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New early Pliocene owls from Langebaanweg, South Africa, with first evidence of *Athene* south of the Sahara and a new species of *Tyto*

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The fossiliferous Upper Varswater Formation at Langebaanweg (South Africa) produced remains of at least five species of owls (Strigiformes). *Tyto richae* sp. nov. is the first palaeospecies of Tytonidae described from an African fossil site, though indeterminate remains referable to the genus *Tyto* are known from the Middle Miocene of Morocco, the early Pliocene of Ethiopia, and the Pliocene of Tanzania. *Athene inexpectata* sp. nov. is not only the earliest documented fossil evidence for the genus worldwide, but also the first record of a species of *Athene* in Africa south of the Sahara. Proportions of its hind limb indicate that *At. inexpectata* sp. nov. probably has been as terrestrial as its modern relative *At. cunicularia*. A few additional remains represent the earliest fossil evidence for the genera *Asio* and *Bubo* on the African continent, though the poor preservation of these bones prevents more detailed identifications. A distal tibiotarsus of a small owl about the size of *At. inexpectata* sp. nov. indicates the presence of a fifth, as yet indeterminate, species of owl at Langebaanweg. Biogeographical and palaeoecological implications of this assemblage of owls are discussed.

Key words: Aves, Strigiformes, Tytonidae, Strigidae, Varswater Formation, Pliocene, Africa, Langebaanweg.

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Introduction

The early Pliocene Upper Varswater Formation (Langebaanweg, West Coast of South Africa) is one of the most important pre-Pleistocene fossil localities in Africa. It has produced a very rich fossil bird bone assemblage with more than 90 species of 35 bird families, and is thus one of the richest fossil avifaunas in the world (Manegold et al. 2013). The study of the fossil birds from this extremely rich fossil locality started at the beginning of the 1980s, when Rich (1980) reported the presence of at least 60 species representing 28 bird families. Several papers were published on various bird groups since then, reviewed in Manegold et al. (2013, 2014), but studies on many taxa are still in progress. Presence of at least two species of Strigidae in the fossil assemblage has already been reported by Rich (1980) and Hendey (1981), though without further details. Thereafter Pippa Haarhoff sorted and identi-

fied 39 fossil bones of Strigiformes, which can be referred to a species of Tytonidae and four species of Strigidae. The fossil material is sufficient for describing a new species of *Tyto* as well as a new species of *Athene* and for distinguishing remains of as yet indeterminate species of the extant genera *Asio* and *Bubo*. A distal tibiotarsus of a small owl about the size of *Athene noctua* can only be referred to Strigidae.

The early Neogene fossil record of *Tyto*, *Athene*, *Bubo*, and *Asio*.—Strigiformes are quite common in the Cenozoic fossil record of birds. The oldest occurrence is dated to the Palaeocene. Strigiformes became quite common during the Eocene and Oligocene in the Northern Hemisphere (Mayr 2009). The order Strigiformes includes six families: four of them (Ogygoptyngidae, Palaeoglaucidae, Protostrigidae, and Sophiornithidae) only contain fossil taxa of Paleogene distribution, while the other two (Strigidae and Tytonidae) comprising fossil and extant species, forming together the crown

group Strigiformes (Mayr 2009). The oldest Strigidae dates back to the Early Miocene, while the Tytonidae are known since the Paleogene (Kurochkin and Dyke 2011; Göhlich and Ballmann 2013). All but one of the fossil remains of strigiforms found at Langebaanweg are referable to modern genera of both Tytonidae and Strigidae: *Tyto*, *Athene*, *Bubo*, and *Asio*.

The fossil history of *Tyto* has been recently summarized by Pavia and Mourer-Chauviré (2011). In particular, starting from the oldest species *Tyto sanctialbani*, it comprises several extinct species, both continental and insular, from the Middle Miocene onwards. All the Neogene fossil species of *Tyto* have been found in Europe or in North Africa together with all the earlier Tytonidae (Mourer-Chauviré and Geraads 2010; Kurochkin and Dyke 2011; Pavia and Mourer-Chauviré 2011; Göhlich and Ballmann 2013), suggesting a Western Palaearctic origin of the genus. The first record of *Tyto alba* is from the late Pliocene–Early Pleistocene of Morocco (Mourer-Chauviré and Geraads 2010), while the earliest record of *T. capensis* is represented by tentatively referred bones from the Late Pleistocene of Tanzania (Harrison 1980).

The first unambiguous record of *Athene* (sensu König and Weick 2008) is represented by the Nearctic *Athene megalopeza* from the late early Pliocene of Idaho and early late Pliocene of Kansas (Ford 1966; Ford and Murray 1967; Bell et al. 2004), a palaeospecies similar in size and proportion to the extant *Athene cunicularia* but more robust. The oldest occurrence of the Recent *At. cunicularia* is found in the late Pliocene of Nebraska, where Feduccia (1970) described *At. c. intermedia*, slightly more robust than the modern *At. cunicularia*. Apart from an as yet unsubstantiated, questionable record of *Athene* from the late Miocene of Hungary (Jánossy in Bernor et al. 2002), the first Palaearctic record of the genus dates from the late Pliocene of Bulgaria (Boev 2002). *Athene noctua* is known since the Early Pleistocene of Italy (Bedetti and Pavia 2013) and for other European localities (Mlíkovský 2002). It is worth mentioning that the islands of Mediterranean Basin during the Middle and Late Pleistocene were inhabited by several endemic forms of *Athene* with different morphological adaptations: *At. angelis*, *At. cretensis*, *At. trinacriae*, and *At. vallgornerensis* (Pavia and Mourer-Chauviré 2002; Guerra et al. 2012).

The genus *Bubo* is known since the early Pliocene of Ukraine and later reported from several Pliocene and Early Pleistocene localities (Mlíkovský 2002). Kurochkin and Dyke (2011) also listed *Bubo florianae* and *B. perpasta* from the Late Miocene of Hungary and Italy respectively, but the identification of the former is doubtful (see Mlíkovský 1998: 13) and the transfer of *Strix? perpasta* into *Bubo* (Mlíkovský 1998: 14) is questionable (MP personal observation). Thus, we note that no fossil species of *Bubo* have been described from the Neogene and that only four fossil species are known from the Pleistocene worldwide, two of them endemic (Kurochkin and Dyke 2011).

The oldest records of *Asio* are from the Western Palaearctic, with *Asio* sp. from the Early Miocene of Germany (Ballmann

1969) and *Asio? ignotus* from the Middle Miocene of France (Cheneval 2000). They are followed by the record of *Asio brevipes* from the early late Pliocene of Idaho (Ford and Murray 1967) and *Asio* sp. from the late Pliocene of Kansas (Ford 1966). Two other fossil species of *Asio* are listed by Kurochkin and Dyke (2011): *Asio longaevus* and *Asio pygmaeus* from the Late Miocene and early Pliocene of Ukraine respectively (Serebrovsky 1941; Umanskaya 1979), with the former originally described as *Bubo longaevus* and subsequently moved to *Asio* by Mlíkovský (1998). The original description of these two taxa does not clarify their taxonomic affinities, and it is impossible to consider these species in any meaningful comparisons of other fossil *Asio* remains. The Recent *Asio flammeus* is known since the late Pliocene of Poland, even if dubitatively (Jánossy 1974), while the oldest record of *Asio otus* is from the Early Pleistocene of Romania (Tyrberg 1998).

However, the identification of most of the fossil Strigidae from the Neogene has to be considered with great caution, because many specimens are only poorly preserved and most of them were only superficially described, as it was already pointed out by Göhlich and Ballmann (2013).

