

## “Old World phorusrhacids” (Aves, Phorusrhacidae): a new look at *Strigogyps* (“*Aenigmavis*”) *sapea* (Peters 1987)

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The discovery of phorusrhacid-like birds (Aves, Phorusrhacidae) in early Tertiary deposits of France and Germany has been of great paleobiogeographic interest, as these flightless birds were previously known only from the New World. In this study, the species from Messel in Germany (“*Aenigmavis*”) *sapea* Peters 1987) is reevaluated and its taxonomy revised. It is shown that *Aenigmavis* Peters 1987 and *Ameghinornis* Mourer-Chauviré 1981, the other European taxon, are junior synonyms of *Strigogyps* Gaillard 1908. *Strigogyps* (“*Ameghinornis*”) *minor* Gaillard 1939 is considered a junior synonym of *Strigogyps dubius* Gaillard 1908. A newly identified, well-preserved wing of *Strigogyps* is described and it is shown that this taxon lacks several derived characters that characterize the Phorusrhacidae, including a dorso-ventrally deep mandible, a strut-like coracoid, an extremely reduced wing, a block-like hypotarsus, and a reduced hindtoe.

### INTRODUCTION

Phorusrhacids or “terror birds” (Aves, Phorusrhacidae) are extinct flightless relatives of the South American seriemas (Cariamidae) that underwent a major radiation in the Tertiary of South America and are assumed to have been carnivorous predators (e.g., Andrews 1899, Sinclair and Farr 1932, Alvarenga and Höfling 2003). Phorusrhacid-like birds also were reported from the early Tertiary of France (Mourer-Chauviré 1981) and Germany (Peters 1987). The French species, “*Ameghinornis minor*” (Gaillard 1939), is known from a humerus, two coracoids, and two carpometacarpi from the Quercy fissure fillings. These bones were not found in association but, because of their strikingly phorusrhacid-like morphology, they were considered to be from the same species by Mourer-Chauviré (1981, 1983). The holotypic humerus of “*A. minor*” was originally described by Gaillard (1939) as *Strigogyps minor*, who (Gaillard 1908) had earlier described a distal tibiotarsus from the Eocene locality Escamps in the Quercy region as *Strigogyps dubius*, the only other species of the genus *Strigogyps*. The original description of the German species, “*Aenigmavis sapea* Peters 1987, is based on a postcranial skeleton (Fig. 1) and a referred foot. Although the wing bones are very poorly preserved in this specimen, Peters (1987) correctly noticed its close relationship to the French phorusrhacid-like taxon.

Being considered birds with weak flight capabilities, or even completely flightless, the European phorusrhacid-like birds subsequently played a central role in discussions on a late Cretaceous/early Tertiary land connection between Europe and South America, either via Africa or North America (Mourer-Chauviré 1981, 1982, 1999, Buffetaut and Rage 1982, Storch and Schaarschmidt 1988, Peters 1991, Peters and Storch 1993, Rage 1999). Recently, however, Alvarenga and Höfling (2003) doubted phorusrhacid affinities of *Ameghinornis* and *Aenigmavis*, and noted that the hypotarsus of *Aenigmavis* “differs substantially from that

of the Phorusrhacidae” and that “the proportions of the *Aenigmavis* skeleton are different from those observed in the Phorusrhacidae (...), thus excluding running habits for *Aenigmavis*” (Alvarenga and Höfling 2003: 63).

Here, I present new evidence that “*Aenigmavis sapea* is not a member of the Phorusrhacidae and show that *Aenigmavis* and *Ameghinornis* are junior synonyms of *Strigogyps*, with which the Messel taxon has not yet been compared.

### MATERIAL AND METHODS

The fossil specimens are deposited in the collection of Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (SMF); osteological terminology follows Baumel and Witmer (1993).

