



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

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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 cucularia* 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 preyed 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

Zusammenfassung

Eulenarten (Aves, Strigiformes) des Jungpleistozäns aus Ecuador, mit Beschreibung einer neuen Art

Es gibt wenige Fossilfunde von Eulenarten der Familie Strigidae und Tytonidae in Südamerika. Das Ziel dieses Beitrags ist es, zum ersten Mal über fossile Strigiformes aus dem Kanton Riobamba der Provinz Chimborazo, Ecuador zu berichten. Die Exemplare stammen aus einer großen Eulenhöhle aus den Schichten des Jungpleistozäns der Cangagua Formation. Wir berichten über die Fossilfunde von *Athene cucularia* und *Tyto* aff. *T. furcata* sowie über den ersten Fossilfund von *Glaucidium* in Ecuador. Weiterhin beschreiben wir eine riesige Art der Gattung *Asio*. Dieses Exemplar stellt die größte bekannte Eulenart dieser Gattung dar, die in etwa die Größe vergleichbar mit einem weiblichen Virginiauhu *Bubo virginianus* hat. Basierend auf Beutefunde aus der fossilen Höhle, lässt sich vermuten, dass sich die neue *Asio*-Art von anderen Eulenarten ernährte. Falls diese Folgerung richtig sein sollte, könnte dies der erste fossile Nachweis für eine Prädation innerhalb der eigenen Ordnung sein.

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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).

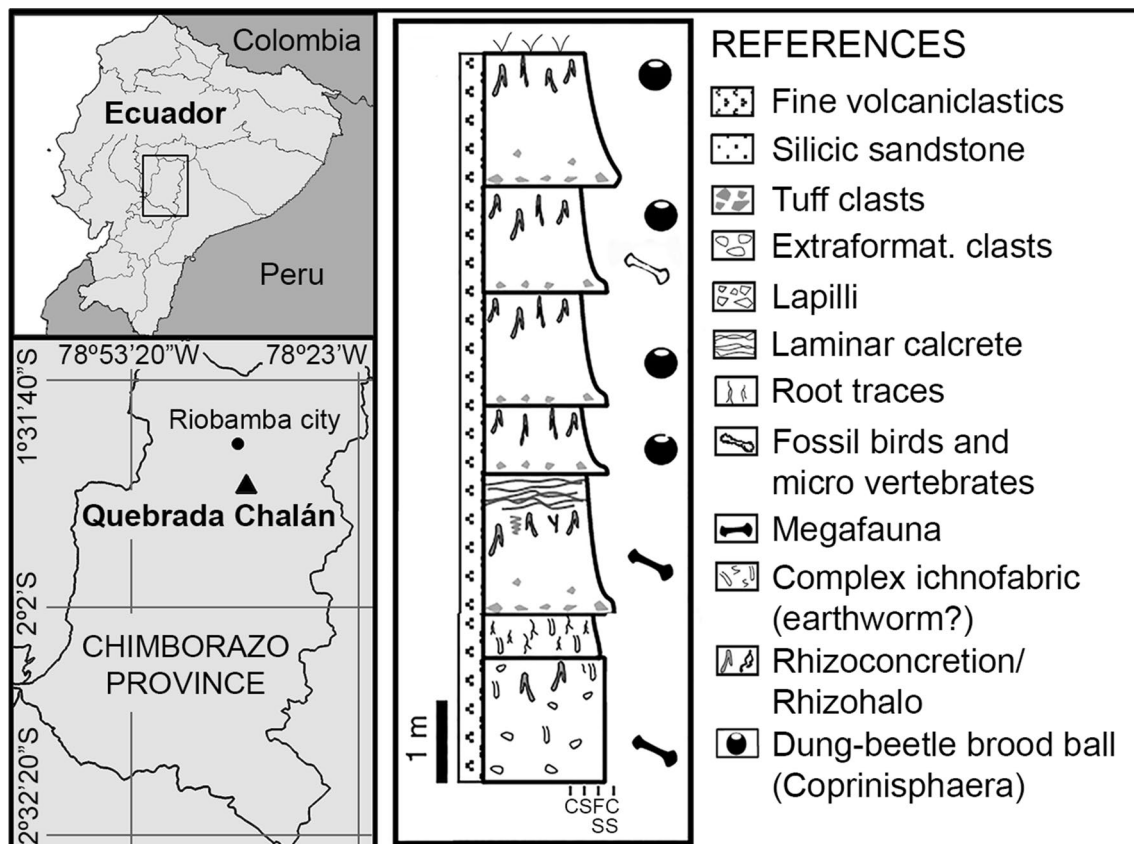


Fig. 1 Schematic map showing Late Pleistocene fossil location of Quebrada Chalán, Riobamba Canton, Chimborazo province, Ecuador and the stratigraphic profile at Quebrada Chalán

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



Referred specimen Distal end of right tarsometatarsus (EPNV, no. 6365; 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).

Remarks The specimen can be referred to *T. furcata* on the basis of the following combination of characters: tarsometatarsus with mediolaterally narrow shaft, slightly divergent distal trochleae, reduced notch between trochleae 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 *T. furcata* (Arredondo 1972a, b; Rich and Bohaska 1976; Suárez and Olson 2015). Because different species previously included within *T. alba* (i.e., *T. furcata*, *T. alba*, *T. javanica*) are not distinguishable on the basis of postcranial elements, we here identify the remains from Ecuador as *Tyto* aff. *T. furcata* based on gross morphological similarity and by geographical criterion, since in South America the only living and extinct species of the genus *Tyto* is *T. furcata* (reported as *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).

