

Chapter 2

A Review of the Systematics of Neotropical Owls (Strigiformes)

Paula L. Enríquez, Knut Eisermann, Heimo Mikkola,
and José Carlos Motta-Junior

Abstract Although birds belong to the best known animal groups, their systematics has not been fully resolved yet. Among the approximately 80 Neotropical owl species, there are monotypic genera such as *Lophostrix*, complex and diverse genera such as *Megascops* or *Glaucidium*, as well as widespread and variable taxa such as *Bubo virginianus* and *Tyto furcata*. Based on a literature review, we provide here an overview of the current taxonomy and nomenclature of Neotropical owls, and indicate knowledge gaps as focus points for future research.

Keywords Owl evolution • Strigiformes classification • Molecular studies • Phylogeny

P.L. Enríquez (✉)

Departamento Conservación de la Biodiversidad, El Colegio de la Frontera Sur,
P. O. Box 63, San Cristóbal de Las Casas 29290, Chiapas, México
e-mail: penrique@ecosur.mx

K. Eisermann

PROEVAL RAXMU Bird Monitoring Program, Cobán, Alta Verapaz, Guatemala

H. Mikkola

Department of Biology, University of Eastern Finland, FIN -70211, Kuopio, Finland

J.C. Motta-Junior

Laboratório de Ecologia de Aves – LABECOAVES Departamento de Ecologia, Instituto de
Biociências da Universidade de São Paulo, 05508-090 São Paulo, SP, Brazil



Birds (Aves) belong to the best studied animal groups, but much remains to be learned about the number of species, taxonomy and systematic position (Barrowclough et al. 2016). Systematics should reflect evolutionary history, but the use of different taxonomic methods has resulted in contradictory phylogenetic positioning (Navarro 1988). Birds in the order Strigiformes (owls) present specific characteristics (i.e. soft plumage, predatory adaptations, binocular vision and nocturnal habits) defining them as a particular group. The phylogenetic position of owls in relation to other birds is controversial (Cracraft 1981; Sibley and Ahlquist 1990; Ericson et al. 2006; Livezey and Zusi 2007; Prum et al. 2015). This chapter provides an overview of the current knowledge on the taxonomy and systematics of Neotropical owls.

The oldest known bird fossil dates back some 225 million years (Pacheco et al. 2011), but the oldest owl-like fossils are from the Paleocene (57–65 million years ago), and more fossil records are known from the Eocene, 34–57 million years ago

(Brodkorb 1971; Mayr 2010). Eocene was obviously the time of the appearance and diversification of many modern groups of organisms including mammals and birds, although the real strigid owls were recorded only 23–24 million years ago (Mikkola 2014). In this time, 80% of the modern bird orders developed and diversified (Welty 1982). None of the real owl fossils recorded so far has provided details on which other bird groups could share the common ancestor with the owls (Grossman and Hamlet 1988). Most of the owl fossils have been found in North America and Europe, and very few in the Neotropical region (Mayr 2010). There are fossil records of pygmy owls in the Americas from Pleistocene deposits (between 2 million and 13,000 years ago) in Mexico and Brazil (Mikkola 2014).

The order Strigiformes (owls) is subdivided into two families: barn owls (Tytonidae) and typical owls (Strigidae). There are several morphological differences separating these families, including the structure of sternum and shape of ears, relative length of toes and serrated or smooth cutting edges to the claw of the middle toe (Ridgway 1914; Sibley and Ahlquist 1972; König et al. 2008). Both families are traditionally divided into two subfamilies (Peters 1940): the Tytonidae is subdivided into the Tytoninae and the Pholinae which together have approximately 20 species (Table 2.1). The genera *Tyto* and *Pholidus* are supported by modern molecular sequence data, and they have diverged from a common ancestor more than 10 million years ago (Wink et al. 2008). The family Strigidae has been divided into the subfamilies Buboninae and Striginae with together more than 200 species (Table 2.1). Some northern species of the latter subfamily have developed bilateral asymmetry of the external ears which help these owls to catch prey hiding underneath of the snow (Norberg 1987). Norberg (1978) indicated that the outer ears are symmetric in the majority of Strigidae genera and that an asymmetrical arrangement is known to involve parts of the skull in four species: Ural owl, *Strix uralensis*; great grey owl, *Strix nebulosa*; Boreal owl, *Aegolius funereus*; and northern saw-whet owl, *Aegolius acadicus*. Research on the skulls of all owl species could prove asymmetry in other species as well, although the majority of owls may have no asymmetry in the hard parts of the head. Barn owls (Tytonidae) of the genera *Tyto* and *Pholidus* show a bilateral asymmetry of the external ears, thus making the skull parts unreliable factors in separating the Strigidae and the Tytonidae (Mikkola 1983). Based on other osteological characters, it has been proposed to divide *Strigidae* family into three subfamilies: Surniinae, Striginae and Asioninae (Ford 1967; Marks et al. 1999). Based on molecular analyses, Wink et al. (2008) recommended a new classification of subfamilies: Surniinae, Striginae and Ninoxinae, in which the subfamily Asioninae should be seen as part of the Striginae to avoid a paraphyletic assemblage.

