OWLS

A GUIDE TO THE OWLS OF THE WORLD

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MOLECULAR EVOLUTION AND SYSTEMATICS OF THE OWLS (STRIGIFORMES)

by

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INTRODUCTION

In 1857 Charles Darwin wrote to his friend T. H. Huxley:

> The time will come, I believe, though I shall not live to see it, when we shall have fairly true genealogical trees of each kingdom of nature...

Darwin was right in both his predictions, for it has taken over 130 years for his expectation to be realised: it is only in recent years that we can claim to have reached the stage when fairly true genealogical (today we use the term 'phylogenetic') trees can be established for nearly every group of organisms.

Phylogeny and systematics of birds and other organisms are traditionally based on morphological and anatomical characters; sometimes ecological, behavioural, acoustical or geographical data are included in the reconstruction of the underlying phylogenies. Since the main criterion is similarity, convergence due to adaptive traits can sometimes obscure the picture.

A real breakthrough for phylogenetic studies came with the advent of molecular and biochemical methods, such as protein electrophoresis, DNA-DNA-hybridisation, DNA restriction analyses (RFLP), or the amplification of marker genes by polymerase chain reaction (PCR) followed by DNA sequencing (overviews in Sibley and Ahlquist 1990, Avise 1994, Hillis and Moritz 1990, Hoelzel 1992, Mindell 1997). In particular, the analysis of nucleotide sequences by powerful computer programs, such as PAUP (Swofford 1993), PHYLIP (Felsenstein 1993) and MEGA (Kumar *et al.* 1993), has facilitated the reconstruction of phylogenies in all kingdoms of life. The molecular approach does not make the traditional analysis obsolete; on the contrary, it is complementary. Indeed, the right questions in molecular analysis can only be asked if we have a solid framework based on morphology, geography, behaviour and/or acoustics.

The analysis of mitochondrial genes is central today in most molecular studies on birds (Mindell 1997), since mtDNA evolves much faster than nuclear DNA. Among mitochondrial genes, many studies use the cytochrome b gene, which has the advantage that deletions, insertions or inversions are usually absent, so that the sequence alignment does not constitute a problem (as compared to ribosomal genes, which are also often used as markers). However, while cytochrome b is usually a good marker at the species and genus level, it loses resolution on divergence events which are more than 50 million years away. This is mainly due to multiple nucleotide substitutions at the same position, which can lead to homoplasy.

Cytochrome b sequences are available today for many groups of birds, such as the ratites, Pelicaniformes, Falconiformes, Ciconiidae, Procellariidae, Alcidae, Gruidae, Laridae, Stercorariidae, Psittacidae, Sylviidae, Paridae, Sittidae and Fringillidae (examples are: Kocher *et al.* 1989, Edwards *et al.* 1991, Birt *et al.* 1992, Cooper *et al.* 1992, Richman & Price 1992, Taberlet *et al.* 1992, Blechschmidt *et al.* 1993, Friesen *et al.* 1993, Helm-Bychowski & Cracraft 1993, Seibold *et al.* 1993, in press, Wink *et al.* 1993a,b, 1998, Avise *et al.* 1994, Hedges and Sibley 1994, Heidrich & Wink 1994, 1998, Wink 1994a,b, 1995, Heidrich *et al.* 1995a,b, 1996, 1998, Helbig *et al.* 1995, 1996, Wink & Seibold 1996, Wittmann *et al.* 1995, Gaucher *et al.* 1996, Griffiths 1997, Leisler *et al.* 1997 and Mindell 1997).

Trees which are based on sequence data are not necessarily unequivocal and correct. Problems can arise if the dataset is incomplete and does not contain all related taxa for a comparison ('undersampling'). The alignment can be critical for datasets containing gaps, insertion or deletions (as in rRNA genes). Nuclear copies of mitochondrial genes can bias a phylogeny (Quinn 1997). Also computer programs (i.e. character state, distance or maximum likely hood methods) and the evolutionary window to be analysed (i.e. problems of homoplasy) are of importance to obtain the correct tree. For mitochondrial genes it should be remembered that we can only trace maternal lineages ('gene trees') and that trees can be distorted by inbreeding and introgression. Some of these limitations have to be kept in mind when interpreting the phylogenetic trees presented in the following.

We have chosen the mitochondrial cytochrome b gene to study speciation and phylogeny of owls. Some results have already been published from our laboratory on tawny, screech and pygmy owls (Heidrich & Wink 1994, 1998, Heidrich *et al.* 1995). In this chapter we present results of our molecular investigation

into the phylogenetic relationships in the genera *Tyto, Phodilus, Otus, Bubo, Ketupa, Nyctea, Strix, Pulsatrix, Glaucidium, Athene, Speotyto, Aegolius, Ninox, Asio* and *Surnia*. The missing genera mostly belong to monotypic genera, so that a general picture on the phylogeny of owls becomes possible with the present dataset. (We would be happy to receive blood, tissue or feather samples from species that are not included in our trees, since we hope eventually to arrive at a complete tree of the Strigiformes.)

MATERIAL AND METHODS

Detailed information on materials and methods use for DNA isolation, PCR, PCR primers, DNA sequencing and tree reconstruction has been produced (Wink 1994a, 1994b, 1995, Heidrich & Wink 1994, 1998, Heidrich *et al.* 1995, Leisler *et al.* 1997, Heidrich 1998). Sequences have been deposited with GeneBank. Details on methodology and sequence information can be obtained from the authors on request.

For most species we have determined cytochrome b sequences (1040 bp) for two or more individuals, so that the sequences used in this analysis are unequivocal and reliable (Heidrich 1998). For the molecular analysis (shown in Fig. 55) we have assembled a dataset consisting of a single cytochrome b sequence per taxon in those cases where significant haplotype differentiation was absent. We had samples of approximately 270 individuals of owls, and determined partial cytochrome b sequences (300 bp) for all of them. The partial sequences are helpful in identifying existing haplotypic differentiation (Fig. 56).

Distances (p-distance) are calculated as the proportion of nucleotide substitutions (in %) between pairs of taxa (Table 1). Distances correlate with divergence time: a 2% nucleotide substitution is estimated to be crudely equivalent to a million years of separation (Shields & Wilson 1987). This molecular clock provides a rough estimate for a temporal framework (Moore & DeFilippis 1997), but needs to be interpreted with caution, since the clock was not calibrated for owls.

Distances can be used to decide whether a taxon can be regarded as a distinct species: in owls a divergence of more than 1.5% is usually indicative of species level, and we advocate species recognition at this threshold when there is clear support from morphological and acoustic characters.

Bootstrap values provide an estimate of how well sequence data support a furcation. Although bootstrap values remain controversial, they can be helpful. On the basis of simulations under a wide range of conditons, Hillis & Bull (1993) concluded that nodes with calculated bootstrap values of 70% and higher actually occurred in 95% and more of simulated phylogenies. This means that a bootstrap value of 70% can be regarded as evidence for a well supported node (Moore & DeFilippis 1997).

PHYLOGENETIC RELATIONSHIPS WITHIN THE STRIGIFORMES

In occupying the niche of a nocturnal raptor, owls underwent several adaptations. Besides specialised hunting strategies, they developed a sophisticated acoustic communication system. Morphology varies relatively little in many owl species but the distinctive calls, which are inherited and not learned, are of considerable taxonomic value (Hekstra 1982, Kõnig 1991a,b, 1994a,b). If phylogenetic relationships are reconstructed on the basis of morphological characters alone, errors may result from the confusion caused by convergent traits that have nothing to do with underlying phylogeny.

The sequence dataset, involving one sequence per taxon, was analysed by Neighbour Joining (NJ) and Maximum Likelihood (ML). The resulting trees are congruent in most groupings (see Fig. 55a, b). Differences can be seen for *Ninox*, which is either placed as a sister group to the *Glaucidium/Athene* complex (ML) or at the base of the Strigidae (NJ). *Pulsatrix* either clusters as a sister group to New World *Otus* (NJ) or sits between *Strix* and *Bubo* (ML). Bootstrap values (NJ) indicate that the position of *Ninox* and *Pulsatrix* is not supported by significant values (Fig. 55b); we consider the ML groupings to be more likely, since ML has been considered as the best tree reconstruction method available at present.

As can be seen from Figs. 55-57, the distinction between the families Tytonidae and Strigidae is evident in all tree reconstructions and well supported by DNA data (Table 1).

Relationships within the family Tytonidae

Traditionally, two genera are distinguished within the Tytonidae: *Tyto* and *Phodilus*. This view is clearly supported by the sequence data (Figs. 55-57). The distance between the two genera is large (Table 1), i.e. their divergence from a common ancestor must have occurred more than nine million years ago.

Although several members of the *Tyto* complex have been recognised as distinct species (Sibley & Monroe 1990), several others are considered to be subspecies of *T. alba, T. novaehollandiae* or *T. capensis*. However, since morphological variation is pronounced, some of the subspecies may constitute sibling species. We have analysed the DNA of more than 20 individuals of *T. alba* and found a considerable degree of sequence variation between birds from different populations (up to 2%), indicating a strong degree of philopatry and reduced gene-flow between them. Fig. 56a shows their phylogeographic

relationships: within Europe and Africa, birds originating from Germany, Ireland, Scotland, Austria or France have developed distinct haplotypes. *T. a. glaucops* from Hispaniola in the Caribbean has been separated as a distinct species since *T. glaucops* and *T. alba* are sympatric and do not interbreed (Sibley and Monroe 1990, Hume 1991). The sequence divergence of 8% (Table 1) definitely supports the treatment of *T. glaucops* as a distinct species. *T. a. pratincola*, which also lives in the West Indies, is clearly distinct from *T. alba* (8% sequence divergence) but less so from *T. glaucops* (1.7%), so might or might not merit species status, and if retained as a subspecies it presumably should be a subspecies of *T. glaucops*. Since barn owls have been introduced to many countries of the world by European settlers, the genetic make-up of local populations may be influenced by hybridisation between native and introduced birds.