### SYSTEMATIC PALEONTOLOGY

AVES Linnaeus 1758

AMEGHINORNITHIDAE Mourer-Chauviré 1981, new rank  
*Strigogyps* Gaillard 1908

*Ameghinornis* Mourer-Chauviré 1981:638–643, pl. 1, figs. 1 and 2

*Aenigmavis* Peters 1987:71–77, figs. 1–12

*Strigogyps sapea* (Peters 1987)

*Aenigmavis sapea* Peters 1987:71–77, figs. 1–12

### COMPARATIVE OSTEOLOGY OF *STRIGOGYPS*

The holotype of *Strigogyps sapea* (SMF-ME 1818, formerly coll. Maschwitz; Fig. 1) has been described in detail by Peters (1987), and the following mentions mainly those features that support the synonymy of *Aenigmavis* Peters 1987 and *Strigogyps* Gaillard 1908.

Only a small fragment of the caudal part of the skull of *Strigogyps sapea* is preserved in the holotype, including the quadrate and what I consider to be the caudal part of the mandible (Fig. 2). Peters (1987) identified the latter bone as

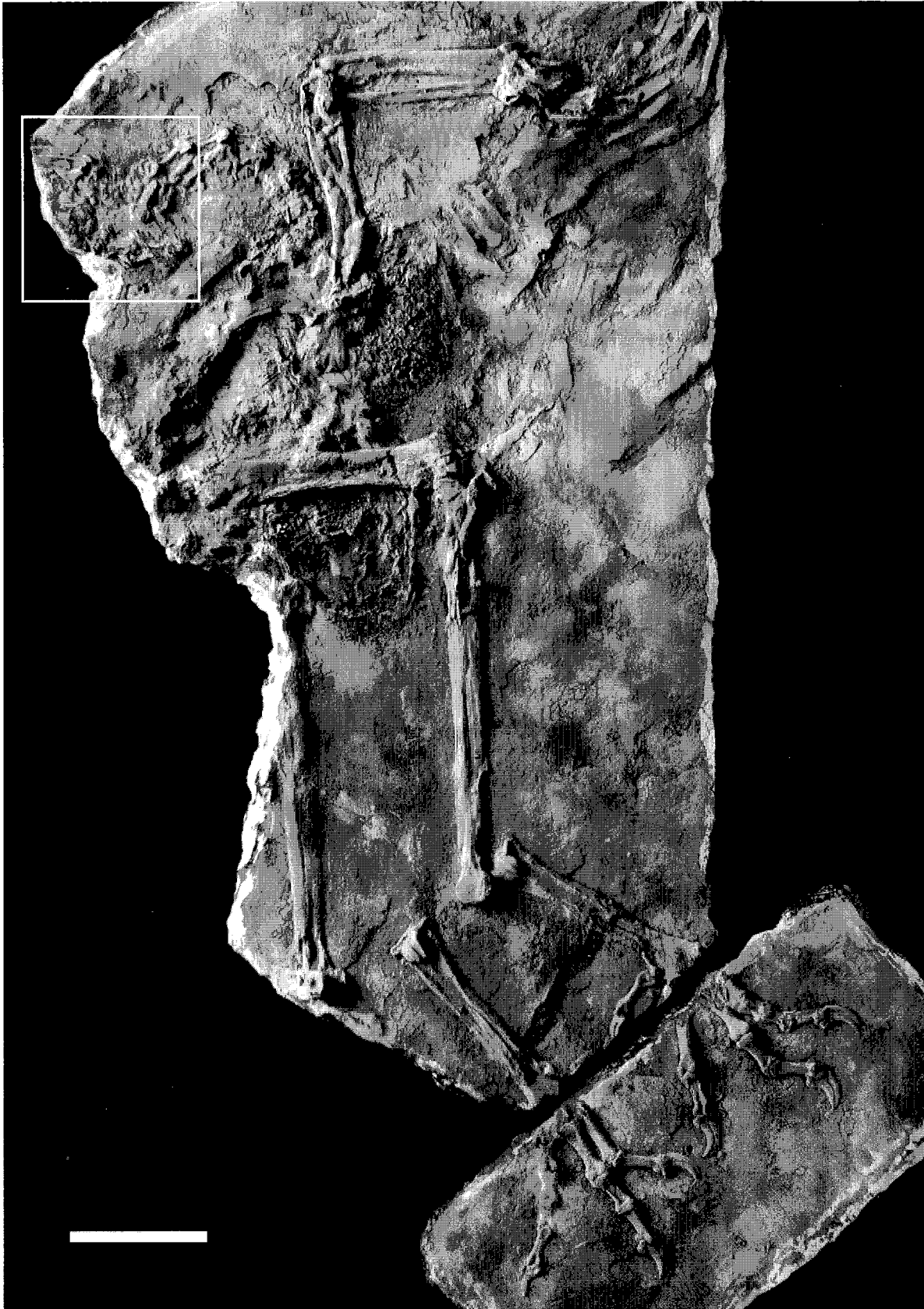


Fig. 1. *Strigogyps sapea* (Peters 1987), holotype (SMF-ME 1818). The frame indicates the position of the detail seen in Fig. 2. Specimen coated with ammonium chloride. Scale bar equals 50 mm.

a pterygoid for which it is, however, proportionally too large given the size of the quadrate (Fig. 2). The proportionally small size of the quadrate indicates that *Strigogyps* had a small skull in relation to its body size as is the case in, for example, modern landfowl (Galliformes) and screamers (Anhimidae), but contrary to phorusrhacids in which the skull is very large. The mandible (Fig. 2) is not nearly as deep dorso-ventrally as that of the Phorusrhacidae.

