distinct from the New World *Megascops/Psilosops* complex. Using 12S mt rDNA sequences, Mindell et al. (1997) showed that *O. mirus*, *O. mindorensis* and *Mimizuku gurneyi* cluster together with *O. megalotis* and *O. longicornis*. Since we studied also the latter two species, we can conclude that *Mimizuku gurneyi* is a

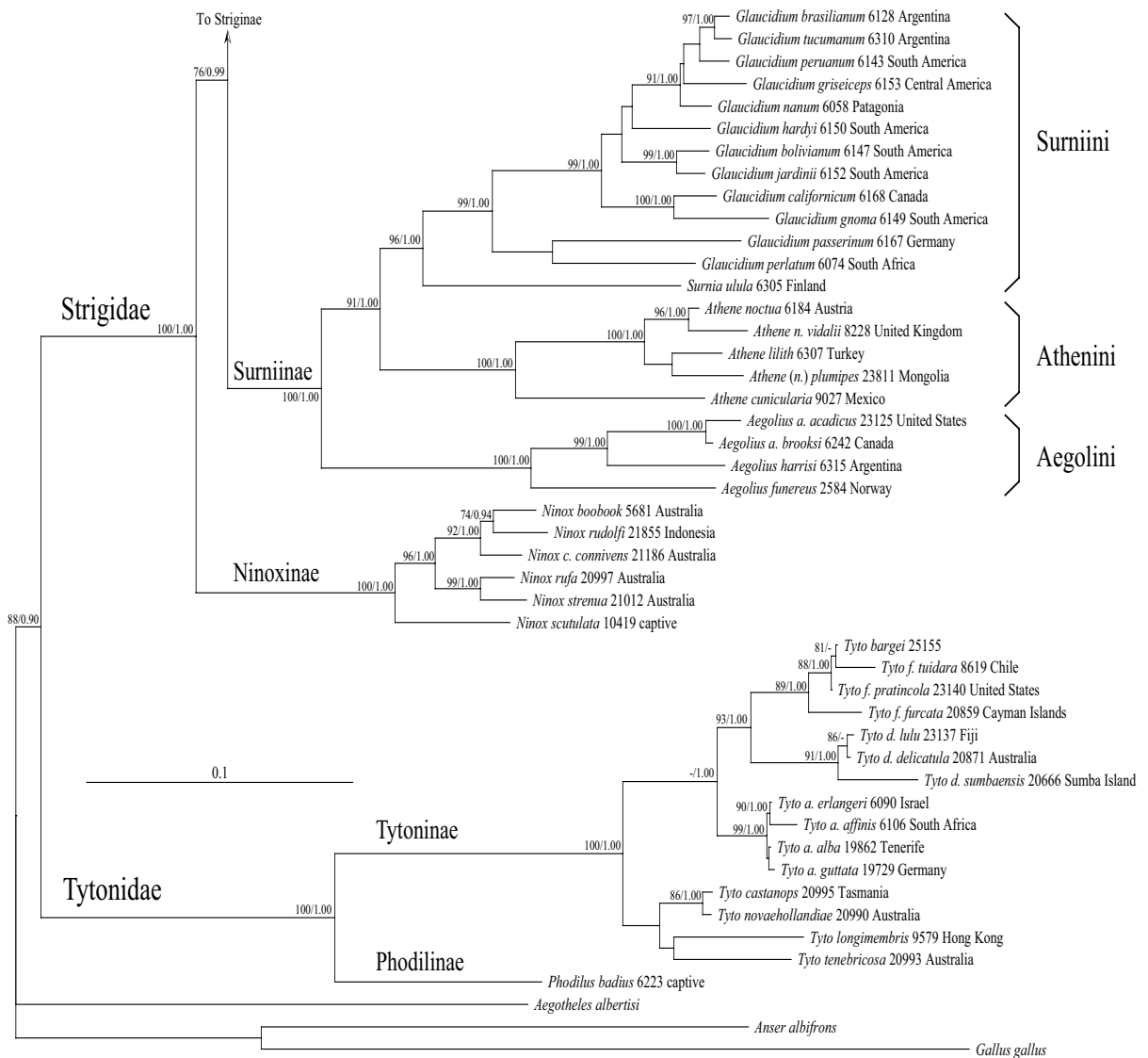


Figure 1. Continued

likely member of the Old World *Otus* group. Since *Mimizuku* clusters within this group it is doubtful whether this monotypic genus is valid.