Relationships within the family Strigidae

Glaucidium Pygmy owls of the genus *Glaucidium* occur in the Old and New World. Although their plumage is very similar in most instances (a factor which makes their taxonomy particularly difficult), they can be distinguished by a unique repertoire of vocalisations (König 1994b). We recently demonstrated that taxonomic classifications based on differing acoustic signals (König 1994b) could be corroborated by DNA sequence data (Heidrich *et al.* 1996). Figure 55 clearly shows that Old and New World species cluster in separate monophyletic clades which possess a common ancestry but diverged more than 7-8 million years ago (Table 1). We can certainly rule out the notion that *G. gnoma/ G. californicum* and *G. passerinum* are conspecific, as has been assumed by some authors based on their similar plumage patterns (Sibley & Monroe 1990). *Glaucidium perlatum* was considered a subspecies of *G. passerinum* by Eck & Busse (1973), but since genetic distances are higher than 6.5% (Fig. 56a) and vocal differences also exist, the taxa can be regarded as distinct species.

Within the *Glaucidium brasilianum* complex of South America, several distinct haplotypes have been recognised (Figs. 55, 57) in different regions of Argentina and Brazil. Because voices and sizes also differ, *G. tucumanum* has been considered a distinct species (Heidrich *et al.*, 1995) and *G. b. stranecki* a new subspecies (König & Wink 1995). *G. brasilianum* shares common ancestry with *G. peruanum, G. griseiceps* and *G. nanum* (Fig. 55), these species forming a monophyletic group. *G. bolivianum, G. jardinii* and *G. hardyi* also cluster in a common, apparently monophyletic group (Fig. 55). Birds of both complexes are clearly separated from *G. californicum* and *G. gnoma*, which have distinctive calls and distributions (*G. californicum* lives in North America, especially the Rocky Mountains, while *G. gnoma* ranges from Mexico to Central America). *G. minutissimum* from eastern Brazil clusters between the *bolivianum* and *californicum* group (Fig. 56a).

Athene/Speotyto Three species have been recognised in the genus *Athene*, i.e. *A. noctua, A. brama* and *A. blewitti*. As can be seen from Fig. 56a, *noctua* and *brama* are clearly separated also at the sequence level. Within *A. noctua*, we encountered a surprising phenomenon. Two genetic clusters are apparent, and are supported by high bootstrap values; genetic differences between both groups account for 6.4% nucleotide substitutions. A genetic distance of more than 1.5% is typical for species. Birds from cluster I derive from Israel and Turkey whereas those from cluster II are from Europe (Figs. 55, 56a). How can we explain these results? Both clusters might represent distinct species which have not been recognised by taxonomy so far. In this case, also morphological and acoustical differences should exist between both forms. Indeed, morphologically distinct subspecies have been described from Israel, which may explain the differences. In this case these birds would represent a separate species: *Athene lilith*.

We had no material of *blewitti* to work with. However, it should be noted that as yet unpublished morphological analysis suggests that it belongs in its own genus *Heteroglaux* (Rasmussen and Collar 1998).

Athene (*Speotyto*) *cunicularia* represents the genus *Athene* in the New World. Since DNA-DNA hybridisation suggested significant differences (Sibley and Monroe 1990), a separation into a monotypic genus appears justified. According to the sequence data, it is clear that *Speotyto* and *Athene* share common ancestry (divergence approximately six million years ago) and that they form a monophyletic group. Because of similarities in morphology, general appearance, vocal patterns, and in behaviour, however, we suggest merging *Speotyto* back in *Athene*.

Surnia The Northern Hawk Owl *Surnia ulula* of northern Eurasia and North America shares common ancestry and forms a monophyletic group with the *Glaucidium* complex of Old World origin (Figs. 1-3). Retention of a monotypic genus is thus open for debate, but might be justified because of morphological, behavioural and, last but not least, genetic differences.

Aegolius Owls of the genus *Aegolius* represent a third major monophyletic group (Figs. 55, 57) besides *Glaucidium/ Surnia* and *Athene*. Within *A. funereus*, some geographical differentiation is apparent (Fig. 56a) which requires further study. The North American *A. acadius* diverges with 12.9% nucleotide substitutions from *A. funereus*, implying divergence well over six million years ago (Table 1). Two

geographically separated subspecies, *A. a. acadius* and *A. a. brooksii*, can be recognised (distance 0.7%). The South American *A. harrisii* is more closely related to the North American *A. acadius* than to *A. funereus* (Fig. 55), suggesting a common ancestor for the New World species. *Aegolius ridgwayi* from Central America could not be studied, as no tissue samples were available.

Ninox The genus *Ninox* comprises at least 20 species of mainly Australasian distribution. On general appearance they might be related to the *Glaucidium/Athene* complex. Indeed, in ML trees (and MP, not shown), *Ninox* clusters as a sister group to this complex (Fig. 55a). Also 12S mt rDNA support such an assumption (Mindell *et al.* 1997). We clearly need more taxa from the genus *Ninox* to resolve its phylogenetic position unambiguously.

Strix Tawny and wood owls (genus *Strix* with 21 species, including *Ciccaba*) always form a monophyletic clade in ML, MP, and NJ trees (Figs. 55-57) and cluster as a sister group to the *Bubo* complex.

DNA data show that *S. butleri* is a distinct species rather than a subspecies of *S. aluco*, and indeed closer to the African *S. woodfordii* than to *S. aluco* (Heidrich & Wink 1994). *Strix uralensis* appears as a sister group of *S. aluco*, as suggested from behaviour and general appearance; genetic distances (Table 1) imply that both taxa diverged from a common ancestor more than four million years ago.

The South American *S. rufipes* always clusters at the base of the *Strix* complex and could belong to a sister group to the Old World *Strix*, the two having diverged from a common ancestor 5-6 million years ago. Future studies of New World species will show whether this assumption is correct.

Within *S. aluco* from various parts of Europe and Israel we found no evidence of haplotypic differentiation, as observed for *Tyto alba* or *Asio otus* (Fig. 56b). Two distinct haplotypes can be seen in *S. uralensis*, probably reflecting phylogeographic differences between Scandinavian and birds from Eastern Europe (Fig. 56b).

Pulsatrix Four species are recognised in the Central and South American genus *Pulsatrix*, of which we were able to study *P. perspicillata* and *P. koeniswaldiana*. The phylogenetic position of *Pulsatrix* cannot, however, be resolved with certainty. In NJ trees (Fig. 55b) it clusters with the South American *Otus* complex, and in ML reconstructions between *Strix* (and *Ciccaba*) and *Bubo* (Fig. 55a); but clusters are not supported by high bootstrap values.

Otus, Mimizuku, Asio and Ptilopsis Morphologically, several owls with ears have been grouped in the genera *Bubo* (eagle owls), *Ketupa* (fish owls), *Otus* (scops and screech owls) and *Asio* ('eared owls'). According to our genetic analysis (Figs. 55-57), members of the genus *Otus* appear in at least three different monophyletic clades, indicating that the genus is polyphyletic; it therefore needs a systematic revision. The screech owls of the New World represent a distinct group which is separated from Old World *Otus* by genetic distances of between 12 and 16%, equivalent to 6-8 million years (Table 1). Within the screech owl complex, which has its centre of radiation in South and Central America, several species have been recognised on account of different acoustic repertoires (König 1994a). Sequence data corroborate these findings (Heidrich *et al.* 1995), thereby supporting the importance of vocalisations in owl taxonomy. *Otus atricapillus*, *O. usta* and *O. roboratus* are distinct species of common ancestry. *Otus sanctaecatarinae*, and probably *O. guatemalae* and *O. asio* (from North America), also belong to this assemblage. *Otus hoyi* and *O. petersoni* appear as sibling species, as do *O. albogularis* and *O. choliba* (Figs. 55, 56b).

Several Old World scops owls have been analysed (overview in Sibley & Monroe 1990). *Otus scops*, *O. lempiji*, *O. megalotis*, *O. longicornis*, *O. brucei* and *O. bakkamoena* have been included here as representatives of this group. As can be seen from Figs. 55 and 56b these birds fall into a common clade which is very distinct from the New World *Otus* 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 also studied the latter two species we can conclude that *O. mirus*, *O. mindorensis* and *Mimizuku gurneyi* are members of the Old World *Otus* group. Since *Mimizuku* clusters within this group it is doubtful whether this monotypic genus is valid (Miranda *et al.* 1997).

The African *O. leucotis* and *O. granti* differ both morphologically and genetically from the other Old World *Otus* species and have been placed in the genus *Ptilopsis*. In all reconstructions (Figs. 55-57) they figure as a sister group to *Asio* (to which they have some superficial resemblance). It is likely that '*P. leucotis*' represents two species: *P. leucotis* and *P. granti*, which are similar in size and plumage, but differ strikingly in voice and range; moreover, our DNA data (Fig. 56b) indicate a clear difference between them. *Asio otus* and *A. flammeus* always fall into the same clade (Fig. 56b) although they may have diverged more than five million years ago.

Altogether it seems obvious that other different monophyletic clades of *Otus* species should also be recognised taxonomically. Some haplotypic differentiation was discovered in *Otus atricapillus*, *O. usta*, *O. hoyi*, *O. petersoni*, *O. guatemalae*, *O. asio*, *Ptilopsis leucotis*, *Asio otus* and *A. flammeus* which deserves further study (Fig. 56b) to determine a possible phylogeographic pattern.

Bubo, Ketupa and Nyctea Eagle owls of the genus *Bubo* represent another prominent group of owls with ear-tufts. To date within this complex we have studied *B. bubo, B. ascalaphus, B. nipalensis, B. virginianus, B. magellanicus, B. africanus, B. bengalensis, B. sumatrana* and *B. lacteus*. According to phylogenetic relationships and distances (Figs. 55 & 56b; Table 1) these are all distinct species, although some have been treated as subspecies of *B. bubo* (Sibley and Monroe 1990).

The southernmost taxon of South American eagle owls differs in size, vocalisations and DNA (Figs. 55 & 56b) from *B. virginianus* and has been considered a distinct species, *B. magellanicus* (König *et al.* 1996).

Bubo ascalaphus, which occurs in North and West Africa, has been treated as a distinct species (Sibley and Monroe 1990). In our analysis nucleotide substitutions differ by 3.5% between *B. bubo* and *B. ascalaphus*. Moreover, *B. b. interpositus*, which is morphologically distinct from *B. bubo* and lives in the Israeli desert, is also genetically distinct (distance 2.8%) (Figs. 55 & 56; Table 1). Since a sequence divergence of more than 1.5% is indicative of species level, we regard it as justified to treat both taxa as distinct species particularly if supported by morphological and accoustic evidence.

