Late Pleistocene owls (Aves, Strigiformes) from Ecuador, with the description of a new species

Gastón E. Lo Coco1,2 · Federico L. Agnolín1,2,4 · José Luis Román Carrión3

Received: 20 October 2019 / Revised: 21 December 2019 / Accepted: 3 February 2020 / Published online: 5 March 2020
© Deutsche Ornithologen-Gesellschaft e.V. 2020

Abstract
The fossil record of owls of the families Strigidae and Tytonidae in South America is poor. The aim of the present contribution is to report for the first time fossil Strigiformes from Riobamba Canton, at Chimborazo province, in Ecuador. The specimens come from a large owl burrow from Late Pleistocene beds of the Cangagua Formation. We report the finding of fossil record of *Athene cunicularia* and *Tyto aff. T. furcata* and the first fossil record of *Glaucidium* from Ecuador. Further, a giant species of the genus *Asio* is described. The specimen constitutes the largest known asionine owl, being approximately of the size of a big female of *Bubo virginianus*. Based on prey content at the fossil burrow, it is possible that the new *Asio* species predated on the other owls. If this inference is correct, it may represent the first evidence indicating intra-ordinal predation in the fossil record.

Keywords  Strigidae · Tytonidae · Glaucidium · Asio · Late Pleistocene · Ecuador

Introduction
The fossil reports of owls of the families Strigidae and Tytonidae in South America is extremely poor. The earliest reports come from the early Miocene of Patagonia, Argentina (Chiappe 1991; Tambussi and Noriega 1996) but remain undescribed. Remaining records are restricted to neospecies found in early-middle Pleistocene of Argentina (Cenizo 2006; Cenizo and De Los Reyes 2008) and Late Pleistocene beds of Argentina, Brazil, and Peru (Winge 1887; Ameghino 1891; Brodkorb 1971; Campbell 1979; Tonni 1983; Guérin et al. 1993; Cenizo et al. 2015).

From Ecuador, the fossil record of birds is still incomplete and most analyses are restricted to the abundant...
avifauna from the Late Pleistocene tar pits at La Carolina (Spillman 1942; Hoffstetter 1952; Campbell 1976), close to the Pacific coast.

**Study area**

The fossil site is located in the Andes, at the south of Riobamba Canton, at Chimborazo province, Ecuador (Fig. 1). Its ravines are part of the Chambo River basin and are known as Quebrada Chalán (01° 46′ 32.3″ S/78° 37′ 41.1″ W; Moreno Cárdenas and Román-Carrión 2017). Today, the area is encompassed within a seasonal shrub ecosystem at 2800 m above sea level (Josse et al. 2009), surrounded by field crops belonging to local populations.

The aim of the present contribution is to report for the first time fossil Strigiformes from the Ecuadorian Andes and to describe a new large owl of the genus *Asio* coming from Late Pleistocene beds.

**Materials and methods**

The fossils we described here were collected by Alejandro Mesías and José Luis Román-Carrión between the years 2009 and 2012, in a small site we interpreted as being a fossil owl burrow (Moreno Cárdenas and Román-Carrión 2017). The fossil assemblage of Quebrada Chalán comprises six specimens of different Strigiformes and several skeletal elements of birds and mammals, including shrews (genus *Cryptotis*, Moreno Cárdenas and Román-Carrión 2017), rabbits, and cricetid rodents. We interpreted these as being prey items of the owner of the owl burrow, including the small strigids and tytonids reported here.

Specimens come from Cangagua Formation loess beds, mainly composed by hard volcanic ashes of eolic origin, assigned to the Late Pleistocene (Sauer 1950; Fig. 1), and based on faunal composition, belonging to the Lujanian South American Mammalian Age/Stage (Sánchez et al. 2013; Moreno Cárdenas and Román-Carrión 2017).

Anatomical nomenclature follows Baumel and Witmer (1993). Bone description follows Campbell (2013).
Institutional abbreviations

MACN Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; EPNV Colección de Paleontología, Escuela Politécnica Nacional, Quito, Ecuador.

