

A LARGE OWL FROM THE PALAEOCENE OF FRANCE

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ABSTRACT. Strigiformes have a very long palaeontological history and were much more diversified in the past than they are at present. *Berruornis orbisantiqui* gen. et sp. nov., from the Upper Palaeocene (Thanetian) of the Reims area, is a large owl, with a stout tarsometatarsus. It belongs to the Sophiornithidae, previously described from the Upper Eocene to Upper Oligocene of the Phosphorites du Quercy, France. The comparison of the distal part of the tarsometatarsus in different extinct forms shows a general trend towards a progressively more semizygodactyl foot, with an internal trochlea more posteriorly oriented, and an external trochlea more medially incurved; correspondingly the size of the internal trochlea compared with the middle trochlea decreases.

BIRD remains found in the Palaeocene deposits of the area of Reims, in north-eastern France, have been known for over a century (Lemoine 1878–1881). They mainly include large forms belonging to *Gastornis* and *Remiornis*. Part of this material was recently revised by Martin (1992), who placed *Gastornis* in the order Gastornithiformes and created for *Remiornis* the new order Remiornithiformes, in the Palaeognathae.

Excavations in the region of Cernay-lès-Reims, and mainly in Mont Berru, have been resumed by D. E. Russell who has collected a large quantity of mammals and a few bird remains. The dating of these localities has been carried out by Russell (1964) on the mammal faunas. Apart from the large forms, the fossil avifauna includes Gruiformes (Cariamidae and Messelornithidae; Mourer-Chauviré in press), Charadriiformes, 'Form-Family' Graculavidae, and a large form of owl, which is relatively abundant, and is the subject of the present study.

The osteological terminology generally follows Howard (1929) and, when necessary, Baumel (1979a). Institutional abbreviations are: AMNH, American Museum of Natural History, New York, USA; KUMNH, Kansas University Museum of Natural History, Lawrence, Kansas, USA; USNM, National Museum of Natural History, Washington D.C., USA.

SYSTEMATIC PALAEOONTOLOGY

Class AVES Linnaeus, 1758

Order STRIGIFORMES Wagler, 1830

Family SOPHIORNITHIDAE Mourer-Chauviré, 1987

Type-genus. *Sophiornis* Mourer-Chauviré, 1987

Other genera. *Berruornis* gen. nov.

Distribution. Palaeocene of the Reims area, and Upper Eocene to Upper Oligocene of Phosphorites du Quercy, France.

Genus BERRUORNIS gen. nov.

Type-species. *Berruornis orbisantiqui* sp. nov.

Distribution. Upper Palaeocene of the Reims area, Thanetian, Mammal Reference-Level MP 6 (Schmidt-Kittler 1987).

Diagnosis. Tarsometatarsus showing the characteristic features of the Sophiornithidae, but differing from *Sophiornis* by 1, proximal part of internal calcaneal ridge situated slightly distally compared with the internal cotyla; 2, internal calcaneal ridge perforated by a foramen. Features unknown in *Sophiornis* are: 3, middle trochlea relatively narrow and slightly longer distally than internal trochlea; 4, external trochlea much shorter distally than middle trochlea, very narrow and prolonged by a posteriorly directed wing. On the distal part of the tibiotarsus; 5, internal condyle relatively narrow and not flattened; 6, supracondylar fossa on the internal side of the shaft.

Derivation of name. 'Berru', from the locality of Mont Berru, and 'ornis', bird.

Berruornis orbisantiqui sp. nov.

Plate 1, figures 1–14

Holotype. Museum national d'Histoire naturelle de Paris, R 4155, incomplete right tarsometatarsus; from Mont Berru, Reims area, France.

Material (all in the same collection as the holotype). Mont Berru: BR 11186, left tibiotarsus, fragment of distal part; BR 11195, right tarsometatarsus, fragment of proximal part and shaft; BR 12482–12483, right tarsometatarsus, fragments of proximal and distal parts; BR 14571, right tarsometatarsus, shaft and incomplete distal part, subadult; Cernay area: L 3096, cast of a complete right tarsometatarsus.

Horizon and localities. Upper Palaeocene, Thanetian, Mammal Reference-Level MP 6 (Schmidt-Kittler 1987), Reims area (Cernay and Mont Berru), Marne Département, France.

Diagnosis. As for the genus.

Dimensions. See Tables 1–2.