We have analysed the sequences of some 20 individuals of *B. bubo* from Western and Central Europe. Many samples derived from birds found dead under powerlines or on roads, most of which were descendants of birds reintroduced to Germany and other countries during breeding programmes. A first analysis of the sequence data (Fig. 56b) shows a strong heterogeneity, indicating that birds from various origins and subspecies have been multiplied and released in the breeding programmes. Analysis before starting the breeding programme could have prevented this genetic mix.

The Snowy Owl *Nyctea scandiaca* shares its ancestry with *Bubo* (Figs. 55-57), especially with the New World *B. virginianus*, a finding which conforms with the arctic distribution of *Nyctea*. The separation from a common ancestor took place more than four million years ago. Since *Nyctea* represents a monotypic genus but unambiguously clusters within the *Bubo*-complex, the taxonomic consequence would be to lump *Nyctea* in *Bubo* and call the species *Bubo scandiaca*.

A similar situation obtains with *Ketupa*, of which four species have been described from South-East Asia. *Ketupa zeylonensis* and *K. ketupu* cluster as close relatives to Asian *Bubo* such as *B. nipalensis* and *B. sumatrana* (Figs. 55 & 56b). Moreover, the general appearance of *Ketupa* is similar to that of *Bubo*; because of genetic relationships (distance 9-10%) we agree with Amadon and Bull (1988) to merge *Ketupa* in *Bubo*.

PHYLOGENETIC POSITION OF OWLS AS COMPARED TO DIURNAL RAPTORS AND NIGHTJARS

Several hypotheses have been advanced concerning the evolution of owls. Linnaeus (1758) placed them with vultures, eagles and falcons in the order Accipitres. In 1827 they were separated from the diurnal raptors as a distict order by L'Herminier; soon afterwards Nitsch (1840) recognised the differences between Tytonidae and Strigidae. This view was supported by Fürbringer (1888) and Gadow (1892), who also stressed a closer relationship between Strigiformes and Caprimulgiformes, a view maintained by Wetmore (1930) and Mayr and Amadon (1951). Cracraft (1981), using a cladistic approach, went against this, concluding a closer relationship between owls and falcons, but Sibley and Ahlquist's (1990) study on DNA-DNA hybridisation reinstated the Caprimulgiformes as the nearest neighbour of the owls.

To test the owl/falcon and owl/nightjar hypotheses, we have assembled a dataset of cytochrome b sequences including the main genera of owls, members of the Galliformes and Casuariformes/Rheiformes as old and distinct outgroups, plus members of the Procellariiformes, Charadriiformes, Falconiformes (Falconidae, Sagittariidae, Pandionidae, Accipitridae, Cathartidae), Psittaciformes, Cuculiformes, Ciconiiformes and Gruiformes. The cytochrome b dataset was analysed by MP methods. The resulting bootstrap cladogram is shown in Figure 57.

Running parallel with our work, Mindell *et al.* (1997), using 12S mt rDNA, concluded that all diurnal raptors could be monophyletic. Our results, on the other hand, suggest that – although deeper (ordinal) branches are not well supported by bootstrap values – the Sagittariidae, Pandionidae and Accipitridae share an ancestry but appear separated from the falcons and Cathartidae. A similar conclusion had already been reached for the New World vultures (König 1982, Avise *et al.* 1994, Wink in press), which are no longer considered members of the Falconiformes (Sibley and Monroe 1990). Similar traits in morphology and behaviour of diurnal raptors are obviously based on convergence due to common life style and not due to common genealogy (Wink 1998, in press).

Figure 57 clearly shows that owls can be subdivided into two major lineages, representing the Tytonidae and Strigidae; together they form a monophyletic group. However, neither nightjars (Caprimulgidae) nor falcons (Falconidae) cluster as a closely related next neighbour to the Strigiformes. These groups usually cluster with unrelated orders (containing the Procellariiformes, Ciconiiformes, Charadiiformes, Pandionidae and Accipitridae). Using different methods for tree-building, such as NJ, MP or ML, we always obtained the same monophyletic groups, such as Strigidae, Tytonidae, Falconidae, Accipitridae,

Laridae, etc., all supported by high bootstrap values, but their positions in relation to each other differed and was not supported by significant bootstrap values. In some trees, we could see a monophyly of Falconidae, Accipitridae, Pandionidae and Sagittariidae; in others a relationship between Tytonidae and Falconidae. Because we could not obtain congruent trees, we conclude that it is difficult to reconstruct higher-order phylogeny of birds using cytochrome b and other mtDNA sequences.

Morphological and anatomical similarities between owls and falcons or nightjars, which were the base for the hypothesis of a closer relationships to owls, are probably based on convergence (as implied already by Bock and McEvey 1969, Mikkola 1983, Feduccia 1996), since they cannot be supported by our sequence data. Since cytochrome b is at its limits for such a comparison, covering probably 100 million years of evolution, a more conserved gene (prefarably a nuclear gene) should be studied to confirm these findings.

CONCLUSION

As can be seen from Figs. 55 & 56, the phylogenetic trees inferred from cytochrome b gene sequences generally agree well with the classical taxonomy of owls (Sibley & Monroe 1990, Hume 1991, Burton 1992). Usually the genetic data agree with the attribution of species to a given genus. Exceptions are evident in *Otus*, where a paraphyletic origin is more likely than the present collection of species in a single genus.

The phylogenetic relationships between different genera could not be resolved with certainty in all instances. However, it is likely that the genera *Glaucidium*, *Athene*, *Aegolius* and *Surnia* derive from a common ancestor; the same applies to *Otus*, *Asio*, *Bubo* and *Strix*, and to *Tyto* and *Phodilus* (Fig. 55).

Cytochrome b sequence data are well suited to resolve phylogenetic relationships within genera and at the species level, but less so at the family and order level (Fig. 3). As mentioned before, several species of the *Glaucidium* and *Otus* complex have been recognised and described mainly by their vocal repertoires, in spite of their weak morphological differentiation. Cytochrome b sequence data have shown that these vocally distinct species are also genetically distinct (König 1994a,b, Heidrich *et al.* 1995, 1996).

In summary, sequence data of the mitochondrial cytochrome b gene provide another powerful tool (besides morphology, anatomy, behaviour and bioacoustics) to elucidate and reconstruct the evolutionary past and speciation in owls. Since the analysis of a single gene only provides a window for a particular evolutionary period, we need to include more progressive or more conservative genes (including both mtDNA and ncDNA) if we intend to solve other problems of microevolution or of higher-level classifications.

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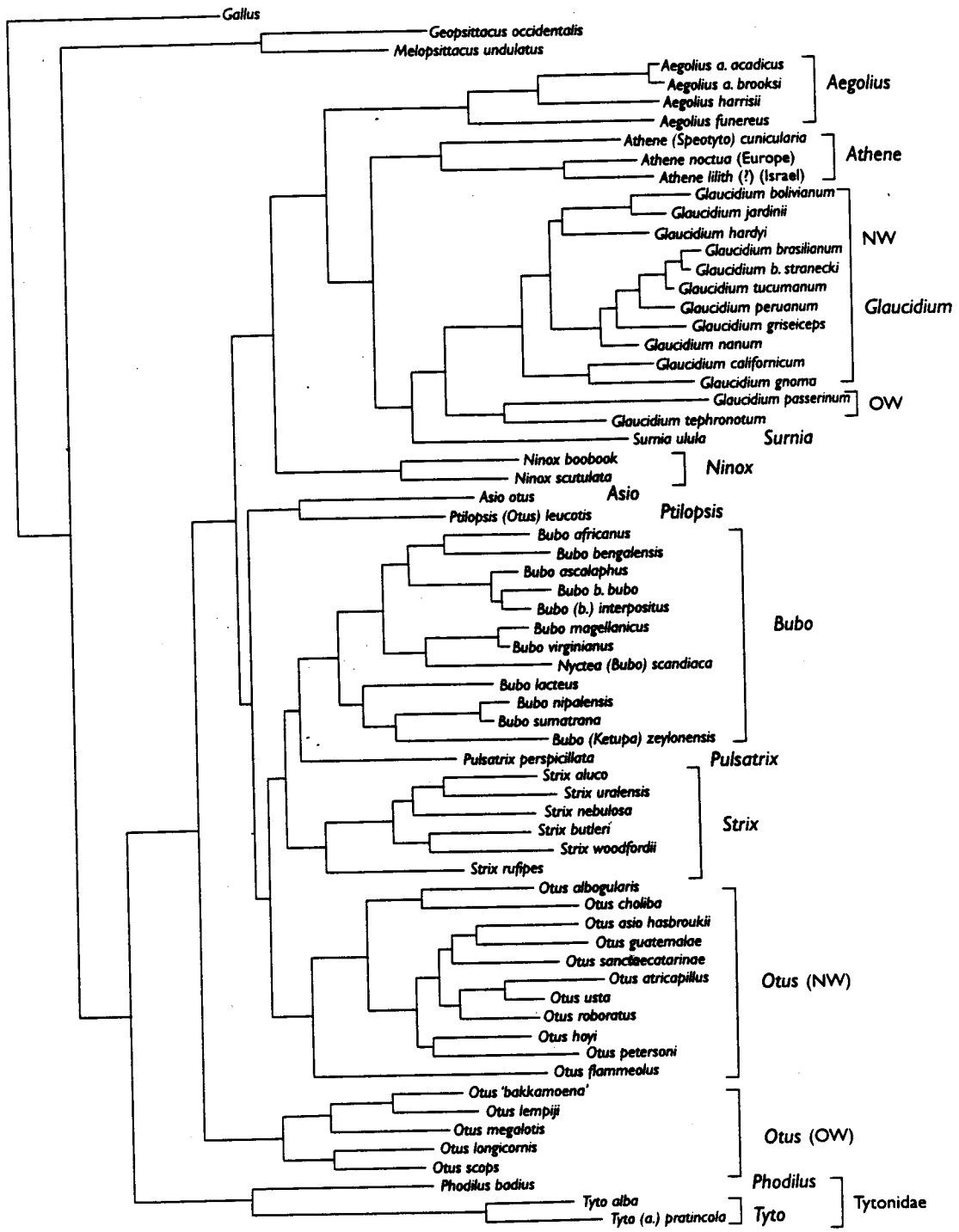


Figure 55a. Genetic relationships within the Tytonidae and Strigidae (based on 1040 nt of the cytochrome b gene): Maximum Likelihood tree. Branch lengths are proportional to genetic distances. (OW = Old World; NW = New World).