Systematic paleontology

Strigiformes Wagler, 1830
Tytonidae Ridgway, 1914
Tyto Billberg, 1828
Tyto aff. T. furcata

Fig. 2 Tyto aff. T. furcata (EPNV, no. 6365; a–e) distal right tarsometatarsus in (a) cranial, (b) lateral, (c) caudal, (d) medial and (e) distal views. *Athene cunicularia* (EPNV, no. 6366; f–h) distal right tarsometatarsus in (f) cranial, (g) caudal and (h) distal views. *Glaucidium* sp. proximal right (EPNV, no. 6363; i–m) and proximal left (EPNV, no. 6364; n–r) tarsometatarsus in (i, n) cranial, (j, o) lateral, (k, p) caudal, (l, q) medial and (m, r) proximal views. Scale bars 1 cm
\textbf{Remarks} The specimen can be referred to \textit{T. furcata} on the basis of the following combination of characters: tarsometatarsus with mediolaterally narrow shaft, slightly divergent distal trochlea, reduced notch between trochlea II and III, narrow second distal trochlea, craniodorsal portion of outer rim of trochlea III flattened, massive and poorly elevated trochlea IV, ventral margin of trochlea IV strongly indented (Ford 1967; Mourer-Chauviré 1987; Suárez and Olson 2015). Further, the size of tarsometatarsus falls within the range of \textit{T. furcata} (Arredondo 1972a, b; Rich and Bohaska 1976; Suárez and Olson 2015). Because different species previously included within \textit{T. alba} (i.e., \textit{T. furcata}, \textit{T. alba}, \textit{T. javanica}) are not distinguishable on the basis of postcranial elements, we here identify the remains from Ecuador as \textit{Tyto} aff. \textit{T. furcata} based on gross morphological similarity and by geographical criterion, since in South America the only living and extinct species of the genus \textit{Tyto} is \textit{T. furcata} (reported as \textit{T. alba} by previous authors; König and Weick 2008; Nijman and Aliabadian 2013).

Oldest fossils of the species come from the early-middle Pleistocene of Buenos Aires province, Argentina (Cenizo and De Los Reyes 2008). By the Late Pleistocene the species is reported from Brazil, Peru and Ecuador (Winge 1887; Campbell 1976, 1979).

\textbf{Strigidae Leach, 1820}
\textbf{Athene Boie, 1822}
\textbf{Athene cunicularia} (Molina 1782)

\textbf{Referred specimen} Distal end of right tarsometatarsus (EPNV, no. 6363; Fig. 2a–e). The specimen shows weathering and breakage on its surface, being typical of stomach acid-derived abrasion of Strigiformes (Dodson and Wexlar 1979).

\textbf{Remarks} The specimens may be referred to the genus \textit{Glaucidium} on the basis of the following combination of characters: shaft, in cranial view, bowing markedly medial, cranial face distal and lateral to extensor groove shallowly excavated, with cranilateral corner of shaft forming an acute and prominent ridge, in caudal view deeply and broadly excavated proximally between hypotarsal crests, extensor groove forming a shallow sulcus in the cranilateral side of intercotylar prominence, strongly proximally extended and subrectangular-shaped crista lateralis hypotarsi, and relatively poorly developed crista medialis hypotarsi (Campbell and Bochenski 2013).

The complex taxonomy of the genus \textit{Glaucidium} in America resulted in the recognition of a large number of species, but authors are far from reaching a consensus about its taxonomic composition (Enríquez et al. 2015). Because of the large number of known species, that are indistinguishable osteologically, the specimens here reported are not identified to the specific level. Nevertheless, the size of specimens falls within the range of the widespread South American species \textit{G. nanum} (Campbell and Bochenski 2013), being much smaller than other strigids as \textit{Athene} and \textit{Tyto}.

The fossil record of \textit{Glaucidium} in South America is restricted to \textit{G. brasiliannum} from the Late Pleistocene of Brazil (Winge 1887). Present finding constitutes the first record for the genus in Ecuador.
Asioninae Vigors, 1825
Asio Brisson, 1760
Asio ecuadoriensis nov. sp.

Holotype Distal end of right tibiotarsus (EPNV, no. 6367; Fig. 3a–e); nearly complete right tarsometatarsus belonging to the same individual (EPNV, no. 6368; Figs. 3f–k and 4a). Both specimens lack abrasion or stomach acid-derived weathering.