The wing is poorly preserved in the *S. sapea* holotype but there is a newly identified and well-preserved wing of *Strigogyps* sp., also from the type locality Messel. This specimen (SMF-ME 11094, Fig. 3) shares with *S. sapea* a derived morphology of the humerus and derived length proportions of the wing bones (see below). It is smaller than the holotype of *Strigogyps sapea* (Table 1) but otherwise very similar in its morphology. It may either belong to a smaller species or to a different sex if *Strigogyps* was sexually dimorphic in size like modern Galliformes (male distinctly larger) or most birds of prey (female distinctly larger). The humerus of SMF-ME 11094 further closely resembles that of “*Ameghinornis minor*” (here synonymized with *Strigogyps dubius*, Fig. 4). As in the latter species and the *S. sapea* holotype, the proximal end of the bone is proportionally very small, the crista bicipitalis and crista deltopectoralis are strongly reduced, and the caput humeri is oriented more obliquely to the longitudinal axis of the bone than in most other avian taxa. As in “*A. minor*” but contrary to phorusrhacid birds (see Alvarenga and Höfling 2003: fig. 5), the processus flexorius is not markedly distally protruding.

In concordance with the *S. sapea* holotype, the wing of specimen SMF-ME 11094 has very unusual proportions in that the ulna is decidedly shorter than the humerus and the hand (carpometacarpus and distal phalanges) is as long as the ulna. The carpometacarpus is proportionally longer than in the Phorusrhacidae, and the os metacarpale minus is not as bowed as in phorusrhacid birds and the specimen referred to “*Ameghinornis minor*” by Mourer-Chauviré (1981).

The coracoid (SMF-ME 11094) lacks a foramen nervi supracoracoidei and is not as elongated and slender as the coracoid referred to “*Ameghinornis minor*” by Mourer-Chauviré (1981) and the coracoid of phorusrhacid birds.