The African White-faced Owl (formerly *Otus leucotis*) differs both morphologically and genetically from the other Old World *Otus* species (Wink & Heidrich 1999) and has therefore been placed in the genus *Ptilopsis*. In Africa two taxa occur, *P. leucotis* in West, Central and East Africa and *P. granti* in southern Africa. In all reconstructions (Fig. 1) *Ptilopsis* figures as a sister group to the genus *Asio*.

Pyrroglaux and *Gymnoglau*x represent monotypic genera. *Pyrroglaux podarginus* has been described from Palau Islands and *Gymnoglau*x *lawrencii* from Cuba. DNA analyses are required to see whether both taxa represent monotypic genera and with which other genus they share ancestry.

Concluding, it seems obvious that the different monophyletic clades of the former *Otus* complex should also be revised taxonomically, i.e., by creating the genera *Otus*, *Megascops*, *Psilosco*ps and *Ptilopsis*, which has been done by several authorities already (Penhallurick 2002, König & Weick 2008). As can be seen from Fig. 1, the former tribe Otini is paraphyletic and interrupted by the Asionini. In order to create a cladistically coherent system, we need to split the former tribe Otini in the tribes Otini, Megascopini and Asionini (taking care of *Ptilopsis*).

Relationships within the subfamily Asioninae

Three genera have been placed in the subfamily Asioninae, *Asio* and the monotypic *Pseudoscops* and *Nesasio*. Within *Asio*, seven species are distinguished (Weick 2006).

Asio otus, *A. clamator*, *A. capensis* and *A. flammeus* always fall into the same clade (Fig. 1); the genetic distances imply a divergence time of more than 5 Myr. *Asio* always clusters as a sister to *Ptilopsis* (Fig. 1). The combined dataset provides strong evidence (94% bootstrap support) that Asioninae does not form a distinct subfamily, but clusters within the Striginae (independent of the tree building methods used). Thus, we suggest merging Asioninae with Striginae in order to avoid paraphyletic groups. The rank of a tribe Asionini containing the genera *Asio* and *Ptilopsis* would be adequate.

Pseudoscops grammicus occurs in Jamaica, *Nesasio solomonensis* on the Solomon Archipelago, Bougainville, Choiseul and Santa Isabel. Without DNA evidence it is difficult to say whether they deserve the status of monotypic taxa and which affiliation they have (probably tribe Asionini).

Relationships within the subfamily Surniinae

The subfamily Surniinae in the traditional circumscription (Weick 2006) is formally subdivided in three tribes: Surniini (with the genera *Surnia*, *Glaucidium*, *Taenioglaux*, *Xenoglaux*, *Micrathene* and *Athene*), Aegolini (*Aegolius*), Ninoxini (*Ninox*, *Uroglaux* and *Sceloglaux*).

TRIBE SURNIINI

Pygmy Owls (32 species) of the former genus *Glaucidium* occur in the Old and New World. Whereas their plumage is very similar in most instances (a fact which makes their taxonomy so difficult), they can be distinguished by a unique repertoire of vocalizations (König 1994b). Recent taxonomical classifications based on differing acoustic signals (König 1994b) have been corroborated with DNA sequence data (Heidrich *et al.* 1995b). Fig. 1 clearly shows that Old and New World species cluster in separate monophyletic clades, which share common ancestry but have diverged more than 7–8 Myr ago (Wink & Heidrich 1999).

In the Pygmy Owls of the Old World two clades are apparent: *G. passerinum*, *G. tephronotum* and *G. perlatum* cluster as a sister to the New World species. Members of the subgenus *Taenioglaux* Kaup 1848, which differ in morphology from members of the genus *Glaucidium* s.str., are represented in our *cytb* dataset by *G. capense* and *G. cuculoides* (Wink *et al.* 2008). Apparently both species cluster in a more distant, separate clade and form a sister group to *Surnia/Glaucidium* s.str. A split of this subgroup into the genus *Taenioglaux* (see König & Weick 2008) is thus supported by molecular evidence.

The Northern Hawk Owl *Surnia ulula* of northern Eurasia and North America shares common ancestry and forms a monophyletic group (96% bootstrap support) with the *Glaucidium* s. str. complex (Fig. 1).