Diagnosis Species of the genus Asio, probably representing the largest known asionine (Fig. 4) showing the following unique combination of characters (autapomorphies marked by an asterisk): tarsometatarsus with robust shaft (similar to A. priscus), well-developed and proximally extended crista lateralis hypotarsi*, proximal end of crista lateralis hypotarsi forming a well-developed subtriangular surface in lateral view (similar to A. flammeus), strongly concave lateral margin of shaft (similar to A. flammeus), crista plantaris medialis well developed and strongly convex (similar to A. priscus), calcaneal ridge proximodistally low and transversally thick (similar to A. priscus), proximally oriented calcaneal ridge (similar to A. flammeus), strongly distally divergent middle trochlear rings* (subparallel in A. flammeus and A. priscus), and tibiotarsus with proximal part of...
the trochlea cartilaginous tibialis lacking a transverse ridge in caudal view* (presence of a ridge in known Asio species; Pavia et al. 2015).

Among the largest South American species, the tarsometatarsus of A. ecuadoriensis sp. nov. are clearly larger than Asio flammeus, A. stygius and Pseudoscops clamator, are more robust than A. flammeus and A. stygius, and slenderer than Bubo virginianus.

**Etymology** ecuadoriensis, for República del Ecuador, honoring the country that yielded the remains of the new species.

**Description** Asio ecuadoriensis sp. nov. had legs the size of a big female Bubo virginianus (see “measurements”). The right tibiotarsus is incompletely preserved, only the distal end is present (Fig. 3a–e). The shaft is transversely narrow and expands distally. The condyles are robust and cranially extended, resulting in a wide U-shaped incisura intercondylaris. The lateral condyle extends distally, not laterally, and is sub-parallel to the lateral edge of shaft. The medial condyle extends distally and medially. The incisura intercondylaris is well developed, deep and transversely wide.

The right tarsometatarsus is nearly complete, only some portions of the shaft are missing (Fig. 3f–k). The bone is relatively robust, with the crista lateralis hypotarsi well developed laterocaudally. The eminentia intercotylaris is wide and the cotylae lateralis is more rounded than the elliptical cotylae medialis. The crista medialis hypotarsi is positioned medially with a broad and elliptical facies plantaris. Between the crista medialis hypotarsi and the lateral edge, there is a subtriangular and broad groove. The sulcus flexorius is broad along all its extension. The distal trochlea III extends slightly distally than trochlea II. The outer rim of trochlea III extends farther caudally and slightly laterally.

**Measurements** Tibiotarsus: total length (as preserved) 81.6 mm; width at mid-shaft (as preserved) 6.1 mm; distal width 14.4 mm; condylus lateralis width 11.1 mm; Condylus medialis width 11.4 mm. Tarsometatarsus: total length 65.2 mm; proximal width 16.2 mm; length of hypotarsus 6.6 mm; width of hypotarsus 3.5 mm; minimum shaft width 7.2 mm; distal width 16.3 mm.

**Remarks** The specimen here reported is referrable to aionines because of the following combination of characters: crista lateralis hypotarsi not laterally flaring, broad arcus extensorius, scar for muscle tibialis cranialis externally displaced, outer rim of middle trochlea much longer than the inner rim (especially in caudal view), outer and inner rims of middle trochlea that are subequally cranially extended, and smoothly curved articular surface of distal trochlea IV in lateral view (Ford 1967; Mlíkovský 1998). The tibiotarsus resembles Asio in the presence of a deep excavation of shaft cranio-proximal to distal trochlea, in having a shallow rounded depression caudally above the distal condyles, narrow shaft, expanded and distally extended distal attachment for fibula, and tuberculum retinaculi musculi fibularis prominent (Howard 1933; Campbell 2013; Pavia et al. 2015). In addition, in spite that A. ecuadoriensis sp. nov. has a distal width of tarsometatarsus similar to Pseudoscops, it differs because the distance between the trochlea is proportionately narrow and the sulcus extensorius poorly distally.

---

**Fig. 4** Right tarsometatarsus of (a) Asio ecuadoriensis nov. sp. (EPNV, no. 6368), (b) Asio flammeus (MACN, no. 2317), (c) Pseudoscops clamator (MACN, no.1404), (d) Asio stygius (MACN, no. 1421), and (e) Bubo virginianus (MACN, no. 54,505), in cranial views. Scale bar 1 cm
extended (Ford 1967). *Nesasio* shows several distinctive features, but its strong robustness clearly distinguishes it from *Asio* (Olson 1995).