Derivation of name. From 'orbis', the world, and 'antiquus', old, because this genus (and family), are known only from the Old World.

Description and comparisons

Tarsometatarsus (Pl. 1, figs 1–13). The tarsometatarsus corresponds to a large form, approximately of the size of the Recent Eagle Owl (*Bubo bubo*). It is very stout, with a wide shaft. This feature is not so well developed in BR 14571, which is subadult.

EXPLANATION OF PLATE 1

Figs 1–14. *Berruornis orbisantiqui*, gen. nov. sp. nov.; collection of the Muséum national d'Histoire naturelle de Paris. 1–5, R 4155, right tarsometatarsus holotype; 1, anterior view; $\times 1$. 2, internal view showing the break of the internal calcaneal ridge at the level of the foramen; $\times 1$. 3, posterior view; $\times 1$. 4, proximal view; $\times 1.5$. 5, distal view; $\times 1.5$. 6–10, L 3096, cast of right tarsometatarsus; 6, anterior view; $\times 1$. 7, internal view showing the break of the internal calcaneal ridge at the level of the foramen; $\times 1$. 8, posterior view; $\times 1$. 9, proximal view; $\times 1.5$. 10, distal view; $\times 1.5$. 11–12, BR 12483; fragment of proximal part of right tarsometatarsus; 11, internal view, showing the foramen in the internal calcaneal ridge; $\times 1.5$. 12, medial view of the internal calcaneal ridge; $\times 1.5$. 13, BR 12482; fragment of distal part of right tarsometatarsus; internal trochlea; internal view; $\times 1.5$. 14, BR 11186; left tibiotarsus, incomplete distal part, anterior view; $\times 1$.

Figs 15–16. *Sophiornis quercynus*, collection Musée Guimet d'Histoire naturelle de Lyon, PQ 1202. 15, anterior view; $\times 1$. 16, posterior view; $\times 1$.

Fig. 17. *Palaeoglaux perrierensis*, collection Université des Sciences et Techniques du Languedoc, Montpellier. PRR 2576; right tarsometatarsus, paratype; distal view; $\times 2$.