Strigidae Leach, 1820

Athene Boie, 1822

Athene cucicularia (Molina 1782)

Referred specimen Distal end of right tarsometatarsus (EPNV, no. 6366; Fig. 2f–h). This specimen shows signs of weathering and breakage on its external surface, being evidence of digestive abrasion by Strigiformes (Dodson and Wexlar 1979).

Remarks The following combination of characters indicates that specimen belongs to genus *Athene*: small size and elongate metatarsal shaft, presence of second foramen vasculare distale, distally extended trochlea metatarsi III, wider and more prominent lateral part of the trochlea metatarsal III than its medial part, medial groove of trochlea metatarsal III deep, and distal trochlea IV relatively small, very proximally located and laterally oriented, with its caudal flange poorly caudally and medially extended (Ford 1967; Olson and Hilgarter 1982; Pavia and Mourer-Chauviré 2002; Guerra et al. 2012). Its size falls within the range of *A. cucicularia*

and the narrow metatarsal shaft that is well excavated caudally, small and poorly divergent distal trochleae, blunt lateral margin of trochlea III in caudal view that is more caudally extended than the medial one indicates that fossil specimen belong to this taxon (Pavia and Mourer-Chauviré 2002; Cenizo 2006; Guerra et al. 2012).

Fossils of this species in South America are reported from the Late Pleistocene of La Carolina, Santa Elena, Ecuador (Campbell 1976), and in Argentina, from Late Pleistocene to Early Holocene of Buenos Aires province (Ameghino 1891; Tonni 1983); an indeterminate probably new, but still unpublished species is known from the Middle Pleistocene of coastal Buenos Aires province (Cenizo 2006).

Glaucidium Boie, 1826

Glaucidium sp.

Referred material Proximal end of right tarsometatarsus (EPNV, no. 6363; Fig. 2i–m); proximal end of left tarsometatarsus (EPNV, no. 6364; Fig. 2n–r), belonging to different individuals. Both tarsometatarsi show signs of weathering and breakage on its external surface, including a broadened foramen vasculare proximale, being probably evidence of digestive abrasion (Dodson and Wexlar 1979).

Remarks The specimens may be referred to the genus *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 cranio-lateral 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 cranio-lateral 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 *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 *G. nanum* (Campbell and Bochenski 2013), being much smaller than other strigids as *Athene* and *Tyto*.

The fossil record of *Glaucidium* in South America is restricted to *G. brasilianum* 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.

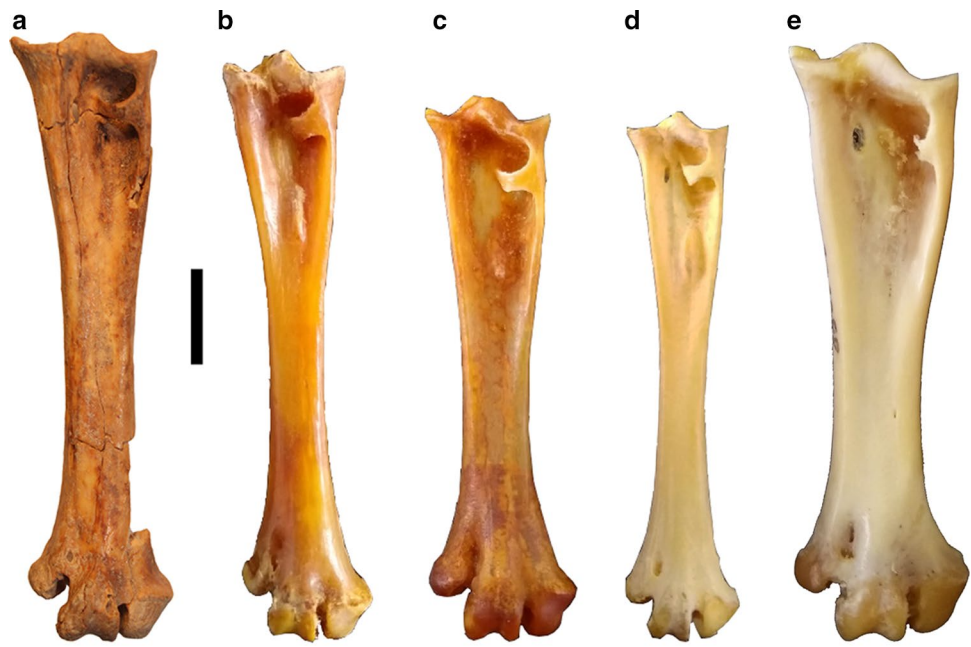
Diagnosis Species of the genus *Asio*, probably representing the largest known asionine (Fig. 4) showing the following unique combination of characters (autapomorphies marked

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

Fig. 3 *Asio ecuadoriensis* nov. sp. distal right tibiotarsus (EPNV, no. 6367; a–e) and right tarsometatarsus (EPNV, no. 6368; f–k) in (a, f) cranial, (b, g) lateral, (c, h) caudal, (d, i) medial and (j) proximal and (e, k) distal views. Scale bar 1 cm



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



the trochlea cartilaginosa 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 referable to asionines 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 trochleae, 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 trochleae is proportionately narrow and the sulcus extensorius poorly distally

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. virginianus* 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 tibiotarsus 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-Carrión 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; Donazar 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.

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Compliance with ethical standards

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

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