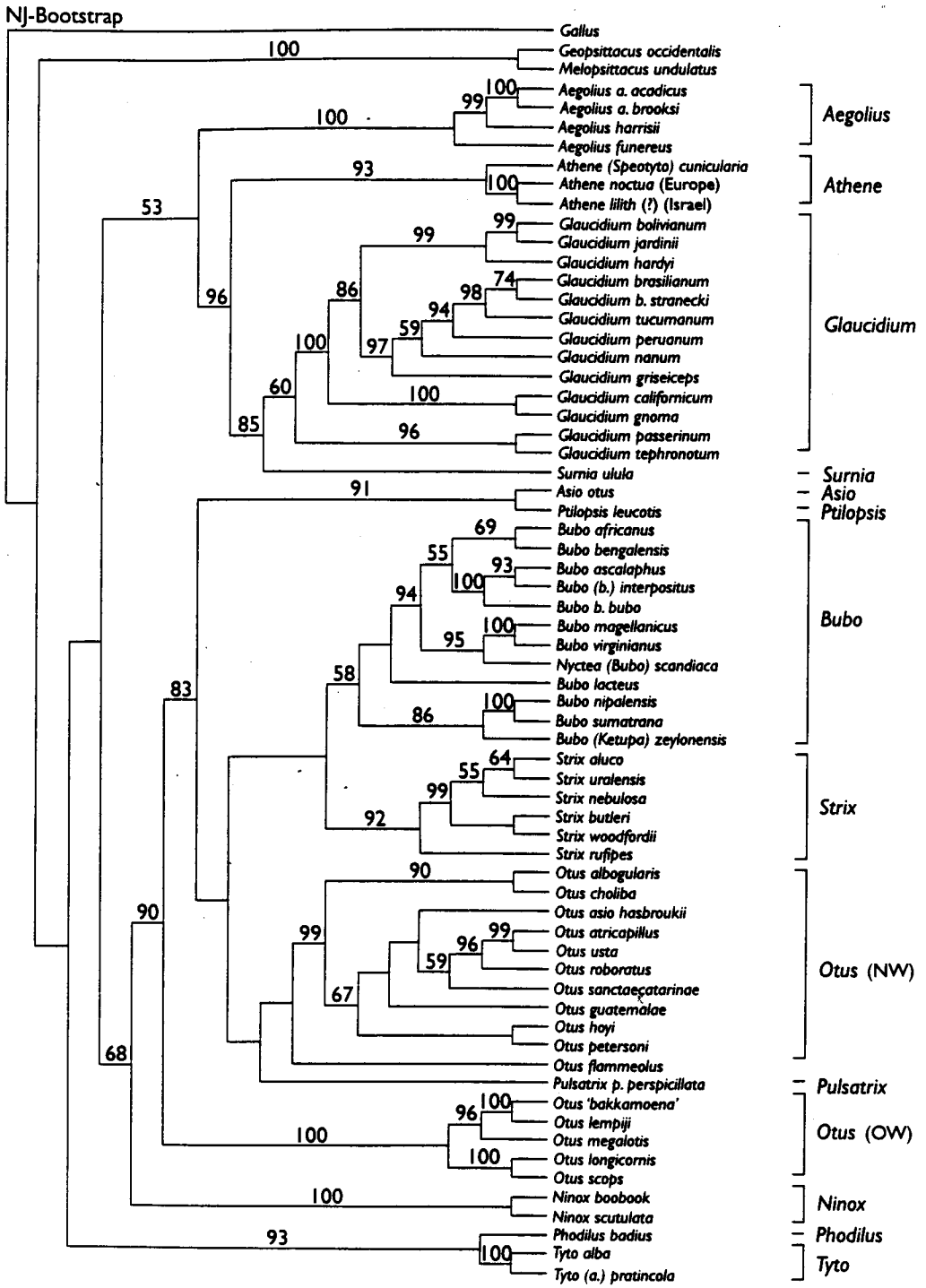


Figure 55b. Genetic relationships within the Tytonidae and Strigidae (based on 1040 nt of the cytochrome b gene): Bootstrap cladogram (100 replicates) reconstructed with the Neighbour Joining method using Jukes Cantor as a distance algorithm (other algorithms, such as Kimura 2, Tamura-Nei, do not change the tree topology). Bootstrap values (above 50%) are given in italics below the branch length values. (OW = Old World; NW = New World).

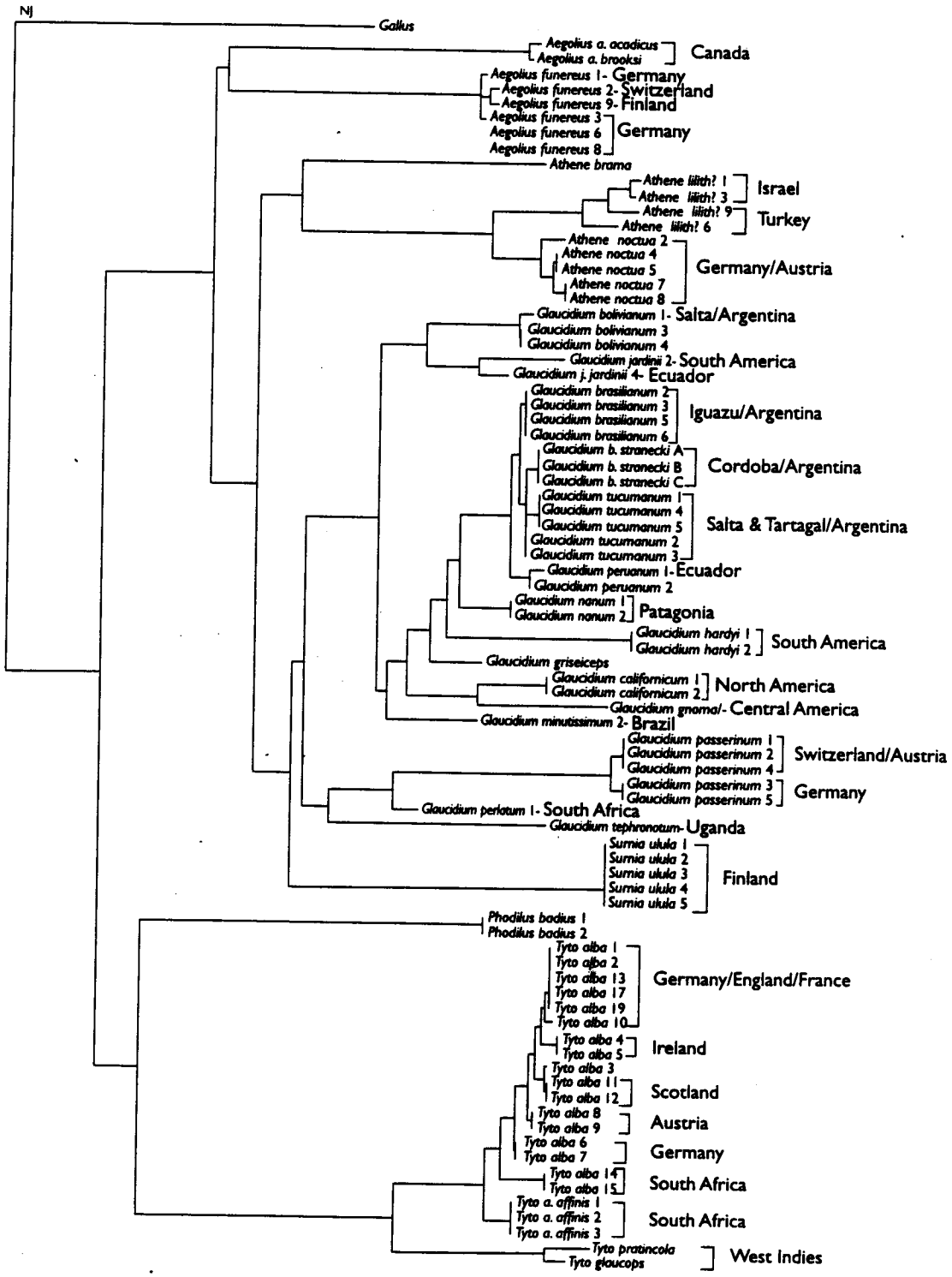
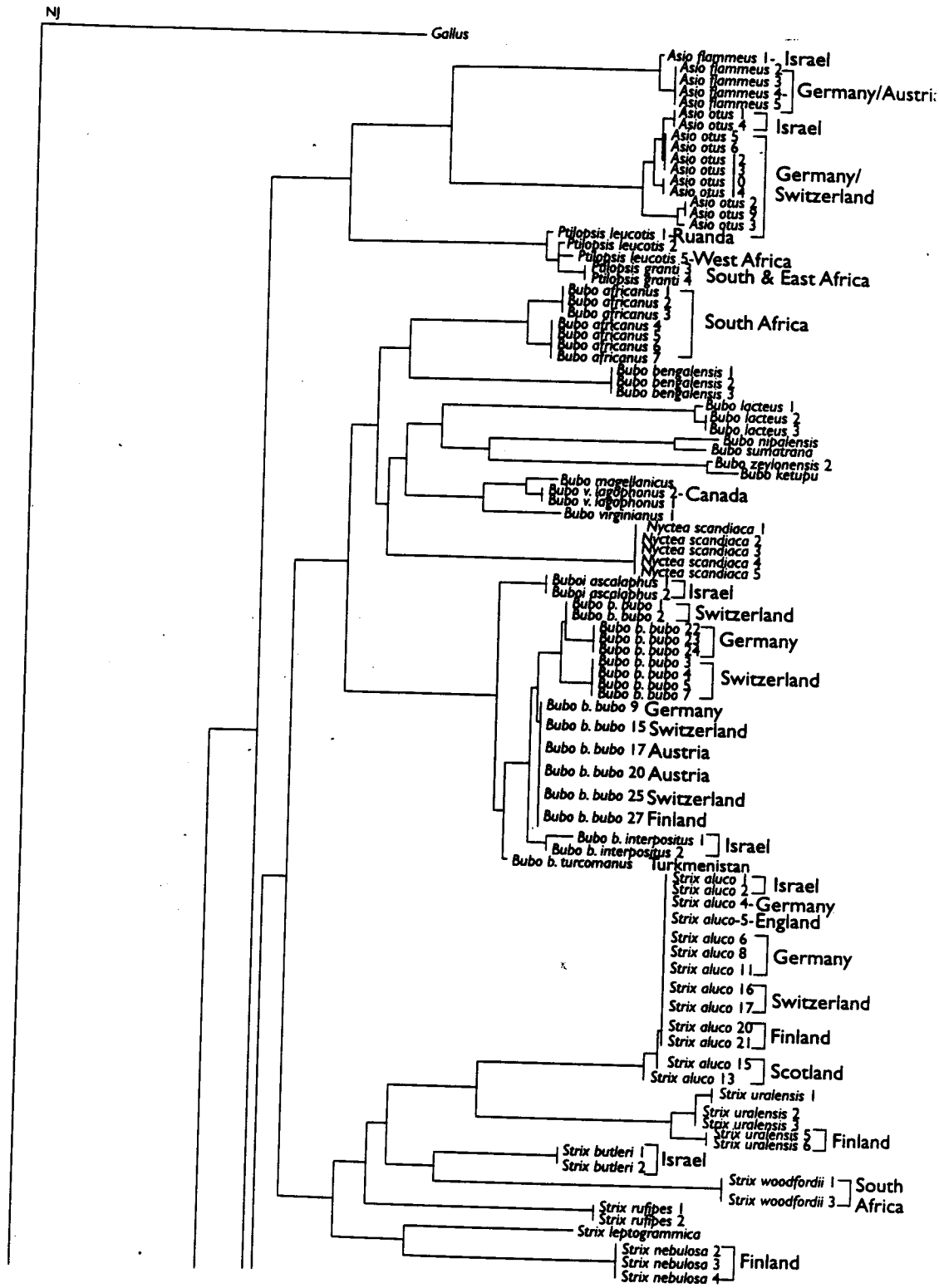