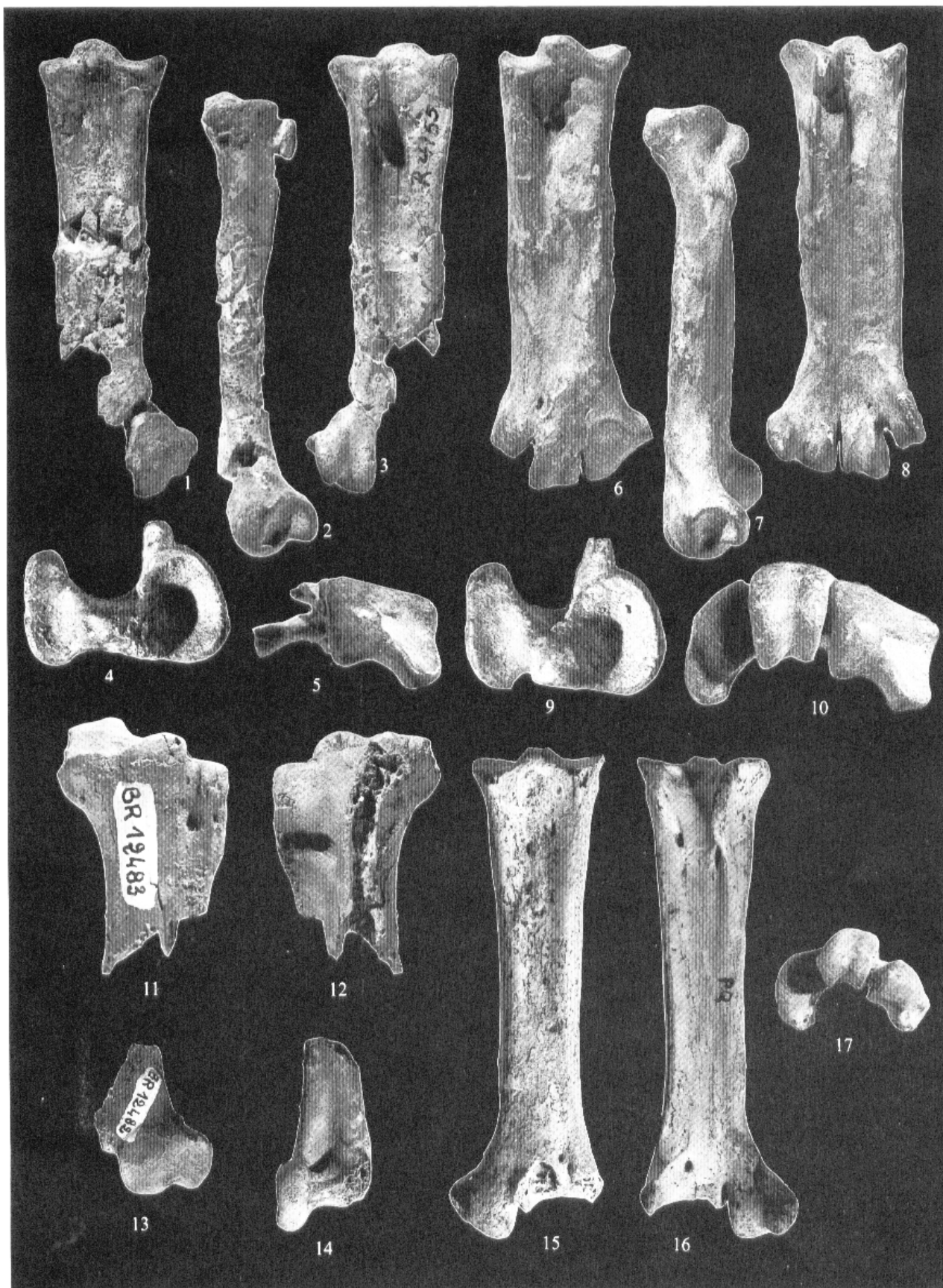


TABLE 1. Dimensions of the tarsometatarsus in *Sophiornithidae*, in mm. (a) Proximal depth from anterior edge of internal cotyle to posterior end of internal calcaneal ridge.

Tarsometatarsus	<i>Berruornis orbisantiqui</i>					<i>Sophiornis quercynus</i>
	R4155 Holotype	L3096	BR12482 and 12483	BR11195	BR14571 juv.	PQ 1202
Total length	69.8 as pres.	68.5	—	—	—	74.0 as pres.
Prox. width	19.9	19.4 as pres.	—	—	—	19.9
Prox. depth (a)	13.7	15.0 as pres.	17.0	—	—	17.2
Width shaft in the middle	14.2 as pres.	16.2	—	11.8	9.1	12.1
Depth shaft in the middle	6.8 as pres.	6.2	—	7.2	5.2	6.0
Distal width	—	24.1	—	—	—	23.7
Distal depth	—	14.0	—	—	—	13.0 as pres.
Width int. trochlea	12.0	12.5	15.8	—	11.7	13.3
Width middle trochlea	—	7.5	—	—	4.3	—
Width ext. trochlea	—	4.8	—	—	—	—
Depth int. trochlea	9.4	9.7	11.7	—	8.7 as pres.	8.7
Depth middle trochlea	—	10.0	—	—	7.0 as pres.	—
Depth ext. trochlea	—	12.7	—	—	—	—

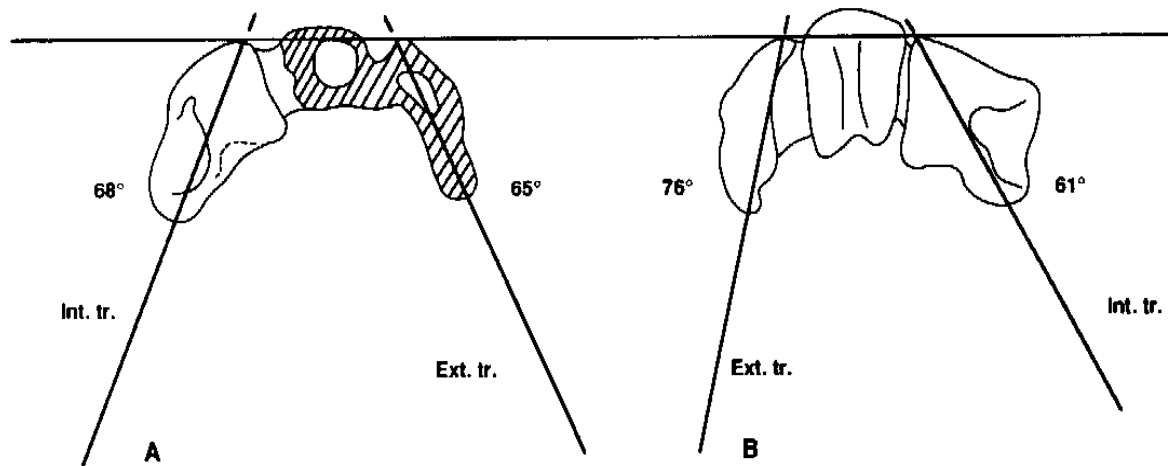
TABLE 2. Dimensions of the distal part of tibiotarsus in some fossil owls, in mm. (a) In Rich (1982) the measurements are given for *Protostrix*, but this generic name is a junior synonym of *Minerva* (Mourer-Chauviré 1983). * measured from the illustrations in Fischer (1983).