Sibley and Ahlquist (1972) established a historic revision of owl classification marking the most important similarities and differences between the two families. They also mentioned family similarities between Strigiformes and Caprimulgiformes (nightjars and relatives, according to Fürbringer 1888, Shufeldt 1904), Falconiformes (hawks and eagles, according to Seebohm 1890, Cracraft 1981) and also Psittaciformes (parrots and parakeets, according to Gadow 1892). Ericson et al. (2006) used a large dataset of five nuclear genes showing that owls are members of

Table 2.1 Number of species of barn owls (Tytonidae) and typical owls (Strigidae) in the world according to different authors

Author(s) Family	Peters (1940)	Burton (1973)	Sibley and Monroe (1990)	Marks et al. (1999)	König et al. (1999)	König et al. (2008)	Dickinson and Rensen (2013)	Mikkola (2014)	Clements et al. (2016)	Gill and Donsker (2016)
<i>Tytonidae</i>	11	10	17	16	11	26	19	27	18	19
<i>Strigidae</i>	133	120	159	189	201	224	191	241	207	223
Total	144	130	176	205	212	250	210	268	225	242

the Coronaves in which owls are in a same clade with diurnal raptors (Accipitridae), vultures (Cathartidae), trogons (Trogonidae) and others, but excluding falcons (Falconidae), which cluster as a sister group to parrots and songbirds. Although there are noticeable similarities between owls and nightjars, and morphological and anatomical similarities between owls and hawks (Livezey and Zusi 2007), other authors have stated that these close family relationships are rather based on convergence since they are not supported by sequence data (Gibb et al. 2007; Wink et al. 2008; Pratt et al. 2009). More recently, Pacheco et al. (2011) have found closer relationship between owls and Psittaciformes, but Prum et al. (2015) established Strigiformes as sister group to the coraciimorph clade including Coliiformes, Leptosomiformes, Trogoniformes, Bucerotiformes, Coraciiformes and Piciformes. Our understanding of the phylogeny of birds keeps developing with the improvement of methodologies of molecular analyses.

The classification of Strigiformes has changed considerably in the last decades, especially in complex groups with highly variable plumages and vocalizations, such as the *Otus* complex (Marshall 1967), including the American species recently separated as genus *Megascops* (Banks et al. 2003). Similar changes have occurred in the genus *Glaucidium* (Howell and Robbins 1995; Robbins and Stiles 1999). Our current knowledge of both genera is based on taxonomic revisions in the last 70 years (Moore and Peters 1939; Buchanan 1964; Howell and Robbins 1995; Wink et al. 2008; Eisermann and Howell 2011). Molecular studies have increased the number of owl species, but the number of accepted species differs considerably between authors (Table 2.1). Gill and Donsker (2016) listed 53 subspecies in the Tytonidae and 432 subspecies in the Strigidae.

In a recent compilation, Mikkola (2014) listed 268 owl species including newly proposed species. Since that time, some new owl species have been proposed (e.g. Kirwan et al. 2015), so the world total could now be over 270 different living owl species.