Although *A. ecuadoriensis* sp. nov. is similar to *B. virgini-anus* in size (the only living species of the genus in South America; Fig. 4), it clearly differs from this species and the extinct Pleistocene Antillean species *B. osvaldoi* in notably slender proportions, lacking a transversely expanded and massive proximal end and a poorly defined and feebly defined scar for the muscle *tibialis cranialis* (Arredondo and Olson 1994).

Despite there being very few specimens of *A. ecuadoriensis* sp. nov., the length and robustness of the holotype indicate that it had longer and more robust legs than any other extant or extinct asionine (Fig. 4; Campbell 2013). In addition, the greater width of the intercondylar groove of tibiotalus is indicative of a notably robust, powerful leg (Campbell 2013). In fact, the robustness of the hindlimb may be correlated with thick and deep muscle scars, which are related to the strength of grip and ability to resist the stresses applied by a struggling prey (Weick and Brown 1980; Ferguson-Lee and Christie 2001; Worthy and Holdaway 2002).

Fossil asionine owls in South America are represented by *Pseudoscops clamator, Asio stygius,* and *Speotyto cunicularia* from the Late Pleistocene of Venezuela (Wetmore 1935), Brazil (Winge 1887), and Ecuador (Campbell 1976). Present finding constitutes the first extinct asionine taxon described for South America.

As indicated above, the fossil owl remains of *Tyto,* *Athene* and *Glaucidium* show breakage and weathering, typical of stomach acid-derived abrasion of Strigiformes (Dodson and Wexlar 1979). This indicates that, as occurs with mammals coming from the site, they would be prey items of the owl that is the owner of the burrow (detailed taphonomical and taxonomical analysis of the site is being carried out by one of the authors; JLRC). The large size of *A. ecuadoriensis* sp. nov., as well as the absence of acid-derived weathering of the bones, may constitute indirect evidence that this taxon is the owner of the burrow. It is worthy to mention that in the fossil record it is very common to find bones of the owner of the nest on its ancient burrows (Pardiñas 1999).

### Discussion

Arredondo and Olson (1994) determined that the Pleistocene of North and Central America show a higher diversity of large owls than nowadays. This is particularly true for the Antilles, among which giant Barn owls and gigantic strigids were highly diversified (Arredondo 1976, 1982; Arredondo and Olson 1994; Suárez and Olson 2015). In the same sense, Olson (1984) reported a giant owl from the Late Pleistocene of North America and Campbell (2013) described in detail the large asionine *Asio priscus* from California (Howard 1933). This is in concordance with the high diversity of giant condors, caracarines, and diurnal raptorial birds reported in the Pleistocene of North and South America (Jones et al. 2015). This diversification may be linked to the aridification of the climate with accompanying expansion of open habitat enabling an increase in the abundance potential food resources (Jacobs et al. 1999).

By the Latest Pleistocene–Early Holocene, the extinction of gigantic mammals is considered as one of the main factors that prompted the disappearance of several genera and species of giant scavengers and raptors (Tyrberg 2008; Jones et al. 2015). The highest proportion of extinct birds in the Pleistocene includes raptorial birds of large size (Tyrberg 2008). However, in spite that scavenger raptorial birds may have been deeply affected by extinction of the giant mammals that constituted their main food resource, the extinction of giant non-scavenger raptors and owls lacks a reliable explanation.

It is probable, as suggested by Pavia (2008), that selective impact that occurred in the Pleistocene extinction eradicated the larger raptorial species more easily, so that the more specialized taxa went extinct first. These taxa should have lower population densities than the smaller ones and usually have higher extinction rates (Peters 1983). This may be also applied to raptorial birds of South and Central America, where a large number of large to gigantic owls, including *Asio ecuadoriensis* sp. nov., disappeared.