Tibiotarsus	<i>Berruornis orbisantiqui</i> BR 11186	<i>Minerva leptosteus</i> (Rich 1982) (a)	<i>Minerva antiqua</i> (Mourer-Chauviré 1983)	<i>Oligostrix rupelensis</i> (Fischer 1983)
Distal width (as preserved)	14.2	13.5	15.8–15.9	7.0
Distal depth (as preserved)	13.3	—	—	6.0
Width internal condyle	5.0	—	6.3–6.8	3.3*
Width of shaft at the level of insertion of retinaculum extensorium tibiotarsi	8.6	—	—	3.7*
Depth of shaft at the same level	5.8	—	—	—

In proximal view, the proximal articular surface is anteroposteriorly narrow at the level of the intercotylar prominence, and this intercotylar prominence is medio-laterally elongated. These features are clearly visible on the holotype, and are slightly different on L 3096 which seems to have suffered some deformation. On the anterior face, the proximal foramina are very small. The internal foramen is situated slightly more distally than the external foramen. It is not possible to see the tubercle for *m. tibialis anticus* because of the poor preservation of the anterior surface of the shafts.

The tarsometatarsus of *Berruornis* exhibits the characteristic features of the *Sophiornithidae*: on the anterior face, a shallow depression below the proximal articular surface but no real anterior metatarsal groove; no ossified supratendinal bridge; posterior metatarsal groove very shallow; cross-section of shaft rectangular; trochleae arranged along a weakly curved line, but differs from the type genus *Sophiornis* by the following features: proximal articular surface very narrow at the level of the intercotylar prominence (wider in *Sophiornis*); proximal surface of the internal calcaneal ridge situated distally compared with the internal cotyle (at the same level as internal cotyle in *Sophiornis*); internal calcaneal ridge wide, straight in internal view, and pierced by a foramen (thin, semi-circular in shape in internal view, proximo-distally elongated, not perforated

in *Sophiornis*); proximal surface of the external calcaneal ridge distinct from the external cotyle (as an extension of the external cotyle in *Sophiornis*); external calcaneal ridge relatively thin and posteriorly directed (wider and postero-externally directed in *Sophiornis*); anterior infracotylar fossa slightly indicated, with traces of insertion of a non-ossified supratendinal bridge (almost missing, with no visible traces of supratendinal bridge in *Sophiornis*); posterior metatarsal groove shallow (almost completely missing in *Sophiornis*); internal trochlea directed internally and posteriorly, with an angle of 61° compared with the anterior face (directed more posteriorly, with an angle of 68° in *Sophiornis*) (Text-fig. 1); deep fossa on the internal face of the internal