The fossil record of Strigiformes in Africa.—Apart from the owl remains from Langebaanweg, the fossil record of Strigiformes in the Neogene of Africa is poor and only spans the time from the Early Miocene to the Middle Pleistocene. The Miocene record is very sparse. It includes a distal humerus from the Lower Miocene of Songhor, Kenya, which was questionably referred to *Otus* (Walker and Dyke 2006), and a proximal phalanx of digitus majoris from the Middle Miocene of Beni Mellal, Morocco, which was originally assigned to *T. alba* (Brunet 1961, 1971), but probably belongs to an extinct species of *Tyto* (Pavia and Mourer-Chauviré 2011). Most of the African Strigiformes have been found in Pliocene and Pleistocene sites, such as the lower Pliocene of Aramis, Ethiopia, where a new, still undescribed, species of *Tyto* has been reported by Louchart et al. (2009) together with a single bone of an indeterminate species of Strigidae. However, the richest Pliocene site in terms of diversity of Strigiformes is Laetoli, Tanzania, with at least four taxa found in the various layers of the succession (Louchart 2011): *Tyto* sp., *Bubo* cf. *lacteus*, *Asio* sp., and an indeterminate small species of Strigidae about the size of *Athene*, *Glaucidium*, or *Taenioglaux*. *Tyto balearica*, *T. alba*, and *Surnia robusta* are documented from the late Pliocene of Ahl al Oughlam, Morocco, each of them by various skeletal elements of several individuals (Mourer-Chauviré and Geraads 2010).

A species of *Tyto* comparable in size to *T. alba*, but morphologically distinct from this species as well as from *T. capensis*, is reported from the Early Pleistocene of Kromdraai, South Africa (Pocock 1970), and Tytonidae are also listed in the preliminary record of birds from the Early Pleistocene of Swartkrans (Watson 1993). *Bubo leakeyae* has been described on the basis of a disarticulated skeleton and some isolated bones of at least 12 individuals from the Early

Pleistocene of Olduvai, Tanzania (Brodkorb and Mourer-Chauviré 1984), together with other remains referable to *T. alba* cf. *affinis* and *Bubo* cf. *lacteus*. A complete skull of a small owl from the Early Pleistocene of Buxton quarry (Taung), South Africa (Rich 1974: 179) has been tentatively referred to *Glaucidium perlatus* by Cooke (1990: 130). The author correctly pointed out the similarities of the fossil with *G. perlatus*, but erroneously listed the skull as cf. *At. noctua* (Cooke 1990: 132). This error was later iterated by Berger and Clarke (1995). Additional remains of owls referable to extant taxa are mentioned for several Pleistocene sites in Africa (Harrison 1980; Watson 1993; Plug and Clark 2008 and references therein), but a review of all these findings was beyond the scope of our study.

Institutional abbreviations.—MGPT-MPOC, Marco Pavia Ornithological Collection, Dipartimento di Scienze della Terra, Torino University, Italy; SAM-PQ-L, Iziko South African Museum Paleontology Quaternary Langebaanweg, Cape Town, South Africa.

Material and methods

The fossil bones described in the following pages are part of the Cenozoic collections of the Iziko South African Museum, Cape Town, South Africa. Osteological comparisons were made with representatives of all Western Palearctic and African genera of Strigiformes, except for the African endemic and monotypic genus *Jubula*, and the genus *Taenioglaux*. The fossil bones were compared to the Recent skeletons housed in Museo Civico di Storia Naturale (Carmagnola, Torino, Italy), Museo Civico di Lentate sul Seveso (Monza, Italy), MGPT-MPOC, Natural History Museum (London/Tring, UK), and Senckenberg Forschungsinstitut und Naturmuseum (Frankfurt/Main, Germany) collections. Comparisons with fossil owls from other African localities were made on the basis of published photographs and sketches (Brunet 1961, 1971; Harrison 1980; Brodkorb and Mourer-Chauviré 1984; Cooke 1990; Mourer-Chauviré and Geraads 2010; Louchart 2011).

The nomenclature of the Strigiformes follows Bruce (1999), Marks et al. (1999) and König and Weick (2008). The anatomical terminology follows Baumel and Witmer (1993). The measurements were taken by using vernier calipers accurate to 0.1 mm in accordance to von den Driesch (1976) and Louchart (2002).

List of Recent taxa used for comparative analyses.—Tytonidae: *Tyto alba alba*, *T. a. guttata*, *T. capensis*. Strigidae: *Aegolius funereus*, *Asio flammeus*, *As. otus*, *As. capensis*, *Athene cunicularia*, *At. noctua*, *Bubo africanus*, *B. ascalaphus*, *B. bubo*, *B. capensis*, *B. cinerascens*, *B. (Nyctea) scandiacus*, *B. (Ketupa) ketupu*, *B. (Scotopelia) bouvieri*, *Glaucidium passerinum*, *Ninox novaeseelandiae*, *Otus scops*, *Ptilopsis granti*, *P. leucotis*, *Strix aluco*, *S. nebulosa*, *S. uralensis*, *S. woodfordi*, *Surnia ulula*.

Systematic palaeontology

Class Aves Linnaeus, 1758

Order Strigiformes Wagler, 1830

Family Tytonidae Ridgway, 1914

Genus *Tyto* Billberg, 1828

Type species: *Tyto alba* (Scopoli, 1769); Recent, Friuli, Italy.

Tyto richae sp. nov.

Fig. 1.

Etymology: Dedicated to Patricia Vickers-Rich, who carried out the preliminary analysis of the Langebaanweg avifauna in 1980 and who has contributed significantly to the record of African fossil birds.

Type material: Holotype: right tarsometatarsus, SAM-PQ-L50354B, distal end. Paratypes: left coracoid, SAM-PQ-L23436, complete; left ulna, SAM-PQ-L50411L, distal end; left tibiotarsus, SAM-PQ-L28197AU, distal end; left tibiotarsus, SAM-PQ-L50022ZA, distal end; right tibiotarsus, SAM-PQ-L50022ZB, distal end.

Type horizon: Muishond Fontein Pelletal Phosphorite Member of the Upper Varswater Formation; early Pliocene (Hendey 1974, 1981; Roberts et al. 2011).

Type locality: Langebaanweg, South Africa.

Referred material.—Right coracoids, SAM-PQ-L30104, cranial end; right tarsometatarsus, SAM-PQ-L28199DT, distal end; right pedal phalanx III/2, SAM-PQ-L56207G; terminal pedal phalanges, SAM-PQ-L56212 A and F.

Diagnosis.—Medium-sized species of *Tyto*, distinctly larger than *T. alba*, coracoid relatively slender showing a well-marked facies articularis clavicularis with a tuberculum on its ventral side, and tarsometatarsus with the trochlea III protruding more distally than the trochlea II and IV.

Description.—*Tyto richae* sp. nov. is described on the basis of eleven more or less fragmentary bones that show a combination of characters previously described as being diagnostic for *Tyto* and which allow the distinction between this genus and *Phodilus* as well as other Tytonidae (Mourer-Chauviré 1987; Pavia 2004; Pavia and Mourer-Chauviré 2011; Göhlich and Ballmann 2013). In particular, coracoid: (i) tuberculum brachiale absent, (ii) processus procoracoideus short and wide at its base, (iii) cranial part of sulcus musculi supra-coracoidei not pneumatized, (iv) shaft ventro-dorsally flattened, (v) processus lateralis wide in cranial view; ulna: (vi) condylus dorsalis ulnaris oblique in ventral view, (vii) condylus ventralis ulnaris pointed and distally well developed; tibiotarsus: (viii) distal part of sulcus extensorius shallow, (ix) condyli caudally extended forming a square angle with the shaft, (x) condyli of similar thin shape in distal view; tarsometatarsus: (xi) trochlea metatarsi III protruding more distally than the remaining trochleae, (xii) medial groove on trochlea metatarsi III limited to the distal part, (xiii) distal edge of trochlea metatarsi IV wide and distally concave in lateral view; pedal phalanx III/2: (xiv) not as shortened as in Strigidae with blunt rather than pointed dorsoproximal process.

Table 1. Measurements (in mm) of the coracoid SAM-PQ-L23436 (paratype) of *Tyto richae* sp. nov. from Langebaanweg in comparison to corresponding measurements of extant *T. alba* and fossil *Tyto* species. Measurements of slightly worn or damaged bones are given in square brackets. Paratype is indicated by an asterisk; ¹ measurements after Brodkorb and Mourer-Chauviré (1984); ² measurements after Pavia and Mourer-Chauviré (2011); ³ measurements after Louchart (2002); n, sample size.