Figure 56a. Haplotypic differentiation in owls based on 300 bp of the cytochrome b gene. Analysis with NJ as in Fig. 55b; branch lengths are proportional to evolutionary distances. Phylogram of genetic relationships between several individuals per taxon of the Tytonidae and in the *Glaucidium/Athene* complex. Geographic origins are given after the species name when reliable data were available; in several instances samples came from zoo birds whose origin could not be established.



(continued on p.49)

(continued from p.48)

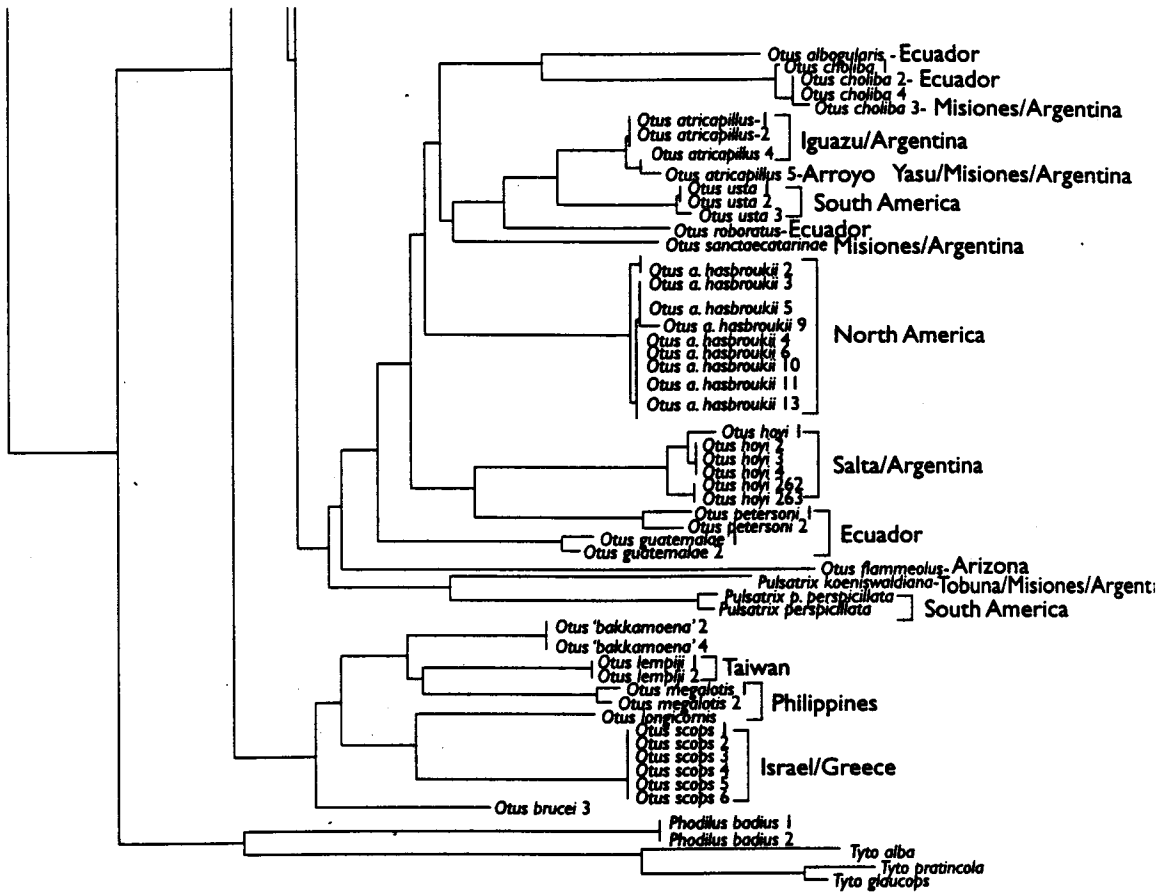


Figure 56b. Haplotypic differentiation in owls based on 300 bp of the cytochrome b gene. Analysis with NJ as in Fig. 55b; branch lengths are proportional to evolutionary distances. Phylogram of genetic relationships within the complex of 'eared owls' and *Strix*. Geographic origins are given after the species name when reliable data were available; in several instances samples came from zoo birds whose origin could not be established.

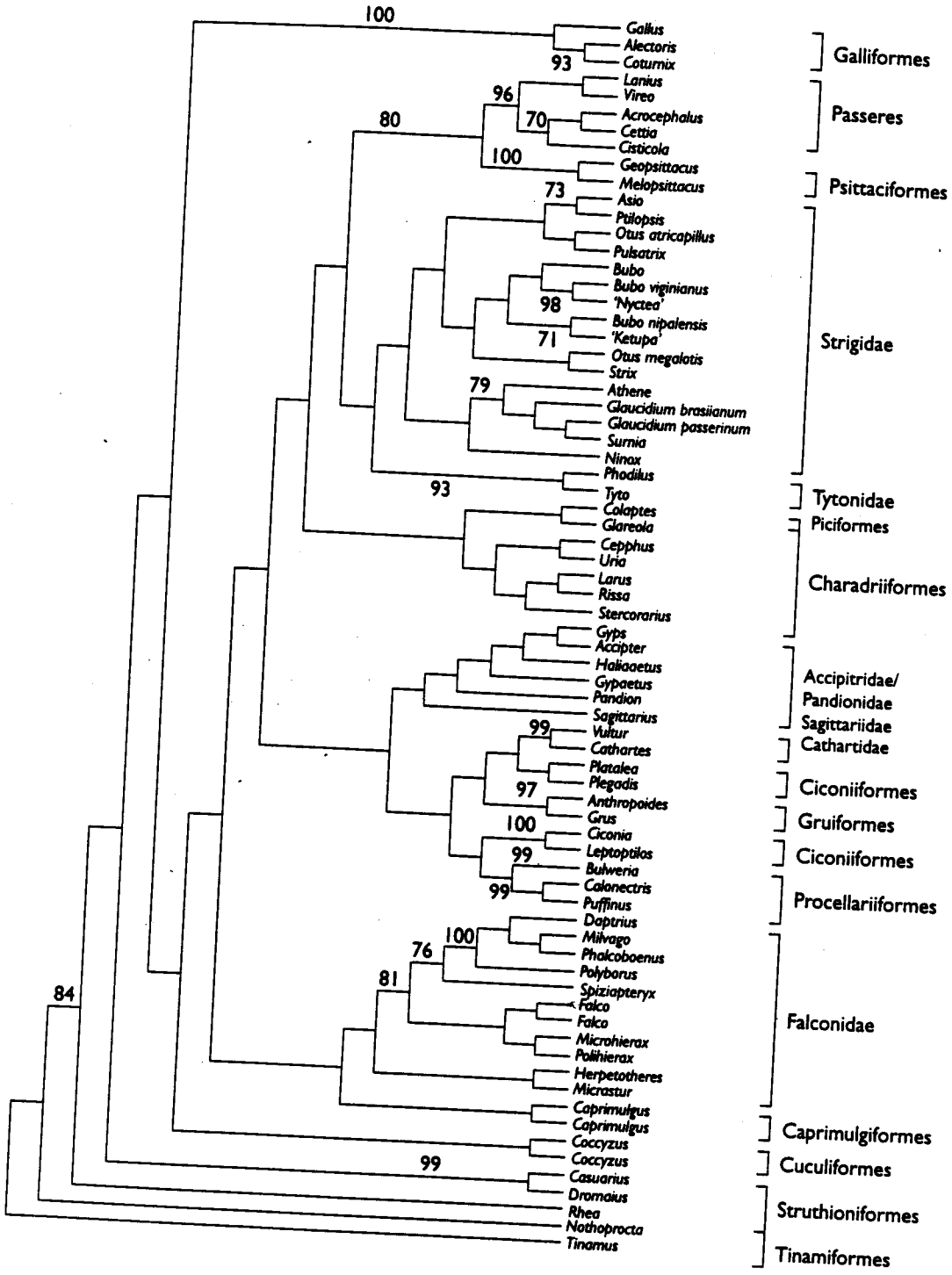


Figure 57. Genetic relationships between members of the Strigiformes and other orders of birds (based on 1040 nt of the cytochrome b gene): Bootstrap analysis (150 replicates) employing the Maximum Parsimony method with heuristic search (TBR branch swapping; tree length 5483 steps [sum of minimal possible lengths 1010, maximally 8114 steps]; consistency index CI= 0.184; retention index RI= 0.370). Sequence data from GeneBank or our own laboratory.