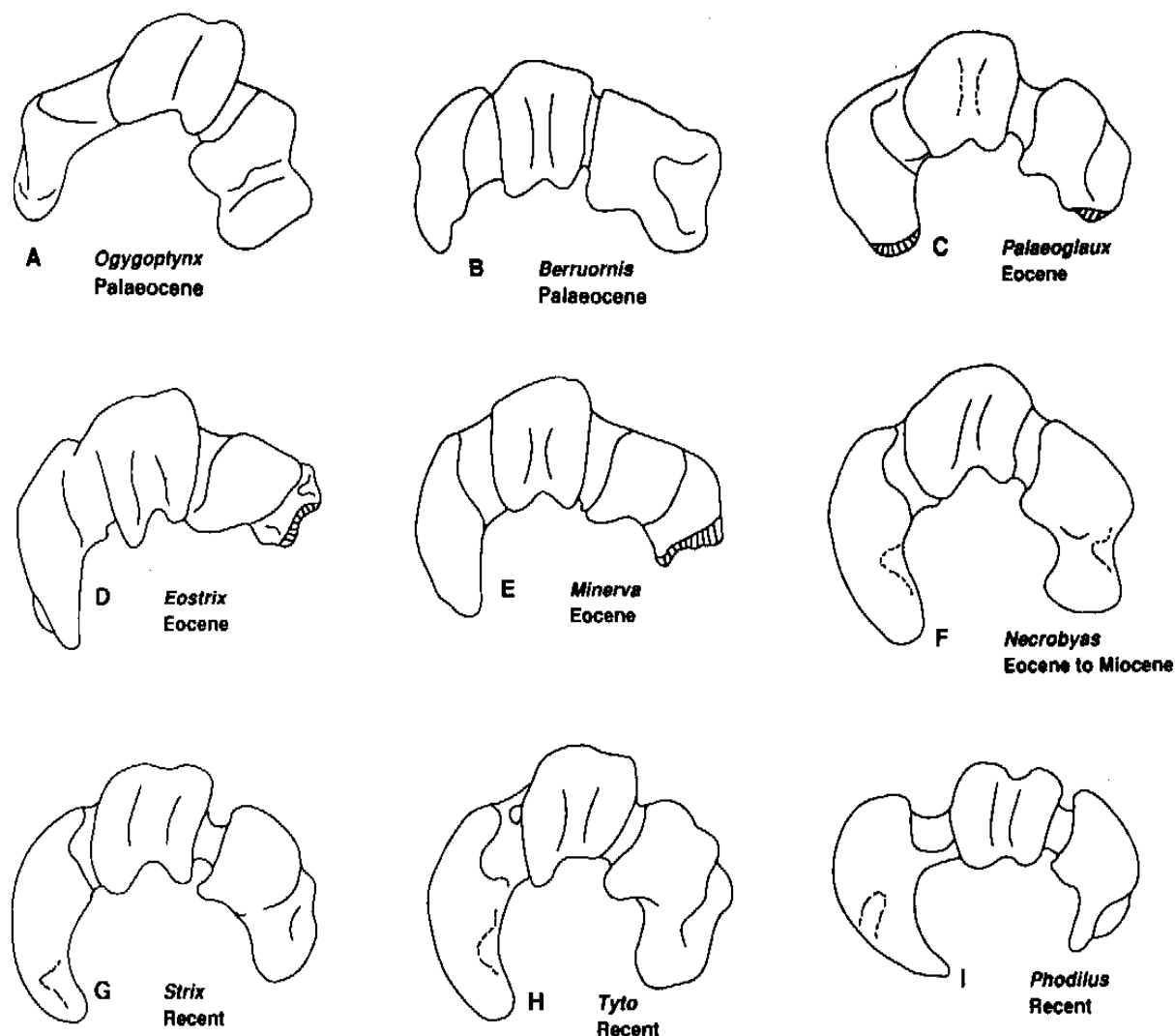
TEXT-FIG. 1. Tarsometatarsus in distal view. Angle of the internal and external trochleae compared with a straight line drawn through the anterior part of these trochleae. A, *Sophiornis quercynus*, PQ 1202, holotype, left tarsometatarsus. Hatched area represents missing parts. B, *Berruornis orbisantiqui*, L 3096; right tarsometatarsus.

trochlea (shallower fossa in *Sophiornis*); articular surface of the internal trochlea forming a spike above the wing of the trochlea, this spike also exists in the protostrigids *Eostrix martinellii* (Martin and Black, 1972) and *Minerva leptosteus* (Rich, 1982) (spike much less developed in *Sophiornis*); external trochlea directed almost posteriorly, with an angle of 76° compared with the anterior face (not so posteriorly directed, with an angle of 65° in *Sophiornis*) (Text-fig. 1); in posterior view, proximal part of external trochlea situated more proximally than the proximal part of internal trochlea (proximal part of external and internal trochleae situated at the same level in *Sophiornis*); metatarsal facet for digit I well marked, in particular on BR 11195, and situated on the internal side of the shaft (more weakly indicated and situated on the postero-internal angle of the shaft in *Sophiornis*).