Specimen	Total length	Internal length	Proximal width	Proximal depth	Distal depth	Minimal width
SAM-PQ-L23436*	38.7	35.7	[7.0]	5.8	[5.8]	4.5
<i>Tyto alba</i>	33.7 (31.9–35.8) n = 36	32.5 (30.4–37.0) n = 26	7.2 (6.2–7.8) n = 17	5.2 (4.3–6.1) n = 30	3.2 (2.6–3.9) n = 36	3.9 (3.4–4.6) n = 26
<i>Tyto a. affinis</i> ¹	–	–	4.3–4.3 n = 4	5.4–5.5 n = 4	–	–
<i>Tyto capensis</i>	39.2 (37.9–40.4) n = 2	37.2 (36.1–38.4) n = 2	7.2 (6.9–7.4) n = 2	5.8 (5.3–6.3) n = 2	3.4 n = 2	4.6 (4.3–4.9) n = 2
<i>Tyto sanctialbani</i> ²	37.8	34.6 (33.0–35.7) n = 4	7.1 (6.9–7.3) n = 6	5.0 (4.2–5.7) n = 7	3.4 (3.3–3.5) n = 3	4.5 (4.1–4.8) n = 4
<i>Tyto b. balearica</i> ³	45.0	42.1	10.0	–	4.9 (4.5–5.7) n = 3	5.6 (5.4–5.9) n = 3
<i>Tyto b. cyrneichnusae</i> ³	41.8	39.5 (38.0–40.5) n = 5	8.1 (7.8–8.4) n = 4	6.4 (6.1–6.6) n = 7	3.8 (3.6–4.2) n = 8	5.2 (4.7–5.6) n = 10

Table 2. Measurements (in mm) of ulna, tibiotarsus, and tarsometatarsus of *Tyto richae* sp. nov. from Langebaanweg in comparison to corresponding measurements of extant *T. alba* and fossil *Tyto* species. Measurements of slightly worn or damaged bones are given in square brackets. The holotype is highlighted in bold, paratypes are indicated by an asterisk; ¹ measurements after Brodkorb and Mourer-Chauviré (1984); ² measurements after Pavia and Mourer-Chauviré (2011); ³ measurements after Jánossy (1991); ⁴ measurements after Louchart (2002); ⁵ measurements after Pavia (2004); n, sample size.

Specimen	Ulna			Tibiotarsus		Tarsometatarsus	
	Distal width	Distal depth	Minimal width	Distal width	Distal depth	Distal width	Distal depth
SAM-PQ-L50411L*	7.5	7.7	4.4	–	–	–	–
SAM-PQ-L28197AU*	–	–	–	11.1	[9.5]	–	–
SAM-PQ-L50022ZA*	–	–	–	11.6	10.3	–	–
SAM-PQ-L50022ZB*	–	–	–	[11.5]	10.0	–	–
SAM-PQ-L28199DT	–	–	–	–	–	[11.8]	–
SAM-PQ-L50354B	–	–	–	–	–	12.7	[9.5]
<i>Tyto alba</i>	6.3 (5.8–7.0) n = 36	6.8 (6–7.3) n = 19	3.6 (3.2–4.0) n = 46	8.9 (8.1–9.4) n = 39	8.8 (8.0–9.4) n = 38	10.0 (9.4–10.4) n = 35	7.8 (7.3–8.3) n = 33
<i>Tyto a. affinis</i> ¹	6.4–6.6 n = 4	6.4–6.6 n = 4	3.8–4.2 n = 4	9.6–9.9 n = 4	3.1–3.4 n = 4	10.7–11.0 n = 4	8.2–8.3 n = 4
<i>Tyto capensis</i>	7.1 (6.7–7.6) n = 2	7.4 (6.9–7.9) n = 2	4.3 (4.2–4.4) n = 2	10.0	10.0	11.7 (11.4–12.0) n = 2	9.3 (8.8–9.8) n = 2
<i>Tyto sanctialbani</i> ²	7.2 (6.8–7.9) n = 3	6.4 (5.6–7.0) n = 3	4.3	9.6 (8.6–10.3) n = 13	8.3 (7.2–9.3) n = 14	11.0 (10.7–11.9) n = 18	8.3 (7.4–8.8) n = 15
<i>Tyto campiterrae</i> ³	–	–	–	10.8 (10.0–11.7) n = 4	–	11.3 (11.0–11.7) n = 5	–
<i>Tyto b. balearica</i> ⁴	–	–	–	–	–	14.4	11.0
<i>Tyto b. cyrneichnusae</i> ⁴	8.0 (7.6–8.4) n = 10	8.8 (8.3–9.2) n = 8	4.7 (4.4–5.4) n = 21	11.9 (10.5–12.75) n = 12	11.4 (11.1–11.7) n = 2	13.5 (12.1–14.0) n = 12	10.9 (10.3–11.2) n = 4
<i>Tyto mourerchauvireae</i> ⁵	9.1 (9.0–9.3) n = 2	10.2 (10.1–10.4) n = 2	–	15.9 (15.0–17.1) n = 3	15.3 (15.1–15.5) n = 2	18.7	13.6

Tyto richae sp. nov. is larger than *T. a. alba*, *T. a. guttata*, and *T. a. ernesti* (see Louchart 2002) the extant European subspecies of cosmopolitan *T. alba*, which lack sexual size dimorphism, and also exceeds *T. a. affinis* of sub-Saharan Africa in size (König and Weick 2008) (Tables 1–3). The new *Tyto* species is similar-in-size to the few *T. capensis* available for comparison, but has stouter coracoid and hind limb bones. *Tyto richae* sp. nov. is larger than *T. sanctialbani* and slightly larger than *T. campiterrae*, but smaller than *T. balearica* and other palaeospecies of *Tyto* described from Europe

and North America (Mourer-Chauviré et al. 1980; Louchart 2002; Pavia 2004; Pavia and Mourer-Chauviré 2011).

The coracoid of *Tyto richae* sp. nov. is more slender than in *T. sanctialbani*, *T. balearica*, and *T. campiterrae*, thus more similar in structure to that of *T. alba*, and is stouter than in *T. capensis* (Table 1). The cranial end of the coracoid in the new species is characterized by a well developed facies articularis clavicularis, with an irregular surface that terminates ventrally into a tuberculum. The facies articularis sternalis is narrower than in *T. alba* and *T. sanctialbani*.