The scientific names (biological nomenclature) of Neotropical Strigiformes have not been standardized. Remsen et al. (2016) listed 44 owl species in South America, and American Ornithologists' Union (AOU 1998 and supplements) listed 44 owl species for Mexico and Central America. In this chapter, we use the nomenclature according to König et al. (2008) but also include in the discussion the American Ornithologists' Union (AOU 1998) and supplements (most recent supplement Chesser et al. 2016). It follows an account of taxonomic changes proposed for the Neotropics in the recent literature:

American Barn Owl (*Tyto furcata*): Previously this owl species was considered a subspecies of Common Barn Owl (*Tyto alba*) of the Old World. Recent molecular studies support the separation of the populations in the Americas, for a high degree of genetic variation which Wink et al. (2008) recognize four subspecies and Mikkola (2014) six. This large number of subspecies is an indication that several of them could be distinct species. AOU (1998 and supplements) and Remsen et al. (2016) have not accepted the separation of *Tyto furcata* from *Tyto alba* and do not recognize Curaçao barn owl (*Tyto bargei*), Lesser Antilles barn owl (*Tyto insularis*) and Galápagos barn owl (*Tyto punctatissima*). Wink et al. (2008) anticipated also the split of *Tyto tuidara* and *Tyto pratincola* from *Tyto furcata*, and Mikkola (2014)

mentioned that *Tyto contempta* could also be a new species. However, recent DNA molecular studies suggest three main clades from *Tyto alba* complex: *Tyto alba* (Africa, Europe), *Tyto furcata* (New World; including *bargei*) and *Tyto javanica* (Australasia; including *delicatula* and *stertens*) (Aliabadian et al. 2016).

Flammulated Owl (*Psiloscoptes flammeolus*): This species was formerly classified as *Otus flammeolus* but differs according to Wink and Heidrich (1999), Penhallurick (2002), König et al. (2008) and Wink et al. (2008) in vocalization and genetics so much that it is now separated into a monotypic genus *Psiloscoptes* (as originally classified by Coues 1899). Nucleotide sequences of the mitochondrial cytochrome b gene study showed that flammulated owl is more directly related to *Megascops* species in the New World rather than being a sister group to *Otus* owls in the Old World (Proudfoot et al. 2007). The closest living relative to the flammulated owl among the Neotropical screech owls appears to be the Puerto Rican endemic *M. nudipes* (Dantas et al. 2016).

The New World screech owl genus *Megascops*, recently split from *Otus* based on vocal and molecular evidence, currently includes 22 species (Dantas et al. 2016) divided into some 63 taxa according to Marks et al. (1999).

Complex of Pacific Screech Owl (*Megascops cooperi*): König et al. (2008) recognize two species: Oaxaca screech owl (*Megascops lambi*) endemic to Oaxaca, Mexico and Pacific screech owl (*M. cooperi*) on the Pacific slope from southern Mexico to Costa Rica. It is not known if this species hybridizes with Oaxaca screech owl in areas where the two overlap (Mikkola 2014). Unfortunately, a genetic study only included samples of the Pacific screech owl (Dantas et al. 2016). AOU (1998 and supplements) does not include *M. lambi*, and Dickinson and Remsen (2013) consider it as subspecies of *M. cooperi*.

Complex of Northern *Megascops watsonii* and Southern Tawny-Bellied Screech Owl (*M. w. usta*): König et al. (2008) separated two species: northern Tawny-bellied screech owl (*Megascops watsonii*) in northern parts of South America as well as in northern Amazonian part of Brazil and southern Tawny-bellied screech owl (*M. usta*) in Amazonian Colombia, Ecuador, Peru and Brazil south to lowland forests in northern Bolivia and Brazilian Mato Grosso. The Brazilian Committee for the Ornithological Records (Piacentini et al. 2015) accepted the status of these two species, but Remsen et al. (2016) recognize only one species as did a recent molecular study, probably due to the lack of broader geographic and population level sampling (Dantas et al. 2016). These last authors considered both *M. watsonii* and *M. usta* as paraphyletic, highlighting the urgent need to a taxonomic review of the *M. watsonii-usta* complex.