In *Berruornis*, on the posterior face, the external proximal foramen is situated at the base of the external calcaneal ridge and the internal proximal foramen on the medial side of the internal calcaneal ridge, but the latter is prolonged by a foramen which goes through the calcaneal ridge and which is clearly visible on fragment BR 12483 (Pl. 1, figs 11–12). The presence of this foramen has produced a weakness in the internal calcaneal ridge, which is broken at the level of this foramen on the other two specimens (R 4155 and L 3096) (Pl. 1, figs 2, 7). In the Recent Strigiformes as well as in *Sophiornis*, the *arteriola tarsalis plantaris* (Baumel 1979b, p. 372, annt. 79) of the inner side goes directly through the internal proximal foramen from the anterior face to the internal side of the internal calcaneal ridge, while in *Berruornis* this arteriola first goes out on the medial side of the internal calcaneal ridge, then crosses through the calcaneal ridge.

At the distal end, in *Berruornis* as in *Sophiornis*, the internal trochlea is very wide and strong. The external and middle trochleae are incompletely preserved in *Sophiornis* and are only known in *Berruornis*. The internal trochlea is slightly shorter than the middle trochlea, while the external trochlea is considerably shorter. In distal view (Text-fig. 2b), the middle trochlea is slightly asymmetrical, with an external border slightly deeper than the internal border. The external trochlea is narrow, with a weakly developed wing, and is directed almost posteriorly.

On the grounds of the morphological differences between the form from Mont Berru and that from Quercy, it seems justified to place them in two different genera. Moreover they are separated by a long interval of time. The Mont Berru form is dated from the Thanetian (between 58 and 54 Ma; Savage and Russell 1983). The age of the Quercy form is not known accurately but lies between the beginning of the Upper Eocene (about 38 Ma),



TEXT-FIG. 2. The right tarsometatarsus, in distal view, in different species of fossil and Recent Strigiformes. All the figures have been brought to the same distal width, and the figures concerning left tarsometatarsi have been reversed in order to make the comparison easier. This figure shows the evolution of the external trochlea which becomes increasingly posteriorly elongated and internally curved in the course of time. The internal trochlea, strongly developed in Sophiornithidae (B) and Protostrigidae (D-E) becomes proportionally smaller and its orientation, internal in Sophiornithidae, becomes increasingly posterior. A, *Ogygoptynx wetmorei*, AMNH 2653; right tarsometatarsus; Palaeocene; $\times 6.5$, after Rich and Bohaska 1976. B, *Berruornis orbisantiqui* gen. et sp. nov. L 3096; right tarsometatarsus; Palaeocene; $\times 2.3$. C, *Palaeoglaux perrierensis*, PRR 2576; right tarsometatarsus; Eocene; $\times 4.9$. D, *Eostrix martinellii*, KUMNH 16601; left tarsometatarsus (reversed); Eocene; $\times 6$, after Martin and Black 1972. E, *Minerva leptosteus*, AMNH 2629, right tarsometatarsus; Eocene; $\times 4$, after Rich 1982. F, *Necrobyas harpax*, QU 16298; left tarsometatarsus (reversed); Oligocene; $\times 5.66$. G, *Strix aluco*, Lyon 252-1; right tarsometatarsus; Recent; $\times 4.8$. H, *Tyto alba*, Lyon 245-1; right tarsometatarsus; Recent; $\times 5.8$. I, *Phodilus badius*, USNM 20310; left tarsometatarsus (reversed); Recent; $\times 4.66$.

and the end of the Upper Oligocene (about 24 Ma; ages after Harland *et al.* 1989). The interval of time which separates the two forms therefore is from a minimum of 16 Ma to a maximum of 34 Ma.

Tibiotarsus (Pl. 1, fig. 14). On the distal part of tibiotarsus BR 11186, only part of one condyle is preserved (only its anterior half). The presence of the tubercle for the attachment of *retinaculum extensorium tibiotarsi* (Baumel 1979a), just below the break of the bone, and the presence on the external side, above the missing condyle, of a longitudinal ridge which limits backwards the groove for *peroneus profundus*, make it possible to state that this tibiotarsus is from the left side, and that the preserved condyle is the internal one.

This condyle is relatively narrow and anteriorly and distally rounded. It is very different from the condition found in the Protostrigidae, where the internal condyle is strongly widened and flattened. This can also be confirmed by the shape of the internal cotyle of the tarsometatarsus, which is hollow. This internal cotyle could not have corresponded to a flattened internal condyle of tibiotarsus.