		77	78	80	84	86	88	89	93	95	97	98	100	113	114
77	*Aegolius acadicus*	-													
78	*A. a. brooksi*	0.00732	-												
80	*A. funereus*	0.12874	0.13210	-											
84	*A. harrisii*	0.08804	0.08910	0.12880	-										
86	*Asio otus*	0.17719	0.17640	0.17810	0.17874	-									
88	*Athene cunicularia*	0.17508	0.17757	0.17047	0.17829	0.18062	-								
89	*A. noctua* (Eur.)	0.18444	0.18270	0.18316	0.18366	0.18741	0.12950	-							
93	*A. (n.) lilith* (Isr.)	0.18792	0.18613	0.18199	0.17739	0.19278	0.13578	0.06467	-						
95	*Bubo africanus*	0.17861	0.17780	0.17396	0.17662	0.14333	0.15945	0.17733	0.17616	-					
97	*B. ascalaphus*	0.18634	0.18451	0.18184	0.19541	0.13901	0.15967	0.17956	0.18434	0.07866	-				
98	*B. bengalensis*	0.18433	0.18255	0.18399	0.18408	0.13853	0.16525	0.17322	0.17868	0.07455	0.08834	-			
100	*B. b. bubo*	0.18707	0.18623	0.18054	0.17935	0.13215	0.16366	0.17793	0.18529	0.08510	0.03499	0.09053	-		
113	*B. (b.) interpositus*	0.19160	0.19097	0.18634	0.18933	0.13801	0.16827	0.18533	0.18961	0.08091	0.02345	0.09278	0.02811	-	
114	*B. lacteus*	0.16164	0.16096	0.16364	0.16687	0.12522	0.14063	0.15879	0.17058	0.09440	0.09629	0.08674	0.09489	0.09999	-
115	*B. magellanicus*	0.18304	0.18353	0.18328	0.18323	0.14300	0.16925	0.16555	0.17856	0.08685	0.09880	0.09612	0.09904	0.09540	0.10531
116	*B. nipalensis*	0.17187	0.16992	0.18782	0.18022	0.13855	0.16531	0.18246	0.18230	0.09727	0.11576	0.11232	0.11889	0.11656	0.09157
117	*B. sumatrana*	0.17516	0.17220	0.18992	0.18382	0.13715	0.16261	0.18218	0.18427	0.09606	0.10902	0.11203	0.11441	0.11114	0.09152
119	*B. virginianus*	0.17934	0.17957	0.17573	0.18057	0.13585	0.16734	0.17147	0.18278	0.08274	0.09478	0.09022	0.09983	0.09580	0.10437
122	*Glaucidium bolivia.*	0.17420	0.17810	0.16117	0.15994	0.17545	0.14471	0.16971	0.17065	0.17736	0.17418	0.17737	0.17677	0.18338	0.16755
124	*G. brasilianum*	0.16297	0.16221	0.17628	0.15411	0.16480	0.13455	0.16594	0.16330	0.17986	0.17661	0.18182	0.17708	0.18071	0.15217
132	*G. b. stranecki*	0.16341	0.16263	0.17815	0.15000	0.16642	0.13841	0.16443	0.16524	0.18173	0.17845	0.18374	0.17899	0.18247	0.15374
136	*G. tucumanum*	0.16637	0.16669	0.17983	0.15308	0.17036	0.13457	0.16398	0.16704	0.18006	0.17903	0.18094	0.18067	0.18410	0.15564
140	*G. californicum*	0.17018	0.17171	0.16251	0.16170	0.17097	0.13781	0.15999	0.16879	0.17608	0.17833	0.17028	0.17380	0.17256	0.15471
141	*G. gnoma*	0.17088	0.17334	0.18932	0.18114	0.18770	0.13959	0.17004	0.17572	0.18445	0.18954	0.18507	0.18862	0.19115	0.15844
142	*G. grnseiceps*	0.16001	0.15927	0.17226	0.15895	0.16267	0.12928	0.16192	0.16143	0.15947	0.15748	0.17208	0.16292	0.17329	0.15287
143	*G. hardyi*	0.16670	0.16702	0.17031	0.16597	0.16713	0.14377	0.15867	0.16844	0.17668	0.17167	0.17350	0.17822	0.17801	0.15031
145	*G. jardinii*	0.17706	0.17853	0.17121	0.16535	0.17118	0.13446	0.15049	0.16147	0.17981	0.17140	0.17239	0.17518	0.17876	0.16372
146	*G. nanum*	0.15306	0.15333	0.16392	0.15945	0.16209	0.13245	0.16581	0.16560	0.16774	0.15912	0.16648	0.16549	0.16299	0.14468
147	*G. passerinum*	0.17400	0.17329	0.17595	0.15686	0.19025	0.16237	0.16848	0.17246	0.18144	0.17166	0.18708	0.18183	0.17776	0.15945
152	*G. peruanum*	0.15879	0.16011	0.16632	0.15975	0.16686	0.13345	0.16091	0.16085	0.17547	0.17338	0.18109	0.17498	0.17990	0.15783
153	*G. tephronotum*	0.15428	0.15342	0.16326	0.15514	0.16541	0.14001	0.16034	0.16703	0.15047	0.15433	0.15859	0.15134	0.15561	0.13746
154	*Bubo zeylonensis*	0.18471	0.18389	0.19503	0.19285	0.15409	0.15736	0.18972	0.19166	0.12072	0.11685	0.11587	0.12200	0.11648	0.10498
155	*Ninox boobook*	0.19593	0.19406	0.19078	0.18899	0.16165	0.17104	0.16349	0.17276	0.16053	0.16698	0.16394	0.15357	0.16450	0.14756
156	*N. scutulata*	0.18630	0.18315	0.19009	0.18245	0.15559	0.15382	0.15349	0.16761	0.15301	0.15505	0.15471	0.14793	0.16007	0.14357
157	*Nyctea scandiaca*	0.18998	0.19029	0.18803	0.18608	0.15261	0.16166	0.17692	0.18428	0.10049	0.10844	0.10789	0.11479	0.10718	0.11467
160	*Otus albogularis*	0.17537	0.17320	0.17993	0.16247	0.15070	0.17389	0.18917	0.18563	0.13686	0.13940	0.13774	0.13637	0.14269	0.13193
161	*O. asio*	0.18202	0.18141	0.18783	0.17083	0.13693	0.15429	0.17700	0.18552	0.12821	0.13304	0.14108	0.12886	0.13099	0.12313
165	*O. atricapillus*	0.17474	0.17705	0.20082	0.17913	0.13916	0.15990	0.19211	0.19918	0.13854	0.14206	0.15134	0.13385	0.12464	0.12270
166	*O 'bakkamoena'*	0.17840	0.17640	0.18185	0.16876	0.15304	0.17869	0.16211	0.17134	0.14412	0.14586	0.14103	0.13535	0.14343	0.12721
169	*O chahba*	0.19294	0.19223	0.19346	0.17381	0.16388	0.17735	0.18325	0.18843	0.13530	0.15103	0.14491	0.14862	0.15170	0.13857
170	*O. flammeolus*	0.19632	0.19432	0.20130	0.18937	0.15794	0.16888	0.19192	0.19621	0.15284	0.15328	0.16144	0.14643	0.14892	0.14355
171	*O. guatemalae*	0.18669	0.18477	0.19213	0.17789	0.14478	0.17216	0.17895	0.18318	0.13613	0.13315	0.13710	0.13088	0.13308	0.12625
172	*O hoy*	0.17664	0.17567	0.19323	0.16733	0.13485	0.16633	0.16644	0.17646	0.13215	0.13293	0.13111	0.12630	0.13199	0.11122
174	*O. lempiji*	0.18979	0.18780	0.19278	0.17784	0.15880	0.18472	0.17672	0.18311	0.14913	0.14432	0.14135	0.14043	0.14325	0.12803
176	*O leucotis*	0.17427	0.17114	0.16600	0.17091	0.11836	0.17102	0.17830	0.18157	0.12400	0.13110	0.13266	0.12387	0.13029	0.11166
179	*O. longicornis*	0.18754	0.18450	0.18576	0.18641	0.15066	0.16592	0.16890	0.17471	0.13951	0.14606	0.14027	0.14452	0.14530	0.12810
180	*O megalotis*	0.18156	0.17851	0.19799	0.18914	0.15475	0.17114	0.17226	0.17421	0.13992	0.13871	0.12422	0.13709	0.14289	0.12534
182	*O. petersoni*	0.19149	0.18970	0.20825	0.18553	0.15873	0.17965	0.18488	0.18775	0.14280	0.15036	0.14750	0.14301	0.15212	0.13471
183	*O. roboratus*	0.18151	0.17961	0.19412	0.16804	0.13390	0.17111	0.17316	0.17733	0.13600	0.13647	0.13286	0.12794	0.13886	0.12124
184	*O. sanctaecat.*	0.17727	0.17640	0.18567	0.16504	0.13663	0.17239	0.18461	0.18265	0.13232	0.13912	0.14982	0.12855	0.13729	0.13288
185	*O. scops*	0.18665	0.18358	0.18940	0.17602	0.15859	0.17855	0.17626	0.17992	0.14633	0.14775	0.13562	0.13874	0.14367	0.12970
187	*O. usta*	0.17989	0.18025	0.18721	0.16705	0.14000	0.16815	0.17720	0.18390	0.11919	0.12745	0.13196	0.12303	0.13419	0.12088
189	*Phodilus badius*	0.17827	0.17845	0.19415	0.19689	0.18558	0.17629	0.18135	0.18835	0.18067	0.17876	0.17523	0.17951	0.17849	0.17460
191	*Pulsatrix perspicill.*	0.17845	0.17515	0.18592	0.17627	0.13752	0.17324	0.18215	0.19181	0.11272	0.12167	0.12549	0.11873	0.12333	0.11447
194	*Strix aluco*	0.17355	0.17378	0.19304	0.17449	0.14367	0.16994	0.18459	0.18446	0.13352	0.13654	0.12776	0.13241	0.13319	0.12274
206	*S. butleri*	0.17616	0.17845	0.17346	0.17828	0.15345	0.17706	0.18257	0.19473	0.12154	0.12065	0.12535	0.10985	0.12451	0.11012
207	*S. nebulosa*	0.17367	0.17501	0.17745	0.17742	0.15395	0.19086	0.18410	0.18274	0.13755	0.13220	0.13925	0.12795	0.12470	0.11810
209	*S. rufipes*	0.18405	0.18110	0.17478	0.17807	0.13157	0.16824	0.16914	0.16899	0.12173	0.12521	0.11864	0.11398	0.12376	0.10293
211	*S. uralensis*	0.18146	0.18071	0.18294	0.18177	0.14569	0.18073	0.19042	0.18946	0.13723	0.13013	0.13411	0.12922	0.12800	0.11340
213	*S. woodfordi*	0.17877	0.17906	0.18039	0.17899	0.14065	0.17755	0.18131	0.17943	0.13625	0.13818	0.13196	0.13038	0.12839	0.13114
216	*Surnia ulula*	0.18891	0.18822	0.20051	0.18040	0.18782	0.15573	0.16910	0.16329	0.17465	0.18119	0.18112	0.18174	0.18733	0.15733
219	*Tyto alba*	0.20761	0.20793	0.18933	0.20312	0.20754	0.20461	0.20300	0.20770	0.19566	0.19924	0.19768	0.19945	0.20157	0.18576
222	*T. (a.) pratincola*	0.21516	0.21699	0.20307	0.20985	0.20236	0.20618	0.21321	0.22102	0.20104	0.19939	0.19632	0.19171	0.19780	0.18759