Three species have been recognized in the genus *Athene*, i.e. *A. noctua* (Eurasia), *A. brama* (southeast Asia) and *A. blewitti* (India). Within *A. noctua* several distinct lineages become visible (similar to the situation in the American *Glaucidium* complex) that indicate a high degree of geographic differentiation. So far we have detected three genetic lineages, which are supported by high bootstrap values; genetic differences (*p*-distance) between these groups account for 5–6%, exceeding the 2% which is typical for 'good' species in owls. Little Owls from Israel, Cyprus and Turkey have been recognised as *A. n. lilith*. On a genetic level, *A. n. lilith* is clearly separated from Little Owls of central and western Europe, representing the subspecies *A. n. noctua* and *A. n. vidalii*, but share ancestry with *A. n. indigena* from southeast Europe (Wink *et al.* 2008). Because of

the significant genetic distances, it would be plausible to recognise *A. lilith* as a distinct species (König et al. 2008). Also *A. n. plumipes* from Mongolia and China shows a distinct genetic lineage (Fig. 1), probably indicating species status; we suggest recognising this taxon as *A. plumipes*.

The former *Speotyto cunicularia* represents the genus *Athene* in the New World and this species has sometimes been considered as a member of the genus *Athene*. Because DNA–DNA hybridization suggested significant differences (Sibley & Monroe 1990), a separation into a monotypic genus appeared justified. However, according to the sequence data, it is clear that *Speotyto* and *Athene* share common ancestry (divergence approximately 6 Myr ago) and that they form a monophyletic group. Because of similarities in morphology, general outlook and in behaviour, we suggested to merge *Speotyto* back into *Athene* (Wink & Heidrich 1999). Most authorities have accepted this suggestion (König et al. 1999, König & Weick 2008).

The genetic analyses of *A. noctua* and *A. cunicularia* are still incomplete. Because of the phylogeographic variation detected in both taxon complexes, a more detailed study, which would cover the whole distribution range, will certainly reveal a more complex pattern with several distinct species and subspecies.

The *Athene* complex clusters as a sister to *Glaucidium/Taenioglaux/Surnia* in all reconstructions, independent of the methods used for tree reconstruction (Fig. 1). This clade corresponds to the tribe Surniini. From a cladistic point of view, such a tribe would agree with basic rules. On the other hand, the subfamily Striginae needs to be subdivided into several smaller tribes, which would make a tribe Surniini rather large. In order to create tribes of more even shape it would also be possible to recognise a distinct tribe Athenini as a sister to Surniini, the latter containing the genera *Glaucidium*, *Taenioglaux* and *Surnia*.

TRIBE AEGOLINI

Owls in the genus *Aegolius* can be found as a third major monophyletic group (Fig. 1) (tribe Aegolini) besides the tribe Surniini with *Glaucidium*, *Surnia* and *Athene*. The North American *A. acadicus* diverges with 12.9% (*p*-distance) from *A. funereus*, implicating a divergence time of more than 6 Myr (Wink & Heidrich 1999). Two geographically separated subspecies, *A. a. acadicus* and *A. a. brooksi* can be recognized (*p*-distance of 0.7%). The South American *A. harrisii* is more closely related to the North American *A. acadicus* than to *A. funereus* (Fig. 1), suggesting a common ancestor for the New World species.

The tribes Aegolini and Surniini share common ancestry with a high bootstrap proportion (100%); this group excludes the tribe Ninoxini (Fig. 1).

TRIBE NINOXINI

The genus *Ninox* comprises 25 species with Australasian distribution. According to the general appearance they could be related to the *Glaucidium/Athene* complex and formally they were recognised as the tribe Ninoxini within the subfamily Surniinae. In our phylogenetic analyses, *Ninox* clusters basal within Strigidae (Fig. 1) indicating that the subfamily Surniinae is paraphyletic. As a consequence, the tribe Ninoxini should be excluded from the Surniinae and possibly form a subfamily of its own, the Ninoxinae (with the genera *Ninox*, *Uroglaux* and *Sceloglaux*).

Recently, a new owl was discovered on Sumba Island, which was assumed to be a member of the genus *Otus*. DNA analysis revealed unequivocally that it is a member of the genus *Ninox*. It was described as *Ninox sumbaiensis* (Olsen et al. 2002).