On the anterior face of the shaft, above the intercondylar groove, there is a shallow, but well indicated, supracondylar fossa, situated on the internal side of the shaft. Unlike the condition of the internal condyle, the presence of a supracondylar fossa situated on the internal side of the shaft is known in all the members of the family Protostrigidae (Wetmore 1933, 1937, 1938; Fischer 1983; Mourer-Chauviré 1983). The position and development of the supracondylar fossa is different in the other Recent and fossil Strigiformes (Mourer-Chauviré 1987). The intercondylar groove is relatively wide, wider than in Recent Strigidae and Tytonidae. On the posterior face, the condyles are not preserved, the posterior intercondylar groove is wide and there is no supracondylar fossa, while this fossa exists in the Recent Strigiformes.

Comparison with other fossil Strigiformes

(a) *Bradycnemidae*. The oldest fossils described as Strigiformes form the basis of the extinct family Bradycnemidae (Harrison and Walker 1975) from the Upper Cretaceous of Romania, but subsequent authors (Brodkorb 1978; Olson 1985) have argued that the remains from which this family was created are not avian.

(b) *Ogygoptyngidae*. The oldest strigiform presently known is *Ogygoptynx* (*Ogygoptyngidae*), from the Palaeocene (Tiffanian) of Colorado (Rich and Bohaska 1976, 1981). Several hypotheses have been proposed for the correlations between the Palaeocene and Lower Eocene of Europe and North America in recent years (Savage and Russell 1983; Russell *et al.* 1990), but according to the latter (1990, p. 29, my translation): 'it seems that there are some indications that a large part of the Middle and Late Paleocene (Torrejonian, Tiffanian, Clarkforkian) of North America could be equivalent to the Thanetian of Europe'. In this case, *Berruornis*, from the Thanetian, could compete with *Ogygoptynx* as the world's oldest owl.

The *Ogygoptyngidae* differ from the *Sophiornithidae* in the following main characteristics: tarsometatarsus slender and elongated; deep anterior metatarsal groove; proximal articular surface in proximal view shaped like a parallelogram; internal trochlea decidedly longer than middle trochlea; in distal view, curvature across the trochleae much more developed (Text-fig. 2A); in distal view, external trochlea not smoothly rounded but slightly grooved laterally (Rich and Bohaska 1976, 1981).

(c) *Protostrigidae*. This family is represented by three genera: *Eostrix*, from the Lower and Middle Eocene of the United States, and to which has been attributed a pedal phalanx from the Lower Eocene of England (Harrison 1980; Olson 1985), *Minerva*, from the Middle and Upper Eocene of the United States (Mourer-Chauviré 1983; Olson 1985), and *Oligostrix*, from the Lower Oligocene of Germany (Fischer 1983). It is the only extinct family of Strigiformes which is known both from Europe and North America. These forms are mainly represented by distal parts of tibiotarsus, distal parts of tarsometatarsus, and pedal phalanges.

The Protostrigidae differ from the *Sophiornithidae* because, in the former the internal condyle of tibiotarsus is distinctly widened and flattened; on the tarsometatarsus the anterior metatarsal groove is deep across the full width of the proximal end (Mourer-Chauviré 1983), and the curvature across the trochleae is much more pronounced (Text-fig. 2D-E). The internal trochlea is strongly developed but not to such an extent as in *Sophiornithidae*.

(d) *Palaeoglaucidae*. This family consists of one genus, *Palaeoglaux*, and two species, *P. artophoron* (Peters 1992), from the Middle Eocene of Messel, in Germany, and *P. perrierensis* (Mourer-Chauviré 1987), from the Upper Eocene of Phosphorites du Quercy. *Palaeoglaux* differs from the *Sophiornithidae* by its tarsometatarsus which is more slender and has an anterior metatarsal groove (Peters 1992). In *P. perrierensis* the distal part of the tarsometatarsus strongly widens at the level of the internal and external trochleae, which distinctly project on the internal and external sides

respectively, and the internal trochlea is almost as wide as the middle trochlea, while in *B. orbisantiqui* the internal trochlea is much wider (Pl. 1, fig. 17; Text-fig. 2c).

(e) *Other fossil forms from the Phosphorites du Quercy*. The other extinct genera from the Phosphorites du Quercy such as *Necrobyas* Milne-Edwards, 1892, *Nocturnavis* Mourer-Chauviré, 1987, *Palaeobyas* Mourer-Chauviré, 1987, *Palaeotyto* Mourer-Chauviré, 1987, and *Selenornis* Mourer-Chauviré, 1987, have been described in detail and ascribed to the Recent family Tytonidae (Mourer-Chauviré 1987).