		115	116	117	119	122	124	132	136	140	141	142	143	145	146
115	*Bubo magellanicus*	-													
116	*B. nipalensis*	0.11502	-												
117	*B. sumatrana*	0.11178	0.01602	-											
119	*B. virginianus*	0.01735	0.10792	0.10462	-										
122	*Glaucidium bolivi.*	0.17017	0.18393	0.18114	0.16721	-									
124	*G. brasilianum*	0.17252	0.17080	0.16879	0.17158	0.07848	-								
132	*G. b. stranecki*	0.17212	0.17267	0.17052	0.17217	0.08369	0.00785	-							
136	*G. tucumanum*	0.17276	0.17656	0.17106	0.17158	0.07747	0.01782	0.01234	-						
140	*G. cobfornicum*	0.16382	0.17885	0.17445	0.16122	0.08816	0.08717	0.09568	0.09289	-					
141	*G. gnoma*	0.18312	0.18282	0.18071	0.17500	0.10874	0.10241	0.10517	0.10603	0.06852	-				
142	*G. griseiceps*	0.16009	0.16163	0.16289	0.15982	0.08527	0.04557	0.04094	0.03840	0.08888	0.10981	-			
143	*G. hardyi*	0.17396	0.18521	0.17387	0.16200	0.08006	0.07704	0.07967	0.07608	0.09095	0.10064	0.08629	-		
145	*G. jardini*	0.16672	0.18061	0.17561	0.16665	0.03672	0.08023	0.08199	0.07559	0.08683	0.11056	0.07977	0.06972	-	
146	*G. nanum*	0.16798	0.16790	0.15938	0.15807	0.07670	0.04224	0.03925	0.04031	0.08698	0.09296	0.04259	0.06808	0.07081	-
147	*G. passerinum*	0.18893	0.18184	0.17871	0.18368	0.14878	0.14916	0.14990	0.15036	0.15259	0.16083	0.14226	0.15420	0.13816	0.14770
152	*G. peruanum*	0.17096	0.17824	0.17368	0.16497	0.07434	0.03229	0.03138	0.02796	0.08965	0.10566	0.04369	0.06898	0.07060	0.04094
153	*G. tephronotum*	0.15352	0.16426	0.16144	0.15544	0.12434	0.11275	0.11552	0.11385	0.11561	0.12278	0.10954	0.11566	0.11826	0.10850
154	*Bubo zeylonensis*	0.12251	0.10201	0.09238	0.11591	0.18437	0.18583	0.18749	0.18922	0.18368	0.19680	0.18364	0.18761	0.18649	0.18369
155	*Ninox boobook*	0.15483	0.15253	0.15130	0.16155	0.17395	0.15993	0.16045	0.15897	0.16253	0.18004	0.14780	0.17390	0.16431	0.15925
156	*N. scutulata*	0.15080	0.15843	0.15730	0.15403	0.16046	0.16312	0.16380	0.16101	0.15387	0.17530	0.15442	0.16091	0.15531	0.16725
157	*Nyctea scandiaca*	0.09007	0.12601	0.12197	0.08124	0.16747	0.17201	0.17267	0.17211	0.18284	0.18552	0.16513	0.17278	0.16302	0.16541
160	*Otus albogularis*	0.14439	0.14932	0.14639	0.13802	0.17680	0.17467	0.17311	0.17351	0.18432	0.18001	0.16217	0.17678	0.18640	0.16637
161	*O. asio*	0.13014	0.13072	0.12598	0.12882	0.16974	0.16733	0.16325	0.16287	0.16753	0.17629	0.14296	0.17057	0.17243	0.15554
165	*O. atricapillus*	0.15025	0.15430	0.13860	0.13012	0.16660	0.16815	0.16179	0.15914	0.18006	0.18703	0.17623	0.18157	0.17543	0.17592
166	*O. 'bakkamoena'*	0.14096	0.14743	0.14562	0.14646	0.19056	0.18595	0.18455	0.18605	0.19460	0.19935	0.17658	0.19534	0.19269	0.17589
169	*O. choliba*	0.14946	0.15542	0.15449	0.14794	0.18024	0.17952	0.17554	0.17849	0.18895	0.18736	0.17066	0.18357	0.18171	0.17475
170	*O. flammeolus*	0.16460	0.14722	0.14247	0.15771	0.18195	0.18259	0.18629	0.18483	0.19355	0.20449	0.18772	0.19212	0.18728	0.18301
171	*O. guatemalae*	0.13340	0.13052	0.12678	0.13305	0.16748	0.17182	0.17009	0.17293	0.16416	0.17703	0.16328	0.17560	0.17743	0.16987
172	*O. hoyi*	0.13770	0.12800	0.12673	0.14041	0.17223	0.16666	0.16477	0.16432	0.16374	0.17348	0.15315	0.17033	0.17363	0.15922
174	*O. lempiji*	0.15268	0.15436	0.15546	0.15348	0.19618	0.19617	0.19808	0.19960	0.19669	0.19216	0.18600	0.19576	0.20101	0.18683
176	*O. leucotis*	0.13046	0.12373	0.12501	0.12726	0.16280	0.15627	0.15811	0.16074	0.16364	0.17418	0.15927	0.16859	0.16167	0.15541
179	*O. longicornis*	0.15096	0.14333	0.14051	0.14601	0.18337	0.18371	0.18449	0.18383	0.16368	0.18428	0.17271	0.18154	0.17368	0.17214
180	*O. megalotis*	0.14080	0.14765	0.14305	0.14152	0.18990	0.18217	0.18173	0.18109	0.18749	0.18584	0.16904	0.18398	0.18010	0.16976
182	*O. petersoni*	0.15235	0.14867	0.14498	0.15147	0.18510	0.17938	0.18009	0.18056	0.17488	0.18849	0.16913	0.17771	0.17656	0.17628
183	*O. roboratus*	0.14072	0.13914	0.13387	0.13877	0.17101	0.16498	0.15974	0.15811	0.17141	0.17081	0.14909	0.17013	0.17526	0.15966
184	*O. sanctaecat.*	0.14236	0.13962	0.13341	0.14138	0.17256	0.17259	0.16752	0.16818	0.16912	0.18212	0.15732	0.17972	0.18173	0.16492
185	*O. scops*	0.14629	0.14153	0.13764	0.14440	0.18515	0.18041	0.18120	0.17941	0.17414	0.18185	0.17740	0.18518	0.17427	0.17356
187	*O. usta*	0.13387	0.13324	0.12899	0.13099	0.17648	0.17059	0.16877	0.16735	0.17659	0.18138	0.16032	0.17266	0.18206	0.16579
189	*Phodilus badius*	0.17796	0.17611	0.17343	0.16886	0.17945	0.19262	0.19660	0.19592	0.17964	0.18382	0.17779	0.17891	0.17966	0.17996
191	*Pulsatrix perspicill.*	0.13044	0.10699	0.09912	0.12219	0.17769	0.17375	0.17335	0.17615	0.17072	0.17861	0.17061	0.17388	0.17627	0.16695
194	*Strix aluco*	0.13235	0.12581	0.12346	0.13127	0.17687	0.17591	0.17669	0.18050	0.17541	0.18845	0.16756	0.18769	0.17645	0.17216
206	*S. butleri*	0.11986	0.12848	0.13255	0.11524	0.16784	0.17429	0.17182	0.17798	0.15087	0.18496	0.16543	0.17497	0.17904	0.16946
207	*S. nebulosa*	0.13420	0.13689	0.13732	0.12842	0.18709	0.18923	0.19183	0.18957	0.17299	0.18938	0.17639	0.18310	0.18046	0.17755
209	*S. rufipes*	0.13169	0.13083	0.12090	0.13142	0.16815	0.17035	0.16985	0.16722	0.17072	0.18280	0.16563	0.16350	0.16040	0.16700
211	*S. uralensis*	0.13493	0.13308	0.13329	0.13303	0.18411	0.17944	0.18019	0.18061	0.18242	0.18745	0.17284	0.18545	0.17697	0.17626
213	*S. woodfordii*	0.13387	0.11953	0.12069	0.13226	0.18448	0.18120	0.18606	0.18334	0.18286	0.18926	0.18523	0.18309	0.18068	0.17618
216	*Surnia ulula*	0.18962	0.18316	0.18106	0.18752	0.15990	0.15015	0.14735	0.14372	0.15053	0.15876	0.14302	0.13889	0.14419	0.14923
219	*Tyto alba*	0.19838	0.20933	0.21019	0.19117	0.20801	0.20909	0.20762	0.20678	0.19405	0.21285	0.19295	0.19536	0.20623	0.19172
222	*T. (a.) pratincola*	0.19686	0.20587	0.20750	0.19903	0.20523	0.21386	0.21356	0.21278	0.20080	0.22087	0.20393	0.20804	0.20079	0.19898