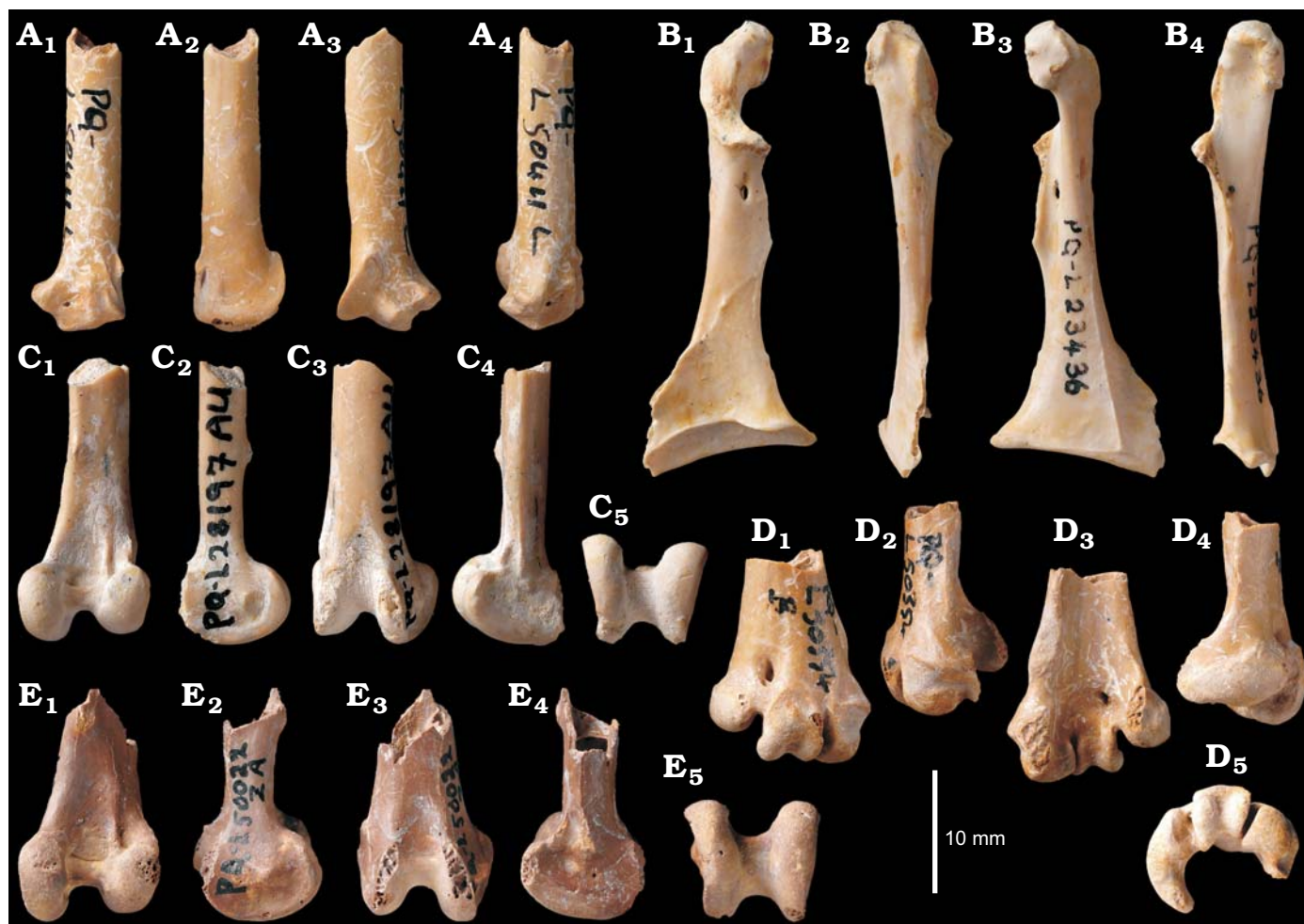


Fig. 1. Tytonid owl *Tyto richae* sp. nov. from the early Pliocene, Upper Varswater Formation at Langebaanweg, South Africa; paratypes (A–C, E), holotype (D). A. Left ulna (SAM-PQ-L50411 L), in dorsal (A₁), caudal (A₂), ventral (A₃), and cranial (A₄) views. B. Left coracoid (SAM-PQ-L23436), in dorsal (B₁), lateral (B₂), medial (B₃), and ventral (B₄) views. C. Left tibiotarsus (SAM-PQ-L28197 AU), in cranial (C₁), lateral (C₂), caudal (C₃), medial (C₄), and distal (C₅) views. D. Right tarsometatarsus (SAM-PQ-L50354 B), in dorsal (D₁), lateral (D₂), plantar (D₃), medial (D₄), and distal (D₅) views. E. Left tibiotarsus (SAM-PQ-L50022 ZA), in cranial (E₁), lateral (E₂), caudal (E₃), medial (E₄), and distal (E₅) views.

Compared to *T. alba*, the condylus ventralis ulnae of *T. richae* sp. nov. does not protrude as far ventrally and the incisura tuberculi carpalis is less marked. In cranial view, the distal tibiotarsus of *Tyto richae* sp. nov. is characterized by a small crest proximal to the medial side of the condylus lateralis. A similar crest is also present in *T. sanctialbani*, but is absent in

all the other *Tyto* species, both fossil and extant. The caudal side of the condylus medialis is wider than in *T. alba*, and the depression situated proximally to the trochlea cartilaginosa tibialis is not deep as in other *Tyto* species, both living and fossil. The two condyli are similar in size and shape and the incisura intercondylaris is proportionately wider than in *T.*

Table 3. Measurements (in mm) of pedal phalanx III/2 SAM-PQ-L56207G of *Tyto richae* sp. nov. from Langebaanweg in comparison to corresponding measurements of extant *T. alba*, *T. capensis*, and fossil *T. b. cyrneichnusae*. ¹ measurements after Brodkorb and Mourer-Chauviré (1984); ² measurements after Louchart (2002); n, sample size.

Specimen	Total length	Proximal width	Proximal depth	Distal width	Distal depth	Minimal width
SAM-PQ-L56207G	13.9	5.3	5.1	4.5	4.9	3.5
<i>Tyto alba</i>	11.3 (10.7–12.0) n = 16	3.6 (3.4–3.9) n = 16	3.8 (3.6–4.2) n = 16	3.0 (2.8–3.1) n = 16	3.2 (3.0–3.4) n = 16	2.4 (2.2–2.5) n = 16
<i>Tyto a. affinis</i> ¹	12.2–13.1 n = 4	–	–	–	–	–
<i>Tyto capensis</i>	13.9 (13.6–14.3) n = 2	4.5 (4.3–4.7) n = 2	4.6 (4.4–4.8) n = 2	3.6 (3.5–3.7) n = 2	4.0 (3.7–4.4) n = 2	2.8 (2.7–2.9) n = 2
<i>Tyto b. cyrneichnusae</i> ²	16.1 (15.3–16.6) n = 5	5.4 (5.1–5.6) n = 5	5.4 (5.2–5.6) n = 5	4.5 (4.4–4.6) n = 4	4.7 (4.6–4.8) n = 2	3.5 (3.5–3.7) n = 5

Table 4. Horizon of specimens of *Tyto richae* sp. nov. from the early Pliocene, Upper Varswater Formation at “E” Quarry, Langebaanweg, South Africa.

Horizon	Specimen
Langeberg Quartz Sand Member	SAM-PQ-L23436, SAM-PQ-L28197AU, SAM-PQ-L28199DT, SAM-PQ-L50022ZA, SAM-PQ-L50022ZB, SAM-PQ-L56207G, SAM-PQ-L56212A, SAM-PQ-L56212F
Muishond Fontein Pelletal Phosphorite Member	SAM-PQ-L30104, SAM-PQ-L50354B, SAM-PQ-L50411L

alba. Although only the distal part of the tarsometatarsus of the new species is known, this bone is apparently stouter than that of *T. capensis*, *T. alba*, and *T. campiterrae* (Table 2). The trochlea metatarsi III extends further distally than the other trochleae, as is the case with *T. sanctialbani*, but not as in other *Tyto* species. The fossil pedal phalanx III/2 is larger and more robust than the corresponding bone of *T. alba* and it is stouter with larger epiphyses than *T. capensis* (Table 3). The terminal pedal phalanges are compatible to the other referred material to *T. richae* sp. nov. They are only slightly curved and equipped with a proximodistally elongated processus extensorius as is typical for Strigiformes in general (Ballmann 1973). The processus flexorius is very small in both specimens as is the case with Tytonidae (Ballmann 1973).

Measurements.—Right distal tarsometatarsus SAM-PQ-L50354B (holotype): distal width 12.7 mm, distal depth >9.5 mm; for additional measurements, see Tables 1–3.

Stratigraphic and geographical range.—Langeberg Quartz Sand Member and Muishond Fontein Pelletal Phosphorite Member of the Upper Varswater Formation at Langebaanweg, early Pliocene of South Africa (Table 4).

Family Strigidae Ridgway, 1914

Genus *Athene* Boie, 1822

Type species: *Athene noctua* (Scopoli, 1769); Recent, Carnia, Friuli, Italy.

Athene inexpectata sp. nov.

Fig. 2A, C–F, G.

Etymology: From Latin *inexpectatus*, unexpected, because it is the first African record of *Athene* South of the Sahara.

Type material: Holotype: right tarsometatarsus, SAM-PQ-L13052N2, complete. Paratypes: sternum, SAM-PQ-L24592J, cranial part; right scapula, SAM-PQ-L25390GA, cranial end; right humerus, SAM-PQ-L33540C, distal half; right ulna, SAM-PQ-L14846, distal half; left tibiotarsus, SAM-PQ-L20700M, almost complete, only lacking proximal end; right tibiotarsus, SAM-PQ-L28927, proximal end; right tibiotarsus, SAM-PQ-L42828A, distal end; left tarsometatarsus, SAM-PQ-L20926, distal half right tarsometatarsus, SAM-PQ-L43568, complete.

Type horizon: Muishond Fontein Pelletal Phosphorite Member of the Upper Varswater Formation; early Pliocene (Hendey 1974, 1981; Roberts et al. 2011).