Two monotypic genera have been included in the tribe Surniini, *Xenoglaux loweryi* from northern Peru and *Micrathene whitneyi* from southwestern North America. Preliminary DNA sequence data only exist for *M. whitneyi*, which would place it outside the tribe Surniini (Wink et al. 2008) but close to the subfamily Surniinae. *Uroglaux dimorpha* (north-western New Guinea) and *Sceloglaux albifacies* (New Zealand) have been included in the tribe Ninoxini, which would make sense in view of distribution and general appearance. DNA samples are needed to see whether their status as monotypic genera and their affiliation can be maintained.

Phylogenetic position of owls as compared to diurnal raptors and nightjars

Linné (1758) placed owls, vultures, eagles and falcons together as an order Accipitres. In 1827 owls were separated from diurnal raptors as a distinct order by L'Herminier; Nitsch (1840) already recognized the differences between Tytonidae and Strigidae. This view was supported by Fürbringer (1888) and Gadow (1892), who also stressed a close relationship between Strigiformes and Caprimulgiformes, a view maintained by Mayr & Amadon (1951). However, Cracraft (1981) using a cladistic approach, concluded a closer relationship between owls and falcons. Sibley & Ahlquist's (1990) study using DNA–DNA hybridisation implied that Caprimulgiformes, rather than falcons, are the nearest neighbour to the owls. However, mtDNA sequences do not support a Strigiformes/Caprimulgiformes clade (Wink and Heidrich 1999).