Complex of Guatemalan Screech Owl (*Megascops guatemalae*) and Vermiculated Screech Owl (*M. vermiculatus*): König et al. (2008) recognized five species based on morphological and vocal differences:

- Guatemalan screech owl (*Megascops guatemalae*) from Mexico to northern Costa Rica
- Vermiculated screech owl (*M. vermiculatus*) from Costa Rica to north-western Colombia and northern Venezuela
- Roraima screech owl (*M. roraimae*) from northern Colombia and Venezuela to Roraima and Duida mountains (northern Brazil and Guyana)

- Rio Napo screech owl (*M. napensis*) from the eastern slopes of the Andes in eastern Colombia to northern Bolivia
- Tumbes screech owl (*M. pacificus*) from the lowland areas in south-western Ecuador and north-western Peru.

Marks et al. (1999), but not Banks et al. (2003), accepted the split between *M. guatemalae* and *M. vermiculatus*, and Hilty (2003) mentioned *M. roraimae* as a separated species. Piacentini et al. (2015) listed only *M. guatemalae* until more complete analysis is provided. Only one species, *M. guatemalae*, was recognized for South America by Remsen et al. (2012) and for Mexico and Central America by AOU (1998 and supplements). The recent molecular data support not only the split between *M. guatemalae* and *M. vermiculatus* but also indicate that three other splits (*M. roraimae*, *napensis* and *pacificus*) are probably best treated as distinct species (Dantas et al. 2016). The southern edge of distribution of *M. guatemalae* is controversial. König et al. (2008) and Mikkola (2014) indicate that this owl ranges into northern Costa Rica, which may be erroneous. According to Marks et al. (1999), *M. guatemalae* and *M. vermiculatus* are allopatric, and the limit between the ranges of both species is located in Nicaragua.

Complex of Great Horned Owl (*Bubo virginianus*): König et al. (2008) separated Magellanic horned owl (*Bubo magellanicus*) in the Andes of Peru, Bolivia, Chile and Argentina and the southern cone of South America, but Remsen et al. (2016) considered these populations part of *B. virginianus*. DNA sequence difference between *B. magellanicus* and *B. virginianus* is 1.6%, maybe justifying their separation as two distinct species, as they also differ clearly in size and colour (König et al. 1996).

Genus *Pulsatrix*: König et al. (2008) list four *Pulsatrix* species: Spectacled owl (*P. perspicillata*), Short-browed owl (*P. pulsatrix*), Band-bellied owl (*P. melanota*), and Tawny-browed owl (*P. koeniswaldiana*). Bencke (2001), Ramírez-Llorens and Bellocq (2007) and Remsen et al. (2016) consider *P. pulsatrix* in eastern Brazil from Bahia south to northeast Argentina too premature to separate as full species as it is rather seen only as the subspecies of the spectacled owl. A study on genetic and voice differences would be needed to confirm the species status of the short-browed owl.

Genus *Ciccaba*: Norberg (1977), Sibley and Ahlquist (1990), Sibley and Monroe (1990), Howell and Webb (1995), Wink and Heidrich (1999), Norberg (2002), Weick (2006), Wink et al. (2008) and König et al. (2008) have incorporated all ex-*Ciccaba* species into the genus *Strix* based on external ear asymmetry and on molecular analysis. Some authors, however, maintain the genus *Ciccaba* (Dickinson and Remsen 2013; Clements et al. 2016; Remsen et al. 2016), and the taxonomic committee of the American Ornithologists' Union has been considering the change but did not approve it (Banks et al. 2003).

Complex of Mottled Owl (*Strix virgata*): König et al. (2008) recognized two species, Mexican wood owl (*Strix squamulata*) from México, south to north-western Colombia and western Ecuador, and mottled owl (*S. virgata*) in most parts of northern and central South America east of the Andes. Only one species, *Ciccaba virgata*, has been accepted by Remsen et al. (2016) for South America and by AOU (1998 and supplements) for Mexico and Central America.