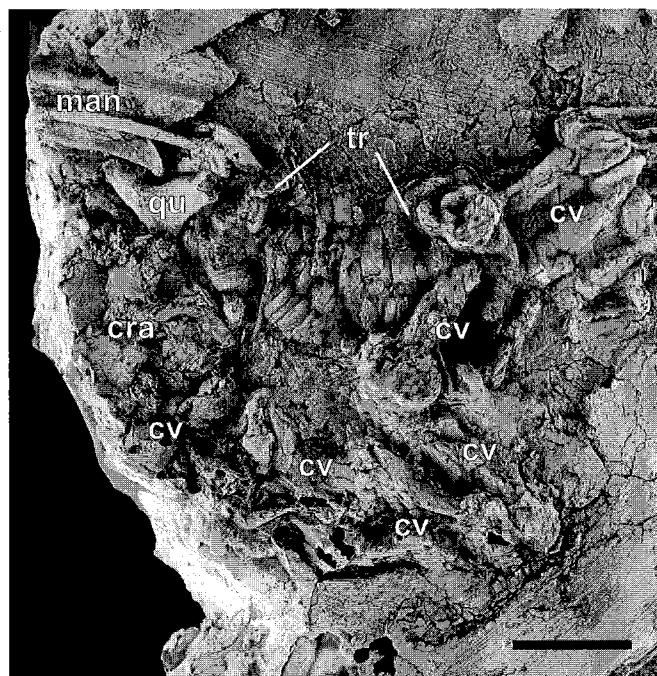


Fig. 2. *Strigogyps sapea* (Peters 1987), holotype (SMF-ME 1818), skull fragment. **Abbreviations:** cra, cranium; cv, cervical vertebra; man, caudal part of mandible; qu, quadrate, tr, tracheal rings. Coated with ammonium chloride to enhance contrast. Scale bar equals 10 mm.

Unfortunately, most of the extremitas omalis of the coracoid of specimen SMF-ME 11094 is hidden behind the overlying acromion of the scapula. The facies articularis scapularis appears to have been cup-like, but only a very small part of it is visible. Contrary to phorusrhacid birds, the processus procoracoideus is well-developed.

Apart from being slightly smaller, the distal tibiotarsus (Fig. 5) of *Strigogyps sapea* very closely resembles that of *Strigogyps dubius* as figured by Gaillard (1908) (Fig. 4). The condyli are of different size, with the condylus lateralis being larger than the condylus medialis. The condylus lateralis has a nearly circular outline in lateral view (Fig. 5). The epicondylus

**Table 1.** Bone dimensions (in mm) of the holotype of *Strigogyps sapea* (Peters 1987), specimen SMF-ME 11094 (*Strigogyps* sp.), and *Strigogyps dubius* Gaillard 1908 in comparison. **Abbreviations:** cmc, carpometacarpus; hum, humerus; tbt, tibiotarsus.

	hum	ulna	cmc	tbt, distal width	Length hum: distal width tbt
<i>Strigogyps sapea</i> (holotype)	~87	~75	~38 <sup>1</sup>	~15 <sup>2</sup>	~5.8
<i>Strigogyps</i> sp. (SMF-ME 11094)	71.8	56.6	37.7	—	—
<i>Strigogyps dubius</i>	120 <sup>3</sup>	—	—	20.2 <sup>3</sup>	5.9

<sup>1</sup>estimated, the bone is strongly deformed in the specimen, Peters (1987) estimated its length with 40–45 mm.

<sup>2</sup>estimated.

<sup>3</sup>after Mourer-Chauviré (1981) and Gaillard (1908).