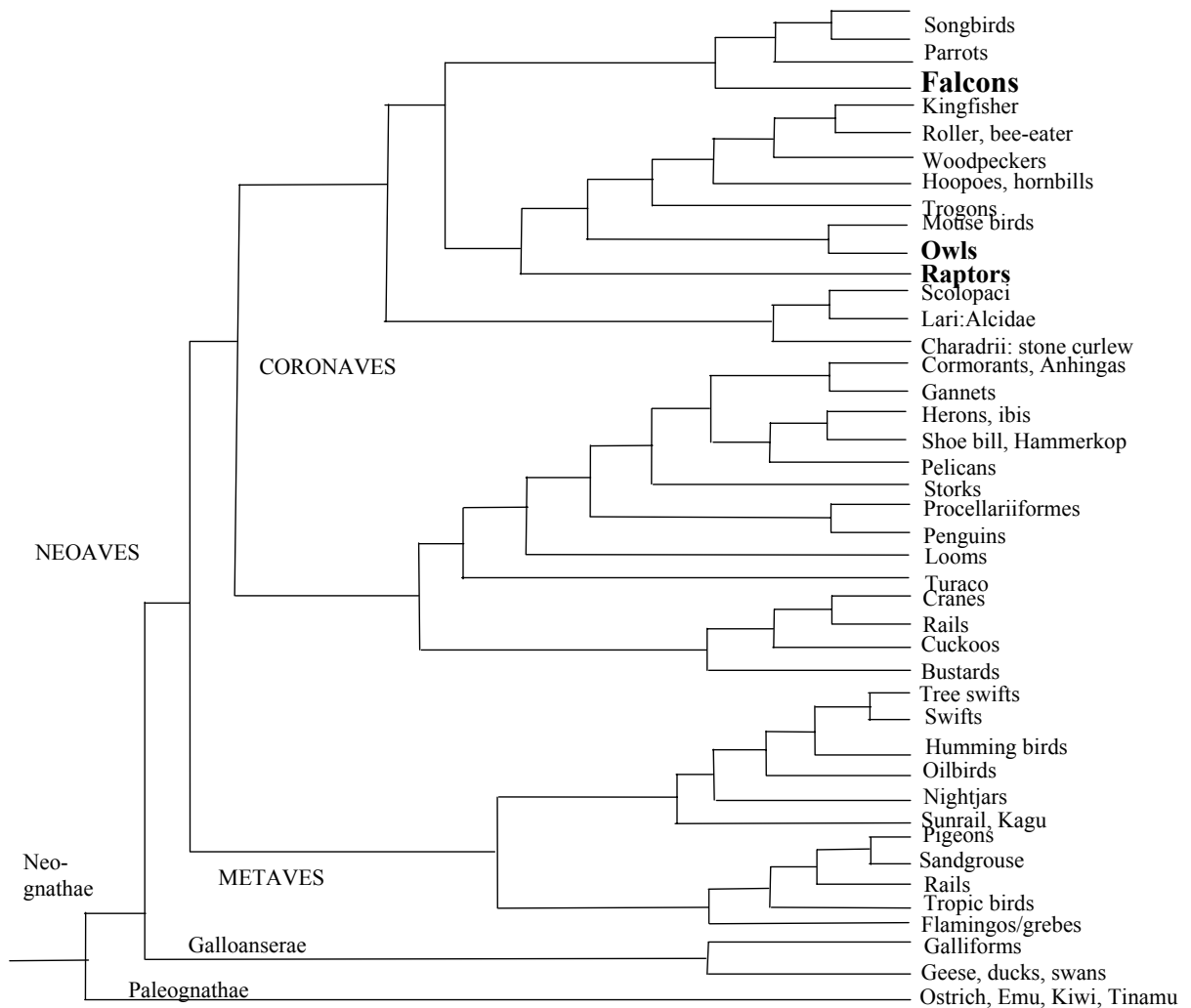


Figure 2. Phylogeny of birds (simplified after Ericson *et al.* 2006 and Hackett *et al.* 2008).

Table 1. Summary of a systematic classification of owls rigorously based on monophyletic groups.

Family	Subfamily	Tribe	Genera
Tytonidae	Tytoninae		<i>Tyto</i>
	Phodilinae		<i>Phodilus</i>
Strigidae	Striginae	Bubonini	<i>Bubo</i> (including the former <i>Nyctea</i> , <i>Ketupa</i> and <i>Scotopelia</i>)
		Strigini	<i>Strix</i> and <i>Jubula</i>
		Pulsatrigini	<i>Pulsatrix</i> and <i>Lophotrix</i>
		Megascopini	<i>Megascops</i> and <i>Psilosops</i>
		Asionini	<i>Asio</i> and <i>Ptilopsis</i> (probably including <i>Nesasio</i> and <i>Pseudoscops</i>)
		Otini	<i>Otus</i> and <i>Mimizuku</i>
	Surniinae	Surnini	<i>Surnia</i> , <i>Glaucidium</i> and <i>Taenioglaux</i>
	Athenini	<i>Athene</i> (including former <i>Speotyto</i>) and <i>Micrathene</i> (?)	
	Aegolini	<i>Aegolius</i>	
	Ninoxinae		<i>Ninox</i> , <i>Uroglaux</i> and <i>Sceloglaux</i>

Recently, a large dataset of five nuclear genes (Fain & Houde 2004, Ericson *et al.* 2006) has provided good evidence that Caprimulgiformes are part of the Metaves, whereas owls are members of the Coronaves. Within the Coronaves, owls are found in a clade with diurnal raptors except falcons, the latter clustering as a sister to parrots and song birds (Fig. 2).

Morphological and anatomical similarities between owls and nightjars, which were the basis for the hypothesis of a closer relationships to owls, are probably influenced by convergence (as implied already by Bock & McEvey 1969, Mikkola 1983, Feduccia 1996), cannot be supported by gene sequence data.

Conclusions

About 120 taxa of the Strigidae and 23 taxa of Tytonidae have been studied so far in our laboratory (Wink *et al.* 2008) and phylogenetic analyses based on cytochrome *b* and nuclear markers (*RAG-1*) provide insight into the evolution of owls. Phylogenetic analyses suggest a few changes in overall owl systematics to generate monophyletic taxa, as has been discussed in this paper (summarized in Table 1). Sequence data of mt and ncDNA provide a powerful tool (besides morphology, anatomy, behaviour and bioacoustics) to elucidate and reconstruct the evolutionary past and speciation in owls.