Type locality: Langebaanweg, South Africa.

Referred material.—Left humerus, SAM-PQ-L20691YE, distal end; left humerus, SAM-PQ-L43566, distal end; right humerus, SAM-PQ-L43565, distal end; left ulna, SAM-PQ-L14849, distal end; right femur, SAM-PQ-L33521H, proximal end; left tarsometatarsus, SAM-PQ-L20691H3, distal end; left tarsometatarsus, SAM-PQ-L20701X, distal half; left tarsometatarsus, SAM-PQ-L56223, proximal end; right tarsometatarsus, SAM-PQ-L25293DZ, proximal end; right tarsometatarsus, SAM-PQ-L25293GM, distal end; right tarsometatarsus, SAM-PQ-L28199FN, distal end; right tarsometatarsus, SAM-PQ-L33704A, distal half; right tarsometatarsus, SAM-PQ-L43569, distal half.

Diagnosis.—Species of the genus *Athene* slightly larger and stouter than *At. noctua* (Tables 5–7). *Athene inexpectata* sp. nov. is distinguished from *At. noctua* by the scapula having pneumatic foramen on the acromion, a pronounced epicondylus dorsalis on the distal humerus, an elongated tibiotarsus, and a stout tarsometatarsus with wide cotylae. The new species also differs from *At. cunicularia* by its less elongated tibiotarsus and stouter tarsometatarsus, from *At. megalopeza* by its stouter tarsometatarsus, and from the various extinct Mediterranean insular species of *Athene*, such as *At. angelis*, *At. cretensis*, *At. trinacriae*, and *At. vallgornerensis* by the different proportions of the hind limb bones (Tables 5–7) and some morphological characters in the various long bones (Weesie 1982; Mourer-Chauviré et al. 1997; Pavia and Mourer-Chauviré 2002; Guerra et al. 2012).

Description.—*Athene inexpectata* sp. nov. is described on the basis of 23 more or less complete bones. It can be referred to *Athene* on the basis of the following morphological characters previously pointed out by Pavia and Mourer-Chauviré (2002): scapula: (i) facies articularis humeralis rounded and mainly mediolaterally oriented, (ii) articular facet on the medial side of the facies articularis humeralis wide, (iii) crista ligamenti acrocoracoacromiali absent; humerus: (iv) fossa musculi brachialis wide and shallow, (v) condylus dorsalis proximally well developed; ulna: (vi) condylus dorsalis ulnaris ventrally well developed and joining the shaft with a square angle; femur: (vii) crista trochanteris weakly developed; tibiotarsus: (viii) proximal part of the crista fibularis separated from the proximal end, (ix) incisura intercotylaris narrow and deep, (x) condylus lateralis wide and expanded laterally in caudal view; tarsometatarsus: (xi) lateral side of the cotyla lateralis rounded in proximal view; (xii) sulcus extensorius exceeding the middle of the shaft; (xiii) tuberositas musculi tibialis cranialis weakly developed; (xiv) medial groove on the trochlea metatarsi III deep; (xv) trochlea metatarsi III protruding more distally than the others.

The area of the foramina pneumatica as well as the labrum internum of the fragmentary sternum of *At. inexpectata* sp. nov. are both wider than in *At. noctua*. The facies articularis humeralis of the scapula of the new species is more square than in *At. noctua*, and the articular facet on the medial side of the facies articularis humeralis is wider. In *At. inexpectata* sp. nov., there is a pneumatic foramen on the medial side of



Fig. 2. Strigid owl *Athene inexpectata* sp. nov. from the early Pliocene, Upper Varswater Formation at Langebaanweg, South Africa; paratypes (A, C–E, G), holotype (F) and *Athene noctua*, Recent (B). **A.** Left tibiotarsus (SAM-PQ-L20700 M), in cranial (A₁), lateral (A₂), caudal (A₃), medial (A₄), and distal (A₅) views. **B.** Reversed right tibiotarsus (MGPT-MPOC 38), in cranial view (B₁), left tarsometatarsus in dorsal view (B₂). **C.** Left scapula (SAM-PQ-L25390 GA), in medial (C₁), cranial (C₂) and lateral (C₃) views. **D.** Right ulna (SAM-PQ-L14846), in dorsal (D₁), caudal (D₂), ventral (D₃) and cranial (D₄) views. **E.** Right tibiotarsus (SAM-PQ-L28927), in cranial (E₁), lateral (E₂), caudal (E₃), medial (E₄), and proximal (E₅) views. **F.** Right tarsometatarsus (SAM-PQ-L13052 N2), in dorsal (F₁), lateral (F₂), plantar (F₃), medial (F₄), proximal (F₅), and distal (F₆) views. **G.** Right humerus (SAM-PQ-L33540 C), in cranial (G₁), dorsal (G₂), caudal (G₃), ventral (G₄), and distal (G₅) views.

Table 5. Measurements (in mm) of humerus and ulna of *Athene inexpectata* sp. nov. from Langebaanweg compared with the corresponding bones of extant and fossil *Athene* species. Measurements of slightly worn or damaged bones are given in square brackets. Paratypes are indicated by an asterisk; ¹ measurements after Mourer-Chauviré et al. (1997); ² measurements after Pavia and Mourer-Chauviré (2002); n, sample size.

Specimen	Humerus			Ulna		
	Distal width	Distal depth	Minimal width	Distal width	Distal depth	Minimal width
SAM-PQ-L20691YE	10.9	5.4	—	—	—	—
SAM-PQ-L33540C*	10.4	5.1	4.3	—	—	—
SAM-PQ-L43565	9.6	4.9	—	—	—	—
SAM-PQ-L43566	9.6	[4.5]	—	—	—	—
SAM-PQ-L14846*	—	—	—	5.7	[6.0]	3.5
SAM-PQ-L14849	—	—	—	5.4	5.3	—
<i>Athene noctua</i>	8.8 (8.3–9.8) n = 22	4.3 (4.3–4.5) n = 22	3.4 (3.3–3.5) n = 22	4.9 (4.2–5.3) n = 21	4.7 (4.1–5.5) n = 21	2.5 (2.3–2.9) n = 21
<i>Athene cunicularia</i>	9.4 (9.2–9.6) n = 3	5.0 (4.9–5.0) n = 3	4.0 (3.9–4.1) n = 3	5.1 (5.1–5.1) n = 3	4.8 (4.7–4.9) n = 3	2.9 (2.7–3.0) n = 3
<i>Athene brama</i>	8.5 (8.0–8.7) n = 9	4.1 (3.8–4.2) n = 9	3.5 (3.2–3.6) n = 9	4.6 (4.4–4.8) n = 9	4.2 (4.0–4.4) n = 9	2.5 (2.3–2.7) n = 9
<i>Athene blewitti</i>	8.7	4.2	3.5	4.6	4.4	2.5
<i>Athene angelis</i> ¹	10.4 (9.5–10.9) n = 10	5.4 (5.3–5.6) n = 9	3.9 (3.6–4.4) n = 23	6.0 (5.6–6.3) n = 13	5.3 (4.8–5.6) n = 12	3.2 (2.6–3.5) n = 22
<i>Athene trinacriae</i> ²	8.9 (8.4–9.1) n = 4	4.3 (4.0–4.7) n = 4	3.5 (3.4–3.5) n = 5	—	—	—

Table 6. Measurements (in mm) of femur and tibiotarsus of *Athene inexpectata* sp. nov. from Langebaanweg compared with the corresponding bones of various living and fossil *Athene* species. Measurements of slightly worn or damaged bones are given in square brackets. Paratypes are indicated by an asterisk; ¹ measurements after Mourer-Chauviré et al. (1997); ² measurements after Louchart (2002); ³ measurements after Pavia and Mourer-Chauviré (2002); n, sample size.