		147	152	153	154	155	156	157	160	161	165	166	169	170	171
147	*Glaucidium pass.*	-													
152	*G. peruanum*	0.14706	-												
153	*G. tephronotum*	0.10878	0.11095	-											
154	*Bubo zeylonensis*	0.19963	0.18663	0.17539	-										
155	*Ninox boobook*	0.18068	0.16308	0.15277	0.16738	-									
156	*N. scutulata*	0.17549	0.16194	0.15000	0.16952	0.08639	-								
157	*Nyctea scandiaca*	0.18538	0.17556	0.16564	0.13109	0.17328	0.16429	-							
160	*Otus albogularis*	0.19285	0.17781	0.16691	0.15008	0.15727	0.14727	0.14677	-						
161	*O. asio*	0.18007	0.16498	0.16022	0.13672	0.15082	0.15143	0.13189	0.10628	-					
165	*O. atricapillus*	0.19418	0.17859	0.15979	0.15819	0.17337	0.16797	0.16007	0.10025	0.08070	-				
166	*O. 'bakkamoena'*	0.18127	0.18696	0.16006	0.15894	0.15102	0.15015	0.15872	0.14512	0.15211	0.16160	-			
169	*O. choliba*	0.19901	0.18270	0.18218	0.16226	0.17256	0.15866	0.14092	0.09807	0.11078	0.11179	0.16549	-		
170	*O. flammeolus*	0.21247	0.18745	0.18808	0.14704	0.16473	0.16124	0.15535	0.13712	0.14786	0.14453	0.15820	0.15858	-	
171	*O. guatemalae*	0.18965	0.17314	0.16833	0.15031	0.16029	0.15656	0.14778	0.10767	0.08665	0.09103	0.15479	0.12006	0.13957	-
172	*O. hoy*	0.17614	0.16746	0.15745	0.14215	0.15236	0.15112	0.14566	0.11105	0.08684	0.10141	0.14536	0.11833	0.14332	0.08589
174	*O. kempp*	0.19018	0.19621	0.18138	0.16620	0.16175	0.16205	0.16296	0.14616	0.15316	0.16752	0.06099	0.16564	0.15942	0.15924
176	*O. leucotis*	0.17506	0.15597	0.15396	0.14196	0.15199	0.15252	0.13489	0.14668	0.13830	0.13129	0.14744	0.14855	0.14282	0.12624
179	*O. longicornis*	0.18071	0.18016	0.15620	0.16029	0.16064	0.14916	0.16017	0.14989	0.14315	0.16038	0.11497	0.15600	0.16579	0.13906
180	*O. megalotis*	0.18354	0.18063	0.16893	0.15593	0.15433	0.15995	0.15297	0.13827	0.14197	0.16814	0.09094	0.15865	0.16309	0.15193
182	*O. petersoni*	0.19155	0.17638	0.17055	0.15764	0.16294	0.15760	0.15583	0.12458	0.10930	0.10801	0.15143	0.11553	0.14647	0.10929
183	*O. roboratus*	0.19096	0.16787	0.15287	0.14737	0.15799	0.15178	0.14899	0.10538	0.08597	0.06500	0.14254	0.11222	0.15142	0.08104
184	*O. sanctaecat.*	0.19503	0.17310	0.16018	0.14689	0.15623	0.15034	0.15752	0.10150	0.08303	0.08004	0.16049	0.11208	0.14511	0.08320
185	*O. scops*	0.18299	0.17399	0.17144	0.16377	0.15859	0.15594	0.15811	0.14760	0.15004	0.16546	0.10311	0.15667	0.17579	0.13706
187	*O. usta*	0.19475	0.17009	0.16608	0.13774	0.15587	0.14760	0.14110	0.09683	0.07668	0.04360	0.14743	0.11378	0.14314	0.08534
189	*Phodilus badius*	0.19143	0.18667	0.17715	0.19770	0.18407	0.18651	0.17758	0.18945	0.16479	0.19166	0.18121	0.19893	0.20143	0.17066
191	*Pulsatrix perspicil.*	0.19076	0.17490	0.16879	0.11617	0.15765	0.15515	0.12902	0.12490	0.12789	0.12097	0.14451	0.13204	0.12960	0.12469
194	*Strix aluco*	0.19184	0.18070	0.16626	0.13584	0.16218	0.15488	0.13393	0.14517	0.14303	0.16013	0.14687	0.15274	0.15324	0.14318
206	*S. butleri*	0.18802	0.17332	0.16152	0.13735	0.17762	0.16142	0.12921	0.13161	0.12014	0.12503	0.13851	0.14039	0.16347	0.12263
207	*S. nebulosa*	0.19120	0.18416	0.16533	0.15160	0.16537	0.16143	0.14577	0.15342	0.14825	0.16208	0.15784	0.15677	0.16060	0.14231
209	*S. rufipes*	0.18883	0.17120	0.15702	0.12936	0.14821	0.13799	0.12867	0.13811	0.13026	0.14439	0.14447	0.13978	0.14354	0.12909
211	*S. uralensis*	0.19740	0.17823	0.16806	0.14309	0.16472	0.16268	0.14078	0.13886	0.14371	0.15411	0.16204	0.15984	0.15001	0.15074
213	*S. woodfordi*	0.20087	0.18151	0.16795	0.13780	0.16295	0.14937	0.14308	0.13974	0.13801	0.13417	0.14845	0.14922	0.14158	0.13891
216	*Surnia ulula*	0.15692	0.14325	0.13434	0.18469	0.17041	0.16429	0.18255	0.18221	0.18416	0.18479	0.17934	0.19760	0.20032	0.18834
219	*Tyto alba*	0.21426	0.20058	0.20548	0.21831	0.20918	0.21189	0.20016	0.19709	0.19569	0.19755	0.21203	0.21008	0.21311	0.20314
222	*T. (a.) pratincola*	0.22072	0.20957	0.20823	0.21323	0.20393	0.20846	0.19460	0.21590	0.18913	0.20039	0.21138	0.21174	0.21706	0.20848

		172	174	176	179	180	182	183	184	185	187	189	191	194	206
172	*Otus hoyi*	-													
174	*O. lempiji*	0.14871	-												
176	*O. leucotis*	0.12421	0.15297	-											
179	*O. longicorni*	0.14169	0.11496	0.14394	-										
180	*O. megalotis*	0.13504	0.09299	0.13704	0.10679	-									
182	*O. petersoni*	0.09289	0.16341	0.14220	0.15459	0.15501	-								
183	*O. roboratus*	0.08025	0.15799	0.12858	0.14129	0.15022	0.08903	-							
184	*O. sanctaecat.*	0.08392	0.16760	0.12489	0.15296	0.16011	0.10351	0.07614	-						
185	*O. scops*	0.14031	0.11192	0.14293	0.07636	0.10759	0.15411	0.14365	0.15538	-					
187	*O. usta*	0.07771	0.15561	0.13141	0.14506	0.14708	0.09201	0.05704	0.07459	0.14323	-				
189	*Phodilus badius*	0.17968	0.18044	0.17174	0.16863	0.17894	0.19049	0.17413	0.17422	0.17401	0.17530	-			
191	*Pulsatrix perspicill.*	0.11929	0.15385	0.12399	0.13703	0.14629	0.13116	0.12445	0.12804	0.13719	0.11595	0.17333	-		
194	*Strix aluco*	0.14982	0.14350	0.13207	0.14741	0.13748	0.15672	0.13972	0.15042	0.14747	0.13716	0.18847	0.12096	-	
206	*S. butleri*	0.12649	0.14849	0.12991	0.14872	0.15565	0.14439	0.12659	0.13041	0.16234	0.13233	0.18072	0.13440	0.08966	-
207	*S. nebulosa*	0.14817	0.15509	0.13632	0.15301	0.15581	0.16434	0.15053	0.14362	0.14905	0.13354	0.19066	0.12988	0.09139	0.08655
209	*S. rufipes*	0.13179	0.15235	0.12222	0.14698	0.13779	0.14560	0.12433	0.13532	0.14511	0.12343	0.17778	0.11324	0.11627	0.10724
211	*S. uralensis*	0.13880	0.15940	0.13357	0.15097	0.15091	0.14773	0.13661	0.14442	0.15793	0.12992	0.18737	0.13249	0.08152	0.10368
213	*S. woodfordii*	0.13600	0.15901	0.13987	0.14816	0.15025	0.14973	0.13476	0.14391	0.15481	0.13915	0.19016	0.12382	0.09167	0.08488
216	*Surnia ulula*	0.17314	0.19243	0.17122	0.19505	0.18489	0.17779	0.17389	0.18556	0.18961	0.17635	0.21015	0.18740	0.18265	0.17145
219	*Tyto alba*	0.19301	0.21986	0.20629	0.19511	0.21043	0.21107	0.19120	0.20284	0.20726	0.19837	0.17490	0.20549	0.23020	0.22080
222	*T. (a.) pratincola*	0.19943	0.21808	0.20319	0.19932	0.21712	0.21006	0.19230	0.20330	0.20846	0.21069	0.18725	0.19888	0.22749	0.22157

		207	209	211	213	216	219	222
207	*S. nebulosa*	-						
209	*S. rufipes*	0.11222	-					
211	*S. uralensis*	0.09247	0.11715	-				
213	*S. woodfordii*	0.10795	0.11074	0.10480	-			
216	*Surnia ulula*	0.17887	0.16384	0.18700	0.18141	-		
219	*Tyto alba*	0.20379	0.20192	0.21127	0.21338	0.22988	-	
222	*T. (a.) pratincola*	0.20451	0.20569	0.20803	0.20525	0.22212	0.08080	-

Table 1. Pairwise nucleotide substitutions between owl taxa. Given are p-distances (in %) which correlate with divergence time (2% roughly equals one million years: Shields & Wilson 1987).

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