Previously reported prey items of *Asio ecuadoriensis* sp. nov. include rodents, shrews and rabbits (Moreno Cárdenas and Román-Carrion 2017). Present contribution adds diverse owls (e.g., *Tyto, Athene, Glaucidium*) that very probably formed part of the diet of *A. ecuadoriensis* sp. nov. This may indicate that this taxon is probably an owl-specialized predator. It is well known that owls usually prey on raptors (e.g., Real and Mañosa 1990; Rohner and Doyle 1992; Tella and Mañosa 1993; Serrano 2000), but predation on owls by owls is uncommon and remains poorly explored in the literature (Mikkola 1976; Donázar 1989; Serrano 2000; Lourenço and Rabaça 2006). If correctly interpreted, the present contribution may constitute the first fossil evidence of owl being killed by owls.

**Acknowledgements** We thank Alejandro Mesías and Pablo Lara for their help during fieldwork. We thank Edith Montalvo (Ornithology curator, EPNV) and Yolanda Davis (Ornithology curator, MACN) and Sergio Bogan (Ornithology curator, Fundación de Historia Natural Félix de Azara) for access to osteological collections under their care. We are grateful to Fernando Novas for his support during the conduct of the present study.
Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Ameghino F (1891) Enumeración de las aves fósiles de la República Argentina. Rev Argent Hist Nat 1:441–453
Arredondo O (1972a) Nueva especie de ave fósil (Strigiformes: Tytonidae) del Pleistoceno superior de Cuba. Bol Soc Venez Cienc Nat 29:415–431
Arredondo O (1972b) Especie nueva de lechuza gigante (Strigiformes: Tytonidae) del Pleistoceno cubano. Bol Soc Venez Cienc Nat 30:129–140
Arredondo O (1982) Los Strigiformes fósiles del Pleistoceno Cubano. Bol Soc Venez Cienc Nat 140:33–55
Arredondo O, Olson SL (1994) A new species of owl of the genus Bubo from the Pleistocene of Cuba (Aves, Strigiformes). Proc Biol Soc Wash 107:436–444
Arredondo O (1976) The great predatory birds of the Pleistocene of Cuba. In: Olson SL (ed) Collected papers in Avian Paleontology honoring the 90th birthday of Alexander Wetmore Smithsonian Contrb Paleobiol, 27th edn. Smithsonian Institution Press, Washington, pp 169–187
Baumel JJ, Witmer LM (1993) Osteologia. In: Baumel JJ, King AS, Mlíkovský J, Pardiñas UFJ (eds) Anatomía de los aves. Academia Nacional de Ciencias, Córdoba, p 100
Brodkorb P (1971) Catalogue of fossil birds. Part 4 (Columbiformes through Piciformes). Bull Fla State Mus Biol Sci 15:163–266
Campbell KE (1976) The late Pleistocene Avifauna of La Carolina, southwestern Ecuador. Smithsonian Contrb Paleobiol 27:155–168
Campbell KE (1979) The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru. R Ont Mus Life Sci Contrb 118(1):203
Campbell KE Jr, Bochenski ZM (2013) Two new late Pleistocene miniature owls from Rancho La Brea, California. Acta Palaeontol Pol 58:707–721
Campbell KE Jr (2013) Revisiting Asio priscus, an extinct eared owl of the California Channel Islands. In: Göhlich UB, Kroh A (eds) Proceedings 8th international meeting of the Society of Avian Paleontology and Evolution. Paleornithological research 2013. Verlag Naturhistorisches Museum, Wien, pp 185–194
Cenizo MM (2006) Un nuevo estrigíforo (Strigiformes, Aves) para el Pleistoceno Tardío de la provincia de Buenos Aires, Argentina Con algunos comentarios sobre la morfología tarsal del género Athene Boie, 1822. 9º Congreso Argentino de Paleontología y Bioestratigrafía. Academia Nacional de Ciencias, Córdoba, p 100
Cenizo MM, de Los Reyes LM (2008) Primeros registros de Tyto alba (Scopoli, 1769) (Strigiformes, Aves) en el Pleistoceno Medio-Tardío de la provincia de Buenos Aires (Argentina) y sus implicancias tafonómicas. Rev Mus Argent Cienc Nat 10:199–209
Cenizo MM, Agnolin FL, Pomi LH (2015) A new Pleistocene bird assemblage from the southern Pampas (Buenos Aires, Argentina). Palaeoecogr, Palaeoclimatol, Palaeoecol 420:65–81