Specimen	Femur		Tibiotarsus				
	Proximal width	Proximal depth	Proximal width	Proximal depth	Distal width	Distal depth	Minimal width
SAM-PQ-L33521H*	8.4	5.7	—	—	—	—	—
SAM-PQ-L20700M*	—	—	—	—	7.5	6.9	3.5
SAM-PQ-L28927*	—	—	[6.7]	8.5	—	—	—
SAM-PQ-L42828A*	—	—	—	—	7.2	6.1	—
<i>Athene noctua</i>	7.2 (7.4–8.1) n = 24	4.7 (4.4–5.5) n = 24	6.4 (5.9–7.2) n = 21	7.4 (7.5–8.2) n = 21	7.2 (6.7–7.7) n = 21	5.7 (5.4–6.2) n = 20	3.0 (2.7–3.5) n = 21
<i>Athene cunicularia</i>	7.8 (7.5–8.1) n = 3	5.4 (5.3–5.4) n = 3	6.9 (6.2–6.9) n = 3	8.3 (8.0–8.5) n = 3	7.2 (6.9–7.5) n = 3	6.3 (6.1–6.5) n = 3	3.4 (3.2–3.5) n = 3
<i>Athene brama</i>	6.9 (6.6–7.1) n = 8	4.3 (4.1–4.7) n = 8	5.6 (5.4–5.9) n = 9	6.8 (6.4–7.2) n = 9	6.4 (6.1–6.7) n = 9	5.4 (5.2–5.6) n = 9	2.7 (2.5–2.8) n = 9
<i>Athene blewitti</i>	—	4.7	6.4	7.5	7.6	6.2	3.3
<i>Athene angelis</i> ^{1,2}	9.4 (8.6–9.8) n = 8	5.6 (5.45–6.0) n = 4	8.3 (7.7–8.7) n = 5	9.2 (8.8–9.6) n = 5	9.1 (8.5–9.7) n = 6	7.5 (7.3–7.7) n = 3	3.7 (3.4–4.2) n = 16
<i>Athene trinacriae</i> ³	7.1 (7.1–7.2) n = 2	4.6 (4.5–4.8) n = 2	—	—	—	—	—

the acromion that is absent in *At. noctua* but present in *At. cunicularia*. The facies articularis clavicularis is more developed in *At. inexpectata* sp. nov. than in *At. noctua*. The sulcus scapulotricipitalis and epicondylus dorsalis of the humerus of the new species are more pronounced than in *At. noctua*. The distal end of the ulna of *At. inexpectata* sp. nov. is characterized by the tuberculum on the ventral side of the condylus ventralis ulnaris being much more obvious than in *At. noctua*. The facies articularis acetabularis and the fovea ligamentum capitis of the femur are larger in *At. inexpectata* sp. nov. than in *At. noctua*. The linea intermusculi cranialis is more pronounced and more medially situated than in *At. noctua* and

the facies articularis antitrochanterica is caudally less developed. The trochanter femoris is generally more developed and more separated from the impressio obturatoria in the new species. Although incompletely preserved, the tibiotarsus of *At. inexpectata* sp. nov. is much more elongated than that of *At. noctua*. In fact, the tibiotarsus of *At. inexpectata* can be estimated to have been as long as 70 mm, whereas the mean for the length of the tibiotarsus in *At. noctua* is 57.5 mm, the minimal width of the tibiotarsus is similar in both species (Fig. 2, Table 6). The proximal tibiotarsus of the new species is characterized by a more distally oriented crista patellaris and a more developed distal part of the crista cranialis lat-

Table 7. Measurements (in mm) of the tarsometatarsus of *Athene inexpectata* sp. nov. from Langebaanweg compared with the corresponding bones of various living and fossil *Athene* species. Measurements of slightly worn or damaged bones are given in square brackets. The holotype is highlighted in bold, paratypes are indicated by an asterisk. ¹ measurements after Mourer-Chauviré et al. (1997); ² measurements after Louchart (2002); ³ measurements after Pavia and Mourer-Chauviré (2002); ⁴ measurements after Guerra et al. (2012); n, sample size.

Specimen	Total length	Proximal width	Proximal depth	Smallest proximal depth	Distal width	Distal depth	Minimal width
SAM-PQ-L13052N2	38.0	[8.2]	[7.8]	5.1	9.1	6.4	4.1
SAM-PQ-L20691H3	—	—	—	—	9.6	6.6	—
SAM-PQ-L20701X	—	—	—	—	[9.6]	[6.0]	4.1
SAM-PQ-L20926*	—	—	—	—	9.5	6.5	4.1
SAM-PQ-L25293DZ	—	8.2	7.7	5.4	—	—	—
SAM-PQ-L25293GM	—	—	—	—	—	[5.3]	—
SAM-PQ-L28199FN	—	—	—	—	9.1	6.3	—
SAM-PQ-L33704A	—	—	—	—	9.2	6.8	4.4
SAM-PQ-L43568*	33.4	7.2	—	4.9	8.3	5.9	4.1
SAM-PQ-L43569	—	—	—	—	8.1	5.9	[4.1]
SAM-PQ-L56223	—	8.3	—	[6.0]	—	—	—
<i>Athene noctua</i>	35.0 (30.2–38.1) n = 21	7.3 (6.7–7.8) n = 21	6.5 (6.2–67.2) n = 21	4.8 (4.2–5.4) n = 5	7.4 (6.5–8.1) n = 21	5.6 (5.1–6.2) n = 21	3.3 (2.8–3.6) n = 21
<i>Athene cucicularia</i>	46.6 (45.4–46.4) n = 3	7.6 (7.3–8.1) n = 3	7.5 (7.2–7.8) n = 3	5.1 (4.9–5.1) n = 3	8.0 (7.7–8.5) n = 3	5.6 (5.4–5.9) n = 3	3.1 (2.7–3.5) n = 3
<i>Athene brama</i>	29.3 (28.0–30.5) n = 9	6.6 (6.1–6.9) n = 9	6.3 (5.9–6.5) n = 9	4.4 (4.1–4.8) n = 8	6.8 (6.7–7.2) n = 9	5.1 (4.7–5.3) n = 9	3.2 (3.0–3.4) n = 9
<i>Athene blewitti</i>	25.8	7.8	7.3	5.2	8.9	6.6	5.1
<i>Athene angelis</i> ^{1, 2}	39.8 (38.2–41.5) n = 10	9.3 (8.7–9.8) n = 12	8.5 (7.9–9.0) n = 10	—	9.3 (8.7–9.7) n = 14	7.2 (7.1–7.3) n = 4	4.2 (4.0–4.6) n = 33
<i>Athene trinacriae</i> ³	40.9 (39.6–42.7) n = 7	6.9 (6.7–7.1) n = 4	6.6 (6.1–6.9) n = 4	—	7.5 (7.2–8.0) n = 5	5.6 (5.4–6.0) n = 5	3.2 (2.6–3.7) n = 7
<i>Athene vullgomerensis</i> ⁴	28.6	6.5	—	—	7.0	—	3.5

eralis, which also has a deeper sulcus intercnemialis. The crista cnemialis lateralis is more medially oriented than in *At. noctua*. The sulcus extensorius on the distal end of the tibiotarsus in the new species is more defined, triangular-shaped, and originates further proximal on the shaft. The medial and lateral margins of the sulcus extensorius are thinner than in *At. noctua*. The tarsometatarsus of *At. inexpectata* sp. nov. is slightly larger and stouter than that of *At. noctua* (Fig. 2, Table 7). The proximal end of the new species is characterized by the cotyla lateralis being wider and more rounded, and by the

eminentia intercotylaris also being wider and less pointed compared with *At. noctua*. The cotyla medialis is less rounded but more extended plantarly in *At. inexpectata* sp. nov. than in *At. noctua*. The trochleae metatarsi are more robust in the new species. In particular, the trochlea metatarsi II of *At. inexpectata* sp. nov. shows the area of the fovea ligamenti collateralis to be more developed whilst the plantar side of the same trochlea is thinner than in *At. noctua*.

Measurements.—Right tarsometatarsus SAM-PQ-L13052N2 (holotype): total length 38.0 mm; distal width 9.1 mm; distal depth 6.4 mm; minimum width of shaft 4.1. For additional measurements, see Tables 5–7.

Stratigraphic and geographical range.—Langeberg Quartz Sand Member and Muishond Fontein Pelletal Phosphorite Member of the Upper Varwater Formation at Langebaanweg, early Pliocene of South Africa (Table 8).

Genus *Bubo* Duméril, 1806

Type species: *Bubo bubo* (Linnaeus, 1758); Recent, Sweden.