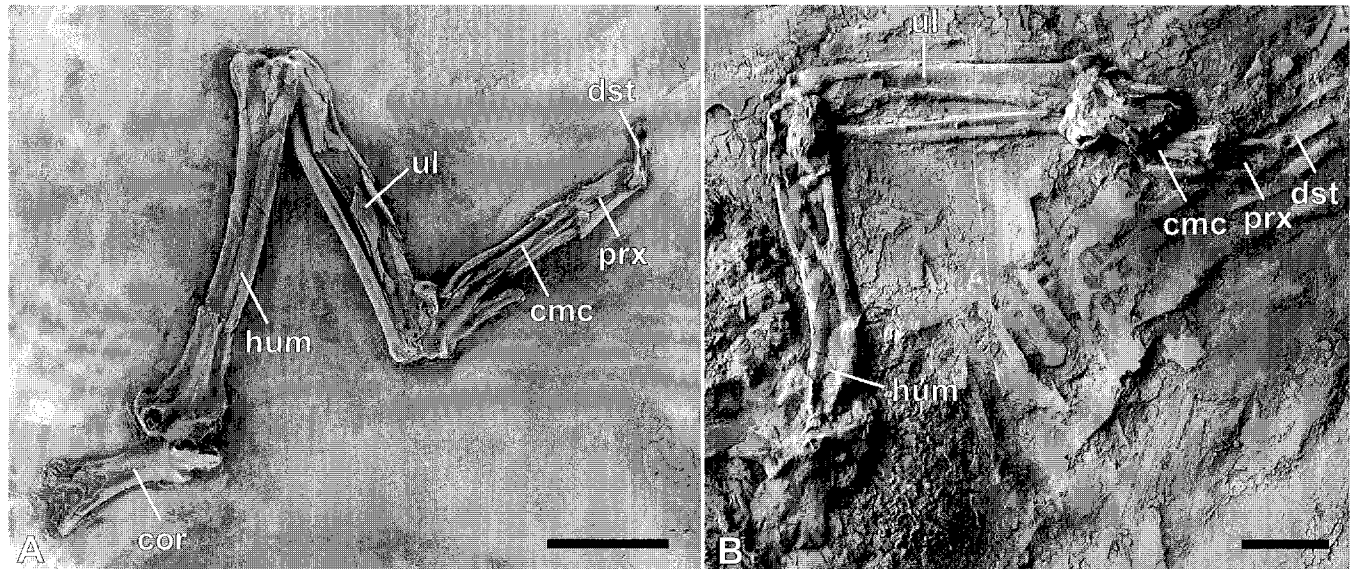


Fig. 3. A. Newly identified left wing of *Strigogyps* sp. (SMF-ME 11094) B. Left wing of the *S. sapea* holotype. Abbreviations: cmc, carpometacarpus; cor, coracoid; dst, phalanx distalis digiti majoris; hum, humerus; prx, phalanx proximalis digiti majoris; ul, ulna. Specimens coated with ammonium chloride. Scale bars equal 20 mm.

medialis protrudes and there is a distinct pit cranial to it on the medial surface of the condylus medialis (Fig. 5). There is a marked sulcus extensorius proximal to the condyles (Fig. 5). The most unusual feature of the tibiotarsus of *Strigogyps* is the complete lack of an ossified pons supratendineus, a feature already noted by Peters (1987) for *Strigogyps sapea*. Among extant birds, an ossified pons supratendineus is absent in most ratites (except moas, Dinornithidae, and kiwis, Apterygidae), the hoazin (Opisthocomidae), few grebes (Podicipedidae), some parrots (Psittacidae), owls (Strigiformes), hornbills (Bucerotidae), the oilbird (Steatornithidae), and potoos (Nyctibiidae). The distal tibiotarsus of these taxa otherwise, however, strongly differs from that of *Strigogyps*.

I identified a well-preserved tarsometatarsus of *Strigogyps sapea* (SMF-ME 1819, Fig. 6) that was found after the publication of Peters' (1987) study and that exhibits more osteological details than the previously known tarsometatarsi of *S. sapea*. This bone differs from the otherwise very similar tarsometatarsus of *Idiornis* spp. (e.g., Mourer-Chauviré 1983) in the proportionally shorter trochlea metatarsi III and the presence of a protruding crista medialis hypotarsi (Fig. 5). Apart from being proportionally shorter and much stouter, the tarsometatarsus of *S. sapea* most closely resembles that of modern Psophiidae, especially in the morphology of its proximal and distal ends. The distal tarsometatarsus of *S. sapea* differs from that of phorusrhacid birds in the proportionally wider trochleae metatarsorum II and IV, which in *S. sapea* bear more strongly developed, plantarly projecting flanges.