Chiappe LM (1991) Fossil birds from the Miocene Pinturas Formation of southern Argentina. J Vertebr Paleontol 11:21A–22A
Dodson P, Weixel D (1979) Taphonomic investigations of owl pellets. Paleobiology 5(3):275–284
Donázar JA (1989) Variaciones geográficas y estacionales en la alimentación del Búho Real (Bubo bubo) en Navarra. Ardeola 36(1):25–39
Enríquez PL, Eisermann K, Motta-Junior JC, Mikkola H (2015) Una revisión de la Taxonomía y Sistemática de los búhos Neotrópicos. In: Enríquez PL (ed) Los Búhos Neotrópicos: Diversidad y Conservación. ECOSUR, México, pp 29–38
Fergusson-Lee J, Christie DA (2001) Raptores de los mundos. Houghton Mifflin Company, Boston
Ford NL (1967) A systematic study of the owls based on comparative osteology. Dissertation, University of Michigan
Guérin C, Hugueney M, MOURER-CHAUVIRÉ C, Faure M (1993) Paléoenvironnement Pleistocène dans l’aire archéologique de Sao Raimundo Nonato (Piaui, Brésil): apport des mammifères et des oiseaux. Doc Lab Géol Lyon 125:187–202
Guerra C, Bover P, Alcover JA (2012) A new species of extinct little owl from the Pleistocene of Mallorca (Balearic Islands). J Ornithol 153:347–354
Hoffstetter R (1952) Les mammifères pléistocènes de la République de l’Équateur. Mém Soc Géol Fr 66:1–391
Howard H (1933) A new species of owl from the Pleistocene of Rancho La Brea, California. Condor 35:66–69
Jacobs BF, Kingston JD, Jacobs LL (1999) The origin of grass-dominated ecosystems. Ann Mo Bot Gard 86:590–643
Jones WW, Cenizo MM, Agnolin FL, Rinderknecht A, Blanco RE (2015) The largest known falconid. N Jahrb Geol Paläontol 277(3):361–372
Josse C, Cuesta F, Navarro G, Barrena V, Cabrera E, Chacón-Moreno E, Ferreira W, Peralvo M, Saito J, Tovar A (2009) Ecosistemas de los Andes del Norte y Centrales. Bolivia, Colombia, Ecuador, Perú y Venezuela. Secretaría General de la Comunidad Andina, Programa Regional ECOBONA-Intercooperation, CONDESAN-Proyecto Páramo Andino, Programa BioAndes, EcoCiencia, Nature Serve, IAvH, LTU-UNALM, ICAE-ULA, CDC-UNALM, RUMBOL SRL, Lima, Peru
König C, Weick F (2008) Owls of the World, 2nd edn. Yale University Press, New Haven
Lourenço R, Raaba J (2006) Intraguild predation by eagle owls in Europe. Aio 16:63–68
Mikkola H (1976) Owls killing and killed by other owls and raptors in Europe. Br Birds 69:144–154
Mlíkovský J (1998) Two new owls (Aves: Strigidae) from the early Miocene of the Czech Republic, with comments on the fossil history of the subfamily Striginae. Buteo 10:5–22
Moreno Cárdenas PA, Román-Carrión JL (2017) Musarañas del género Cryptotis (Eulipotyphla: Soricidae) en el Pleistoceno Tardío de los Andes Ecuatorianos. Bol Soc Geol Mex 69(2):421–432
Mourer-Chauviré C (1987) Les Strigiformes (Aves) des Phosphorites de l’Équateur. Mém Soc Géol Fr 66:1–391
Nijman V, Aliabadian M (2013) DNA barcoding as a tool for elucidating species delineation in wide-ranging species as illustrated by owls (Tytonidae and Strigidae). Zool Sci 30:1005–1009
Olson SL, Hilgartner W (1982) Fossil and Subfossil Birds from the Bahamas. In: Olson SL (ed) Fossil Vertebrates from the Bahamas. Smithsonian Contrb Paleobiol, 48th edn. Smithsonian Institution Press, Washington, pp 22–56
Olson SL (1984) A very large enigmatic owl (Aves: Strigidae) from the late Pleistocene of Ladds, Georgia. In: Genoways HH, Dawson MR (eds) Contributions in quaternary vertebrate paleontology: a volume in memorial to John E. Guilday, vol 8. Carnegie Museum of Natural History Special Publication, pp 44–46
Olson SL (1995) The genera of owls in the Asioninae. Bull Brit Ornithol Club 115:35–39
Pardiñas UFJ (1999) Tafonomía de microvertebrados en yacimientos arqueológicos de Patagonia (Argentina). Arqueol 9:265–339
Pavia M (2008) The evolution dynamics of the Strigiformes in the Mediterranean Islands with the description of Aegolius martae n. sp. (Aves, Strigidae). Quat Int 182(1):80–89