Bubo sp.

Fig. 3C.

Material.—Left tibiotarsus, SAM-PQ-L28439C, distal end from Langeberg Quartz Sand Member or Muishond Fontein

Table 8. Horizon of specimens of *Athene inexpectata* sp. nov. from the early Pliocene, Upper Varwater Formation at “E” Quarry, Langebaanweg, South Africa.

Horizon	Specimen
Langeberg Quartz Sand Member (LQSM)	SAM-PQ-L13052N2, SAM-PQ-L14846, SAM-PQ-L14849, SAM-PQ-L20691H3, SAM-PQ-L20691YE, SAM-PQ-L20700M, SAM-PQ-L20701X, SAM-PQ-L20704EI, SAM-PQ-L20926, SAM-PQ-L25293DZ, SAM-PQ-L25293GM, SAM-PQ-L25390GA, SAM-PQ-L28199FN, SAM-PQ-L56223
Muishond Fontein Pelletal Phosphorite Member (MPPM)	SAM-PQ-L24592J, SAM-PQ-L33521H, SAM-PQ-L33540C, SAM-PQ-L33704A, SAM-PQ-L43508, SAM-PQ-L43565, SAM-PQ-L43566, SAM-PQ-L43569
LQSM or MPPM	SAM-PQ-L28927, SAM-PQ-L42828A

Table 9. Measurements (in mm) of the tibiotarsus of *Bubo* sp. from Langebaanweg in comparison with corresponding measurements of extant and extinct *Bubo* species. Measurements of slightly worn or damaged bones are given in square brackets. ¹ measurements after Brodkorb and Mourer-Chauviré (1984); n, sample size.

Specimen	Distal width	Distal depth	Minimal width
SAM-PQ-L28439C	13.3	[10.5]	—
<i>Bubo africanus</i> ¹	11.1–12.5 n = 8	9.0–10.7 n = 8	—
<i>Bubo bubo</i>	18.7 (17.2–20.8) n = 7	15.1 (13.6–16.6) n = 7	10.1 (9.4–11.3) n = 7
<i>Bubo lacteus</i>	18.5	15.2	8.1
<i>Bubo shelley</i>	20.6	16.0	8.4
<i>Bubo capensis</i>	12.2	10.2	6.2
<i>Bubo leakeyae</i> ¹	12.2–15.6 n = 4	10.7 n = 2	—

Table 10. Measurements (in mm) of the tibiotarsus of *Asio* sp. from Langebaanweg in comparison with corresponding measurements of extant *Asio* species; n, sample size.

Specimen	Distal width	Distal depth	Minimal width
SAM-PQ-L33521I	8.4	7.2	3.5
SAM-PQ-L20691L3	—	—	3.5
<i>Asio flammeus</i>	8.8 (8.2–9.6) (n = 6)	7.0 (6.7–7.7) (n = 6)	3.9 (3.7–4.1) (n = 6)
<i>Asio capensis</i>	9.1	7.8	3.9
<i>Asio otus</i>	8.8 (8.0–9.0) (n = 10)	7.0 (6.5–7.4) (n = 10)	3.7 (3.2–4.0) (n = 10)

Pelletal Phosphorite Member of the Upper Varswater Formation at Langebaanweg, early Pliocene of South Africa.

Measurements.—Distal width 13.3 mm; distal depth >10.5 mm (see Table 9).

Remarks.—The distal tibiotarsus can be referred to Strigidae rather than to Tytonidae because of the following morphological characteristics: (i) two condyli parallel and wide in distal view; (ii) condylus medialis not tilted medially; (iii) depression on the distal part of the shaft just above the trochlea cartilaginosa tibialis deep in caudal view; (iv) epicondylus lateralis well developed. The specimen is comparable in size to the extinct *B. leakeyae* from the Early Pleistocene of Olduvai (Brodkorb and Mourer-Chauviré 1984), thus bigger than the Recent *B. africanus* and smaller than *B. lacteus* (Table 9). According to Brodkorb and Mourer-Chauviré (1984: 22), *B. leakeyae* and *B. africanus* are distinguished from *B. bubo* by a more developed and more medially situated tuberositas retinaculi medialis, but, unfortunately, this character is not discernible in the Langebaanweg specimen. The fossil here described is also not comparable to *Bubo* cf. *lacteus* from the Pliocene of Laetoli and the Pleistocene of Olduvai (Brodkorb and Mourer-Chauviré 1984; Louchart 2011) as no distal tibiotarsi are known for these taxa from the aforementioned localities. The fossil tibiotarsus from Langebaanweg is thus referable to a medium-sized species of the genus *Bubo*, apparently smaller than the largest extant species of eagle owls

in Africa, i.e., *B. lacteus*, *B. shelleyi*, and *B. (Scotopelia) peli*. Because the specimen is only poorly preserved, we abstain from referring it to any particular species of this genus.

Genus *Asio* Brisson, 1760

Type species: *Asio otus* (Linnaeus, 1758); Recent, Sweden.

Asio sp.

Fig. 3A.

Material.—Left tibiotarsus (SAM-PQ-L20691L3, shaft) from Langeberg Quartz Sand Member; right tibiotarsus (SAM-PQ-L33521I, distal part) from Muishond Fontein Pelletal Phosphorite Member; the Upper Varswater Formation at Langebaanweg, early Pliocene of South Africa.

Measurements.—Distal right tibiotarsus SAM-PQ-L33521I: distal width 8.4 mm; distal depth 7.2 mm; minimal width of shaft 3.5 mm (see Table 10).

Description.—The two tibiotarsi from Langebaanweg are more similar to the corresponding bones of *Asio* than to that of other Strigidae in having: (i) distal attachment of the fibula very close to the distal end of the bone; (ii) proximal part of the trochlea cartilaginosa tibialis terminates in a ridge in caudal view; (iii) tuberculum retinaculi musculi fibularis prominent. The fossils are distinguished from *As. otus*, but are similar to *As. flammeus* and *As. capensis*, because of the less medially tilted condylus medialis and of the general shape of the epicondylus ventralis and medialis. It is further distinguishable from *As. flammeus* and *As. capensis* by its narrower incisura intercotylaris. The fossil specimens could not be compared with corresponding bones of the extant *As. abyssinicus*, a species endemic to the East African rift and often considered a subspecies of *As. otus*, and their preservation does not allow their assignment to any particular taxon of *Asio*. The ungual phalanx of *Asio* sp. reported from Laetoli is comparable in size with *As. capensis*, *As. abyssinicus* and *As. flammeus*, shows no diagnostic feature that would allow an assignment to a particular species of long-eared owl (Louchart 2011).

Strigidae gen. et sp. indet.

Fig. 3B.

Material.—Left tibiotarsus, SAM-PQ-L28479 C, distal end from Langeberg Quartz Sand Member or Muishond Fontein Pelletal Phosphorite Member of the Upper Varswater Formation at Langebaanweg, early Pliocene of South Africa.

Measurements.—Distal width 8.0 mm; distal depth 6.5 mm.

Remarks.—The distal tibiotarsus is similar in size to *At. inexpectata* sp. nov., but can be distinguished from *Athene* by its wider epicondylus medialis and wider condylus medialis. It further differs from *Asio*, *Otus*, and *Ptilopsis* by a differently shaped condylus medialis and a distally very deep sulcus extensorius. This tibiotarsus thus indicates the presence of another small species of Strigidae at Langebaanweg, but due to its fragmentary preservation, it cannot be referred to any taxon of owl below the family level.