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SAMENVATTING

Op grond van moleculair onderzoek is de onderlinge verwantschap van 97 uilensoorten vastgesteld. Dergelijke gegevens zijn tegenwoordig een belangrijke basis voor de naamgeving en ordening van soorten. De orde van de Uilen is opgesplitst in de families Tytonidae en Strigidae. De Tytonidae zijn onderverdeeld in de onderfamilies Tytoninae (met het geslacht *Tyto*) en Phodilinae (met *Phodilus*). De Strigidae zijn onderverdeeld in de onderfamilies Striginae, Surniinae en Ninoxinae (met het geslacht *Ninox*, en mogelijk de monotypische *Uroglaux* and *Sceloglaux*). De Surniinae zijn onderverdeeld in de takken Surnini (met *Surnia*, *Glaucidium* en *Taenioglaux*), Athenini (met *Athene*) en Aegolini (met *Aegolius*). De Striginae zijn onderverdeeld in de takken Bubonini (met *Bubo* waaronder de vroeger geheten *Nyctea*, *Ketupa* en *Scotopelia*), Strigini (met *Strix* en *Jubula*), Pulsatrigini (met *Pulsatrix* en *Lophostrix*), Megascopini (met *Megascops* en *Psiloscops*), Otini (met *Otus* en *Mimizuku*) en Asionini (met *Asio*, *Ptilopsis* en mogelijk de monotypische *Nesasio* en *Pseudoscops*).

Appendix 1. Origin, collection codes and accession numbers of owl taxa investigated in this study. Taxa are in alphabetical order.