Fulvous Owl (*Strix fulvescens*): This owl is morphologically similar to the barred owl (*Strix varia*) of North America and Northern Mexico and was until recently recognized only as subspecies of barred owl (J.T. Marshall, pers.com; Enríquez et al. 1993). Both species form possibly a superspecies (AOU 1998). The voice of fulvous owl resembles that of spotted owl (*Strix occidentalis*); it has been speculated that fulvous owl may form a superspecies together with spotted and barred owls which are known to hybridize in North America (Hamer et al. 1994). Recent records from Mexico confirm the distribution of fulvous owl west of the Isthmus of Tehuantepec in Oaxaca suggesting sympatric distribution with the barred owl in that area (Gómez de Silva 2010; Ramírez-Julián et al. 2011). Superspecies speculation requires comparative studies, molecular and biological (Mikkola 2014).

Complex of Mountain Pygmy Owl (*Glaucidium gnoma*): König et al. (2008) separated three different Neotropical species out of this complex, Baja pygmy owl (*Glaucidium hoskinsii*; in Baja California peninsula), Mountain pygmy owl (*G. gnoma*; in Mexico west of the Isthmus of Tehuantepec) and Guatemalan pygmy owl (*G. cobanense*; in México east of the Isthmus of Tehuantepec, Guatemala and Honduras). Other authors have classified all or some of the four taxa as subspecies of *G. gnoma* (Weick 2006; Dickinson and Remsen 2013; Clements et al. 2016). A recent comparative study on vocalizations of *G. cobanense* and *G. gnoma* (Eisermann and Howell 2011; Howell and Eisermann 2011) found differences supporting the species status of *G. cobanense*, as originally proposed (Sharpe 1875; Griscom 1931). Molecular studies are required in order to confirm the new taxonomic status of pygmy owls in northern Central America (Heidrich et al. 1995). AOU (1998 and supplements) recognizes only one species *Glaucidium gnoma*.

Complex of Least Pygmy Owl (*Glaucidium minutissimum*): König et al. (2008) recognized five species:

- Tamaulipas pygmy owl (*Glaucidium sanchezi*) in the mountains of north-eastern Mexico
- Colima pygmy owl (*G. palmarum*) along the Pacific coast of Mexico
- Central American pygmy owl (*G. griseiceps*) from south-eastern Mexico to northern and western Colombia and north-western Ecuador
- Sick's pygmy owl (*G. sicki*) in eastern Brazil south to eastern Paraguay and eastern Peru, possibly extending to north-eastern Argentina
- Pernambuco pygmy owl (*G. minutissimum*) from the state of Pernambuco in north-eastern Brazil

Earlier the least pygmy owl complex was considered to be polymorphic with eight different subspecies (Peters 1940). Buchanan (1964) classified five subspecies in Mexico based on morphological differences. Later Howell and Robbins (1995) proposed distribution limits of four species: *G. palmarum*, which included three subspecies *palmarum*, *oberholseri* and *griscomi*, occurring in western Mexico; *G. sanchezi*, with distribution in north-eastern Mexico; *G. griseiceps*, occurring from south-eastern Mexico through Central America to the Pacific coast of South America (including three subspecies: *griseiceps*, *rarum* and *occultum*); and *G. minutissimum*, with distribution in south-eastern Brazil and Paraguay. Piacentini et al. (2015)

and Remsen et al. (2016) consider *G. sicki* a synonym of *G. minutissimum*. Populations, which König et al. (2008) named as Pernambuco pygmy owl (*Glaucidium minutissimum*), were referred to as *G. mooreorum* by Remsen et al. (2016). Recently, Grantsau (2010) proposed *Glaucidium pumila* as a pygmy owl species living in south-eastern and south-western Brazil, but other authors have not recognized this species (Sigrist 2006; König et al. 2008; Mikkola 2014; Piacentini et al. 2015; Remsen et al. 2016).

Complex of Ferruginous Pygmy Owl (*Glaucidium brasilianum*): König et al. (2008) separated three species, Ridgway's pygmy owl (*Glaucidium ridgwayi*) from southern Arizona and Texas, USA, throughout Mexico and Central America and south- to north-western Colombia; ferruginous pygmy owl (*G. brasilianum*) in South America east of the Andes; and Chaco pygmy owl (*G. tucumanum*) from Bolivia, Paraguay and northern Argentina, possibly to south-western Brazil. Other authors accept also *G. ridgwayi* (Heidrich et al. 1995; Wink and Heidrich 1999; Weick 2006; Proudfoot et al. 2006; Wink et al. 2008). American Ornithologists' Union (AOU 1998 and supplements) and Remsen et al. (2012) recognize only *G. brasilianum*.