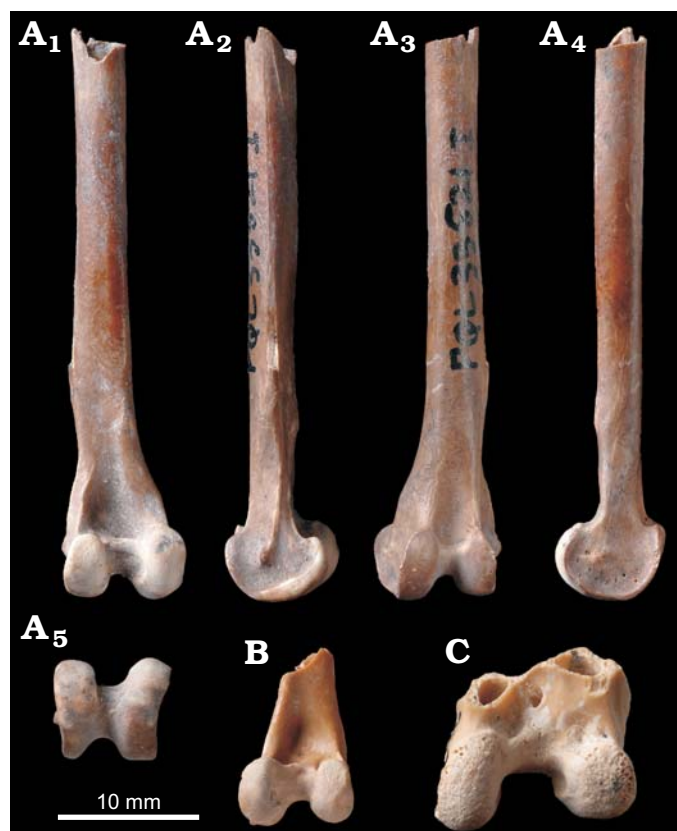


Fig. 3. Strigid owls from the early Pliocene, Upper Varswater Formation at Langebaanweg, South Africa. **A.** *Asio* sp. (SAM-PQ-L33521 I), right tibiotarsus, in cranial (A_1), lateral (A_2), caudal (A_3), medial (A_4), and distal (A_5) views. **B.** Strigidae gen. et sp. indet. (SAM-PQ-L28479 C), left tibiotarsus in cranial view. **C.** *Bubo* sp. (SAM-PQ-L28439 C), left tibiotarsus in cranial view.

Discussion

The extraordinarily rich fossil avifauna found at Langebaanweg makes it one of the most important bird localities of the world (Manegold et al. 2013), but, despite this great diversity, it has a relatively low number of owl taxa. This could be related to the fact that the fossil bearing sediments of the Upper Varswater Formation were deposited in coastal and fluvial environments. It appears that the fossil strigiforms are generally better represented, in terms of species diversity and number of bones, in karst-related fossil localities, such as Quercy, France, and Gargano, Italy, where at least 11 and 7 owl taxa have been found respectively (Ballmann 1973, 1976; Mourer-Chauviré 1987), than in non-cavity sites, such as Saint-Gérard-le-Puy, France, where only 3 owl taxa are recorded (Mourer-Chauviré et al. 2013). Furthermore, several insular fossil bird associations are especially complex as it comes to the diversity of owls represented therein (Louchart 2005; Pavia 2008; Guerra et al. 2013). However, the diversity of owl species recorded at Langebaanweg is comparable, even higher, than that of most of the Neogene and Early Pleistocene African and European continental fos-

sil localities (e.g., Ballmann 1969; Brodkorb and Mourer-Chauviré 1984; Tyrberg 1998; Louchart et al. 2009; Bedetti and Pavia 2013; Mourer-Chauviré et al. 2013). Four owl species, referable to *Tyto*, *Asio*, *Bubo* and at least one additional indeterminate taxon, are also recorded from the Pliocene of Laetoli (Louchart 2011).

Palaeoenvironmental implications.—Extant species of the owl genera *Tyto*, *Asio*, *Athene*, and *Bubo* are rather generalist taxa occurring in various environments ranging from open grasslands to tropical rainforests and taiga forests. Thus, evidence for these genera at Langebaanweg provides no indication for any particular palaeoenvironments in this area during the early Pliocene. Many extant owl species, in fact, breed in tree cavities or adopt abandoned nests built in trees by other bird species, while a few species, such as *As. flammeus* and *As. capensis* breed on the ground in open grasslands as well as in thick bush lands. We suppose that the proportionally more elongated hind limb elements of *At. inexpectata* (Fig. 2A, F) indicate that this species was more terrestrial than *At. noctua*. Similarly elongated hind limbs are known for the fossil taxa *At. cretensis*, *At. megalopeza*, and *At. trinacriae*, and especially pronounced in the extant terrestrial *At. cunicularia* (Pavia and Mourer-Chauviré 2002; Louchart 2005; König and Weick 2008). Unfortunately, no complete tibiotarsus is known for the fossil species making more detailed comparisons of hind limb proportions in fossil and modern *Athene* species impossible. The tarsometatarsus of *At. inexpectata* seems to be as robust as in *At. angelis* from the Pleistocene of Corsica (Antoine Louchart, written communication 2014), which is supposed to have been an arboreal species as suggested by the stoutness of the hind limb bones (Louchart 2002). In general the strigiforms found at Langebaanweg agree with the palaeoenvironmental reconstruction, based on the other vertebrate taxa, of mosaic of different habitats ranging from almost arid areas and open grasslands to fresh- and saltwater wetlands, and woodlands (Manegold et al. 2013).

Palaeobiogeographical implications.—Although it is very difficult to understand the relationships between *Tyto richae* sp. nov. and the other species of *Tyto*, both living and fossil, on the basis of the known material from Langebaanweg, it seems reasonable to speculate that the closest relatives of *T. richae* sp. nov. are the Neogene Palaearctic *Tyto* species such as *T. sanctialbani* and *T. campiterrae* rather than *T. alba* or *T. capensis*, which are known only from the upper Pliocene and Upper Pleistocene respectively (Harrison 1980; Mourer-Chauviré and Geraads 2010). Aside its age, such a relationship of *T. richae* sp. nov. is suggested by its greater resemblance to *T. sanctialbani* than to *T. alba* and *T. capensis*. *Tyto richae* sp. nov. is biogeographically well separated from its Palaearctic counterparts by the Sahara, which affected the past and current distributions of African taxa since its formation during the Middle-Late Miocene (Douady et al. 2003; Schuster et al. 2006; Brito et al. 2011). As a yet undescribed *Tyto* remains from the Pliocene of

Ethiopia (Louchart et al. 2009), which was larger than *T. alba* (Antoine Louchart personal communication), might be referable to *T. richae* sp. nov., it would further suggest that this species had have a much wider distribution on the African continent.

Evidence for a species of *Athene* in southern Africa challenges earlier hypotheses on the early diversity and centre of origin of this taxon. The previously known pre-Pleistocene fossil record of *Athene* was limited to a few taxa with probable close affinities to *At. cunicularia* from the early Pliocene of Idaho and the early late Pliocene of Kansas and Nebraska (Ford 1966; Ford and Murray 1967; Feduccia 1970; Bell et al. 2004), and *Athene* sp. from the late Pliocene of Bulgaria (Boev 2002). The fossil record of *At. noctua* does not pre-date the Early Pleistocene and is limited to European localities (Mlíkovský 2002; Bedetti and Pavia 2013), as is the case with the additional four palaeospecies of *Athene* from the Mediterranean Basin (Guerra et al. 2012). Thus, it was hitherto reasonable to suppose that *Athene* originated in the Northern Hemisphere and became a typical element of the Palaearctic fauna. This hypothesis is also supported by the great diversification of the genus in the Western Palaearctic from the Pleistocene onwards, as testified by the recognition of several fossil and living taxa (Pavia and Mourer-Chauviré 2002; König and Weick 2008; Guerra et al. 2012; Pellegrino et al. 2014). *Athene inexpectata* sp. nov. now provides evidence for a former much wider distribution of the genus and one could speculate that this taxon in fact originated in Africa. Be that as it may, the presence of an otherwise primarily Eurasian taxon such as *Athene* in the extreme South of Africa is not without parallels: Langebaanweg has also produced remains of the bear *Agriotherium africanum* and the wolverine *Plesiogulo monspessulanus* (Hendey 1980; Werdelin and Peigné 2010), whose closest relatives were once widespread in the Northern Hemisphere. This fact can be interpreted as additional evidence of the biogeographical links between Eurasia and South Africa subsequent to the Late Miocene collision of the African and Eurasian plates that allowed the mixing of taxa previously endemic to each of these continents (Roberts et al. 2011). Finally, it is noteworthy that evidence for owl taxa now endemic to Africa, such as *Ptilopsis*, is still lacking for any African fossil sites including Langebaanweg.

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