Taxon	IPMB Code ^a	Accession numbers ^b		Taxon	IPMB Code ^a	Accession numbers ^b	
		cytb	RAG-1			cytb	RAG-1
<i>Aegolius acadicus acadicus</i>	23125	EU348958	EU348862	<i>Ninox connivens connivens</i>	21186	EU348981	EU348913
<i>Aegolius acadicus brooksi</i>	6242	EU348959	EU348863	<i>Ninox boobook</i>	5681	AJ004007	EU348914
<i>Aegolius funereus</i>	2584	AJ004353	EU348864	<i>Ninox rudolfi</i>	21855	EU348982	EU348915
<i>Aegolius harrisi</i>	6315	AJ003940	EU348865	<i>Ninox rufa</i>	20997	EU348983	EU348916
<i>Asio capensis</i>	8232	EU348960	EU348866	<i>Ninox scutulata</i>	10419	AJ004008	EU348917
<i>Asio clamator</i>	8231	EU348961	EU348867	<i>Ninox strenua</i>	21012	EU348984	EU348918
<i>Asio flammeus</i>	465	EU348962	EU348868	<i>Otus bakkamoena</i>	6216	AJ004020	EU348919
<i>Asio otus otus</i>	2621	EU348963	EU348869	<i>Otus brucei</i>	9569	EU348985	EU348920
<i>Asio otus canariensis</i>	19772	EU348964	EU348870	<i>Otus lettia glabripes</i>	6272	EU348986	EU348921
<i>Athene cucularia</i>	9027	EU348965	EU348871	<i>Otus lempiji</i>	8863	EU348987	EU348922
<i>Athene noctua</i>	6184	AJ003945	EU348872	<i>Otus lettia erythrocampe</i>	9572	EU348988	EU348923
<i>Athene lilith</i>	6307	AJ003949	EU348873	<i>Otus megalotis nigrorum</i>	9560	AJ004032	EU348924
<i>Athene noctua plumipes</i>	23811	EU348966	EU348874	<i>Otus scops scops</i>	6213	AJ004037	EU348925
<i>Athene noctua vidalii</i>	8228	EU348967	EU348875	<i>Otus spilocephalus latouchi</i>	9574	EU348989	EU348926
<i>Asio otus otus</i>	2191	EU348968	EU348876	<i>Otus sunia malayanus</i>	9575	EU348990	EU348927
<i>Bubo bengalensis</i>	6118	AJ003954	EU348877	<i>Phodilus badius</i>	6223	AJ004042	EU348928
<i>Bubo bubo bubo</i>	6320	AJ003969	EU348878	<i>Ptilopsis granti</i>	6226	EU348991	EU348929
<i>Bubo bubo interpositus</i>	6077	EU348969	EU348879	<i>Ptilopsis leucotis</i>	22331	EU348992	EU348930
<i>Bubo bubo sibiricus</i>	9580	EU348970	EU348880	<i>Pulsatrix koeniswaldiana</i>	6055	EU348993	EU348931
<i>Bubo bubo swinhoi</i>	9571	EU348971	EU348881	<i>Pulsatrix perspicillata</i>	22408	AJ004043	EU348932
<i>Bubo bubo turcomanus</i>	6115	EU348972	EU348882	<i>Strix aluco sylvatica</i>	6160	AJ004051	EU348933
<i>Bubo bubo yenisenseis</i>	9581	EU348973	EU348883	<i>Strix aluco wilkenskii</i>	6082	AJ004045	EU348934
<i>Bubo ketupu</i>	6094	EU348974	EU348884	<i>Strix butleri</i>	6080	EU348994	EU348935
<i>Bubo lacteus</i>	6110	AJ003970	EU348885	<i>Strix nebulosa lapponica</i>	28328	AJ004058	EU348936
<i>Bubo nipalensis</i>	6095	AJ003972	EU348886	<i>Strix rufipes</i>	6299	AJ004060	EU348937
<i>Bubo scandiacus</i>	23126	AJ004011	EU348887	<i>Strix uralensis liturata</i>	6330	AJ004063	EU348938
<i>Bubo zeylonensis</i>	3938	EU348975	EU348888	<i>Strix uralensis macroura</i>	6191	AJ004062	EU348939
<i>Bubo africanus africanus</i>	6260	AJ003951	EU348889	<i>Strix woodfordii woodfordii</i>	6111	AJ004064	EU348940
<i>Bubo ascalaphus</i>	9567	EU348976	EU348890	<i>Strix woodfordii nigricantior</i>	8235	EU348995	EU348941
<i>Bubo capensis capensis</i>	6116	EU348977	EU348891	<i>Surnia ulula</i>	6305	AJ004068	EU348942
<i>Bubo capensis mackinderi</i>	9292	EU348978	EU348892	<i>Tyto delicatula lulu</i>	23137	EU348996	EU348943
<i>Bubo virginianus virginianus</i>	6239	AJ003973	EU348893	<i>Tyto alba erlangeri</i>	6090	EU348997	EU348944
<i>Glaucidium bolivianum</i>	6147	AJ003975	EU348894	<i>Tyto alba affinis</i>	6106	EU348998	EU348945
<i>Glaucidium brasilianum</i>	6128	AJ003983	EU348895	<i>Tyto alba alba</i>	19862	EU348999	EU348946
<i>Glaucidium californicum</i>	6168	AJ003993	EU348896	<i>Tyto bargei</i>	25155	EU349000	EU348947
<i>Glaucidium gnoma</i>	6149	AJ003994	EU348897	<i>Tyto delicatula delicatula</i>	20871	EU349001	EU348948
<i>Glaucidium griseiceps</i>	6153	AJ003995	EU348898	<i>Tyto furcata furcata</i>	20859	EU349002	EU348949
<i>Glaucidium hardyi</i>	6150	AJ003996	EU348899	<i>Tyto alba guttata</i>	19729	EU349003	EU348950
<i>Glaucidium jardinii</i>	6152	AJ003998	EU348900	<i>Tyto furcata pratincola</i>	23140	EU349004	EU348951
<i>Glaucidium nanum</i>	6058	AJ003999	EU348901	<i>Tyto delicatula sumbaensis</i>	20666	EU349005	EU348952
<i>Glaucidium passerinum</i>	6167	AJ004002	EU348902	<i>Tyto furcata tuidara</i>	8619	EU349006	EU348953
<i>Glaucidium perlatum</i>	6074	EU348979	EU348903	<i>Tyto castanops</i>	20995	EU349007	EU348954
<i>Glaucidium peruanum</i>	6143	AJ004005	EU348904	<i>Tyto longimembris</i>	9579	EU349008	EU348955
<i>Glaucidium tucumanum</i>	6310	AJ003988	EU348905	<i>Tyto novaehollandiae</i>	20990	EU349009	EU348956
<i>Megascops asio hasbroucki</i>	6274	AJ004015	EU348906	<i>Tyto tenebrosa</i>	20993	EU349010	EU348957
<i>Megascops atricapillus</i>	6054	AJ004013	EU348907				
<i>Megascops choliba</i>	6056	AJ004021	EU348908				
<i>Psiloscoptes flammeolus</i>	23123	AJ004022	EU348909				
<i>Megascops napensis</i>	6154	AJ004023	EU348910				
<i>Megascops hoyi</i>	6049	AJ004024	EU348911				
<i>Megascops kennicottii</i>	6170	EU348980	EU348912				

^a IPMB: Institut für Pharmazie und Molekulare Biotechnologie, Heidelberg University.^b cytb = cytochrome b gene, RAG-1 = recombination activating gene 1.

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