#### DISCUSSION

Both morphology and proportions (Tab. 1) of the somewhat smaller *Strigogyps sapea* holotype suggest that the distal

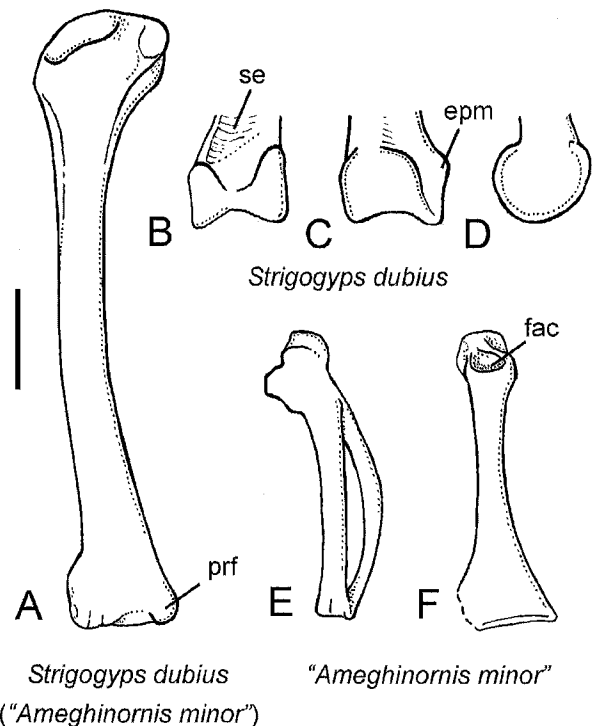


Fig. 4. Humerus (A) and distal tibiotarsus (B–D) of *Strigogyps dubius* Gaillard 1908, and carpometacarpus (E) and coracoid (F) referred to "*Ameghinornis minor*" by Mourer-Chauviré (1981). The humerus is the type specimen of *Strigogyps (Ameghinornis) minor* Gaillard 1939. A. Caudal aspect (after Mourer-Chauviré 1981, 1983). B. Cranial aspect (after Gaillard, 1908). C. Caudal aspect (after Gaillard, 1908). D. Lateral aspect (after Gaillard, 1908). E. Dorsal aspect (after Mourer-Chauviré 1981, 1983). F. Dorsal aspect (after Mourer-Chauviré 1981, 1983). Abbreviations: epm, epicondylus medialis; fac, facies articularis scapularis; prf, processus flexorius; se, sulcus extensorius. Scale bar equals 20 mm.

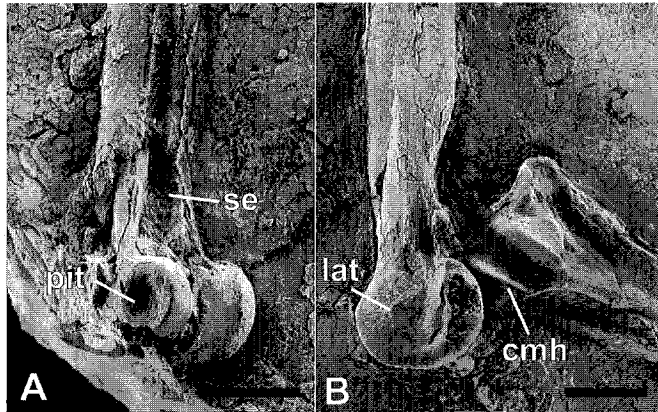


Fig. 5. *Strigogyys sapea* (Peters 1987), holotype (SMF-ME 1818). A. Distal end of left tibiotarsus. B. Distal end of right tibiotarsus and proximal end of right tarsometatarsus. Abbreviations: cmh, crista medialis hypotarsi; pit, pit cranial to the epicondylus medialis; lat, condylus lateralis; se, sulcus extensorius. Coated with ammonium chloride to enhance contrast. Scale bars equal 10 mm.

tibiotarsus from the Quercy locality Escamps, described as *Strigogyys dubius* by Gaillard (1908), belongs to the same species as the humerus from an unknown Quercy locality, which Gaillard (1939) described as *Strigogyys minor*. Thus, *Strigogyys minor* Gaillard 1939 (“*Ameghinornis minor*”) is a junior synonym of *Strigogyys dubius* Gaillard 1908. Although being the more appropriate and euphonic names, *Aenigmavis* Peters 1987 and *Ameghinornis* Mourer-Chauviré 1981 are junior synonyms of *Strigogyys* Gaillard 1908, a taxon that is very well characterized by the derived morphology of its reduced wing and distal tibiotarsus (see description above and Figs. 3–5).