Pavia M, Mourer-Cauviré C (2002) An overview of the genus Athene in the Pleistocene of the Mediterranean Islands, with the description of Athene trinacriae n. sp. (Aves: Strigidae). In: Zhou Z, Zhang F (eds) Proceedings of the 5th symposium of the Society of Avian Paleontology and Evolution. China Science Press, Beijing, pp 13–27

Pavia M, Manegold A, Haarhoff P (2015) Early Pliocene owls from Langebaanweg, South Africa, with first evidence of the genus Athene south of the Sahara and the description of a new species of Tyto. Acta Palaeontol Pol 60(4):815–828

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Real J, Mañosa S (1990) Eagle Owl (Bubo bubo) predation on juvenile Bonelli’s Eagles (Hieraaetus fasciatus). J Raptor Res 24(3):69–71

Rich PV, Bohaska D (1976) The world’s oldest owl: a new strigiform from the Paleocene of southwestern Colorado. In: Olson SL (ed) Collected papers in avian paleontology honoring the 90th birthday of Alexander Wetmore. Smithson Contrib Paleobiol 27:87–93

Rohner C, Doyle FI (1992) Food-stressed great horned owl kills adult goshawk: exceptional observation or community process? J Raptor Res 26(4):261–263

Sánchez MV, Genise JF, Bellosi ES, Román-Carrión JL, Cantil LF (2013) Dung beetle brood balls from Pleistocene highland palaeosols of Andean Ecuador: a reassessment of Sauer’s Coprinisphaera and their palaeoenvironments. Palaeogeogr, Palaeoclimatol, Palaeoecol 386:257–274

Sauer W (1950) Contribuciones para el Conocimiento del Cuaternario en el Ecuador. Anales Univ Central Quito 77:327–364

Serrano D (2000) Relationship between raptors and rabbits in the diet of eagle owls in southwestern Europe: competition removal or food stress? J Raptor Res 34(4):305–310

Spillmann F (1942) Contribución al conocimiento de fósiles nuevos de la avifauna Ecuatoriana en el Pleistoceno de Santa Elena. Proc Eight Am Sci Congr 4:375–389

Suárez W, Olson SL (2015) Systematics and distribution of the giant fossil Barn owls of the West Indies (Aves: Strigiformes: Tytonidae). Zootaxa 4020(3):533–553

Tambussi C, Noriega JI (1996) Summary of the Avian fossil record from southern South America. In: Arratia G (ed) Contributions of southern South America to Vertebrate Paleontology. Müncher Geowiss Abh, 30:245–264

Tella JL, Mañosa S (1993) Eagle Owl predation on Egyptian Vulture and Northern Goshawk: possible effect of a decrease in European rabbit availability. J Raptor Res 27(2):111–112

Tonni EP (1983) Aves de un sitio arqueológico del área interserrana de la provincia de Buenos Aires. Ameghiniana 20(1–2):3–10

Tyrberg T (2008) The Late Pleistocene continental avian extinction—an evaluation of the fossil evidence. Oryctos 7:249–269

Weick F, Brown L (1980) Birds of prey of the world: a colored guide to identification of all the diurnal species order Falconiformes. Verlag Paul Parey, Hamburg

Wetmore A (1935) Pre-Columbian bird remains from Venezuela Auk 52(3):328–329

Winge H (1887) Jordfundne og nulevende Gnave (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. E Museo Lundii 1:1–200

Worthy TH, Holdaway RN (2002) The lost world of the moa: prehistoric life of New Zealand. Indiana University Press, Bloomington

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.