(f) *Eoglaucidium pallas* Fischer, 1987. This genus and species, from the Middle Eocene of Geiseltal, Mammalian Reference-levels MP 11, 12, and 13 (Schmidt-Kittler 1987) is known from eight humeri. It was classified in the Recent family Strigidae but, according to Peters (1992) and to Mlikovsky (1992), who is studying other elements associated with these humeri, it may belong to the Coraciiformes.

(g) *Genus incertae sedis Eupternis Lemoine, 1878*. Lemoine (1878–1881, 1884) described from the locality of Cernay the genus *Eupternis*, the type of which is a distal part of ulna, strongly flattened and which looks somewhat like the ulna of a loon (Gaviidae). Its systematic position is not yet defined (Lambrecht 1933; Brodkorb 1963; Olson 1985), and it is better to consider it as incertae sedis. The illustrations of the holotype and of a wing phalanx referred to the same species, do not show any resemblances to Strigiformes and therefore the tibiotarsus and tarsometatarsi from Cernay and Mont Berru cannot be attributed to that genus.

(h) *Strigiform from the Upper Palaeocene of Kazakhstan*. A pedal phalanx of a large-sized strigiform has been reported and illustrated by Nessonov (1992, fig. 5j and k) from the Upper Palaeocene (Landenian) of the Zhylga locality in Kazakhstan. From its size, this phalanx could correspond to *Berruornis*. This indicates that large owls were also present during the Palaeocene in Central Asia.

CONCLUSIONS

The Strigiformes, which are represented today by only two families, were already very diverse during the Palaeocene, where they are represented by two families, the Ogygoptyngidae, which are known only from one small form, and the Sophiornithidae, which are, on the contrary, large forms.

This diversification continued during the Eocene, where four families are known, three extinct, namely the Protostrigidae, the Sophiornithidae, and the Palaeoglaucidae, and the Recent family Tytonidae, which is represented in the Phosphorites du Quercy deposits by two extinct subfamilies, the Necrobyinae, and the Selenornithinae. The Protostrigidae are themselves very diverse and could belong to two distinct families (Olson 1985).

These families, with the exception of Palaeoglaucidae, persisted during the Oligocene, and there is in the United States a large quantity of Oligocene owl material which has not yet been studied (Olson 1985). Among the Recent suprageneric taxa, the Tytoninae and the Strigidae appear in Europe from the Lower Miocene (Mourer-Chauviré 1987). The Strigiformes have, therefore, a very long palaeontological history and in the past they were more diverse than they are now.

The Recent Strigiformes have a semizygodactyl foot, which means that digit IV can be directed forwards or backwards. According to Raikow (1985, p. 119): 'Presumably this ability enhances the functional potential of the foot'.

In the Ogygoptyngidae the shape of the foot, in distal view, is very peculiar (Text-fig. 2A). It seems that digits II and IV could be strongly splayed and that the foot could have developed into an ectropodactyl type, similar to that which can be observed in the Piciformes when climbing on a vertical surface (Raikow 1985).

In families other than Ogygoptyngidae it is possible to see, from the Sophiornithidae (Text-fig. 2B), then the Protostrigidae (Text-fig. 2D and 2E), then the Palaeoglaucidae (Text-fig. 2C), to the

Necrobyinae (Text-fig. 2F) and the Recent forms, Strigidae (Text-fig. 2G), Tytoninae (Text-fig. 2H), Phodilinae (Text-fig. 2I), an evolution towards a more and more semizygodactyl type, with the trochlea for digit IV directed first extero-posteriorly, then more and more posteriorly, then more and more curved medially, the maximum being reached in the Recent genus *Phodilus* (Text-fig. 2I). At the same time the trochlea for digit II, strongly developed in the Sophiornithidae and Protostrigidae, becomes proportionally smaller, and its orientation also changes. The wing of this trochlea is predominantly oriented internally in the Sophiornithidae and becomes more posteriorly oriented in the other families. This can be explained from the functional point of view either by progressively more pronounced perching habits, or by a better adaptation to the capture of prey. In the first case, that would indicate that the Sophiornithidae were more terrestrial than the Recent Strigiformes.

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