The phorusrhacid-like coracoid and carpometacarpus assigned to “*Ameghinornis minor*” by Mourer-Chauviré (1981) differ from the corresponding elements of *Strigogyys*, as exemplified by the referred wing SMF-ME 11094, and may belong to a flightless species of the Idiornithidae, such as the large *Propelargus* Lydekker, 1891 (see Mourer-Chauviré 1983:119).

Despite a similar humerus morphology, *Strigogyys* lacks derived characters that characterize members of the Phorusrhacidae. Most notably, the skull is not large with a dorsoventrally deep mandible, the coracoid (visible in specimen SMF-ME 11094) is not strut-like with a narrow shaft, the wing is not as greatly reduced, the carpometacarpus is proportionally longer and with a less bowed os metacarpale minus (SMF-ME 11094), the hypotarsus is not block-like (i.e., without protruding cristae, cf. Alvarenga and Höfling 2003), and the hindtoe is not as strongly reduced. *Strigogyys* is also distinguished from phorusrhacid birds by the absence of an ossified pons supratendineus at the distal tibiotarsus, although this characteristic may well be an apomorphy of *Strigogyys*.

I concur with Alvarenga and Höfling (2003) that *Strigogyys sapea* and *S. dubius* are not members of the Phorusrha-

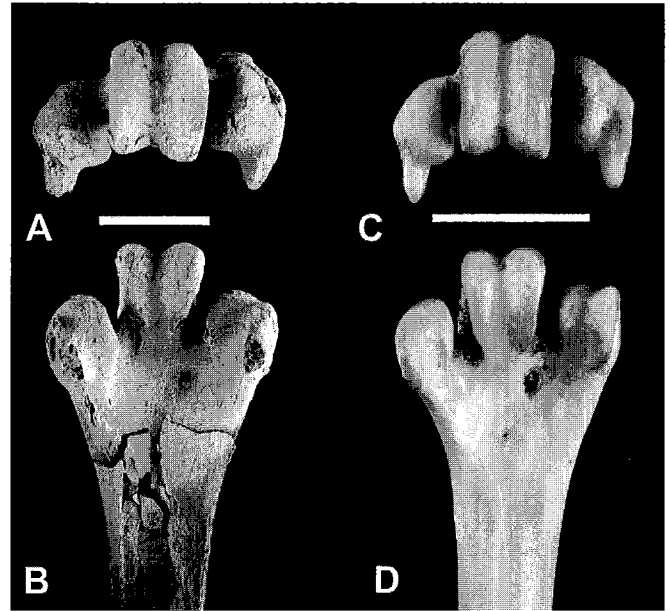


Fig. 6. A, B. *Strigogyys sapea* (Peters 1987), distal end of left tarsometatarsus (specimen SMF-ME 1819). C, D. Modern *Psophia crepitans* (Psophiidae), distal end of left tarsometatarsus. A, C. Distal view. B, D. Plantar view. Fossil specimen coated with ammonium chloride. Scale bars equal 10 mm.

cidae, although their phylogenetic affinities to modern birds are uncertain. As I noted previously (Mayr 2000), *Strigogyys* may be a relative of the equally enigmatic Messel bird *Salmilla robusta* that also appears to lack an ossified pons supratendineus (Mayr 2000: 192) and, apart from the less reduced wing, exhibits a similar overall morphology to *Strigogyys sapea* with equally robust hind limbs. *Salmilla robusta* shares derived characters with modern Psophiidae and Cariamidae (Mayr 2000, 2002). *Strigogyys sapea* further resembles the late Eocene North American species *Neocathartes grallator* Wetmore 1944. The tibiotarsus of the only known specimen of *N. grallator* lacks an ossified pons supratendineus, although Wetmore (1944: 66) assumed that it “has been broken away”. *Neocathartes* was described as a New World Vulture (Cathartidae) by Wetmore (1944) but assigned to the Cariamae by Olson (1985).

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