Burrowing Owl (*Athene cunicularia*): This owl was once separated from *Athene* into its own monotypic genus *Speotyto* (Clark 1997), but based on recent anatomic, molecular, behavioural, vocal and osteological data, it was reclassified back into the genus *Athene* (AOU 1998; König et al. 1999, 2008).

Unspotted Saw-whet Owl (*Aegolius ridgwayi*): Briggs (1954) and Mayr and Short (1970) consider this as a subspecies of northern saw-whet owl (*A. acadicus*). AOU (1998) mentioned that both taxa form a superspecies. Ecology and biology of unspotted saw-whet owl are little known explaining the lack of feather or blood samples, so the molecular status of *A. ridgwayi* remains unknown (Wink and Heidrich 1999; Wink et al. 2008) although a detailed study of its vocalizations is now available (Eisermann 2013).

Striped Owl (*Asio clamator*): This species has been placed previously in the genera *Rhinoptynx* and *Pseudoscops* (Olson 1995). It has been placed in the genus *Asio* together with long-eared owl (*Asio otus*), marsh owl (*A. capensis*) and short-eared owl (*A. flammeus*) based on molecular studies (Wink et al. 2008; König et al. 2008). AOU (1998 and supplements) kept this species in the genus *Pseudoscops*, and Remsen et al. (2016) listed it in the genus *Asio*.

Owls are much more difficult to find and study than many other birds, especially diurnal birds, explaining why they are relatively little known, with even new species still discovered. During the last 40 years, several new owl species have been found in the Neotropical region including a new genus *Xenoglaux* (O'Neill and Graves 1977). A list of these newly found or reclassified (based on molecular and/or vocal differences) Neotropical owl species in chronological order starting from 1977 follows:

- Long-whiskered owl (*Xenoglaux loweryi*) described by O'Neill and Graves (1977)
- Cloud-forest screech owl (*Megascops marshalli*) by Weske and Terborgh (1981)
- Tumbes screech owl (*Megascops pacificus*) and Koepcke's screech owl (*M. koepckeae*) by Hekstra (1982)

- Cinnamon screech owl (*Megascops petersoni*) by Fitzpatrick and O'Neill (1986)
- Montane forest screech owl (*Megascops hoyi*) by König and Stranek (1989)
- Amazonian pygmy owl (*Glaucidium hardyi*) by Vielliard (1989)
- Yungas pygmy owl (*Glaucidium bolivianum*), Peruvian pygmy owl (*G. peruanum*) and Chaco pygmy owl (*G. tucumanum*) by König (1991)
- Subtropical pygmy owl (*G. parkeri*) by Robbins and Howell (1995)
- Cloud-forest pygmy owl (*G. nubicola*) by Robbins and Stiles (1999)
- Pernambuco pygmy owl (*Glaucidium mooreorum*) by Silva et al. (2002)
- Sick's pygmy owl (*Glaucidium sicki*) by König and Weick (2005)

New description of the Koepcke's screech owl (*Megascops koepckeae*) and its subspecies *M. k. hockingi* was made by Fjeldså et al. (2012). Recent molecular studies have now reconfirmed the independent species status of *M. koepckeae* (Dantas et al. 2016). In 2007, a new species of *Megascops* was located in Minca Village, Sierra Nevada de Santa Marta mountain range in northern Colombia, but this species is still waiting to be officially described (König et al. 2008; Chaparro-Herrera et al. 2015). *Megascops vermiculatus pallidus* from northern Venezuela and the Sierra Perija of northern Colombia may deserve species status based on distinct vocalizations (N. K. Krabbe, unpub. data, see Dantas et al. 2016).

Systematics and taxonomy of the Neotropical owl species are still developing. New samples of feathers, tissue and blood, voice recordings and new photographs are extending our knowledge and understanding on the evolution, taxonomy and molecular phylogeny of these birds. "The last word on owl taxonomy is yet to be spoken!" as so well concluded König et al. (2008).

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