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A POSTCRANIAL SKELETON OF *PALAEOPSITTACUS* HARRISON, 1982 (AVES INCERTAE SEDIS) FROM THE MIDDLE EOCENE OF MESSEL (GERMANY)

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Abstract : A nearly complete postcranial skeleton of *Palaeopsittacus* cf. *georgei* Harrison, 1982 (Aves incertae sedis) is described from the Middle Eocene of Messel, Germany. This is the first articulated skeleton assigned to *Palaeopsittacus*, which before was only known from a few isolated bones from the Lower Eocene of England. Further, the new specimen is the first record of *Palaeopsittacus* outside the type locality Walton-on-the-Naze. *Palaeopsittacus* is not closely related to the Psittaciformes (parrots) to which it was originally assigned, though its true systematic affinities remain uncertain. In the morphology of its tarsometatarsus, the Eocene genus resembles recent Podargidae (Caprimulgiformes). An isolated skull from Messel is figured which might also belong to *Palaeopsittacus*.

Key words : Fossil birds, Middle Eocene, Messel, Palaeopsittacus georgei, new specimen

Un squelette post-crânien de *Palaeopsittacus* Harrison, 1982 (Aves) de l'Éocène moyen de Messel (Allemagne)

Résumé : Un squelette post-crânien presque complet de *Palaeopsittacus* cf. *georgei* Harrison, 1982 (Aves incertae sedis) est décrit de l'Éocène moyen de Messel, Allemagne. C'est le premier squelette articulé attribué à *Palaeopsittacus* qui n'était connu, auparavant, que par quelques ossements isolés de l'Éocène inférieur d'Angleterre. Le nouveau spécimen est la découverte la plus ancienne du genre *Palaeopsittacus*, en dehors de la localité type de Walton-on-the-Naze. *Palaeopsittacus* n'est pas apparenté aux Psittaciformes (perroquets) auxquels il était originellement attribué, bien que ses réelles relations systématiques restent incertaines. Par la morphologie de ses tarsométatarses, le genre éocène ressemble aux Podargidae (Caprimulgiformes) actuels. Un crâne isolé de Messel est figuré; il appartient probablement au genre *Palaeopsittacus*.

Mots clés : Oiseaux fossiles, Éocène moyen, Messel, Palaeopsittacus georgei, nouveaux spécimen

INTRODUCTION

The avian species *Palaeopsittacus georgei* was described by Harrison (1982) from the Lower Eocene London Clay of Walton-on-the-Naze (Essex, England). The type specimen (BMNH A 5163) consists of 11 bones, including a nearly complete coracoid, both ends of the ulna, the proximal half of the scapula, the distal end of the carpometacarpus, the distal end of the tibiotarsus, and the proximal end of the tarsometatarsus. Harrison (1982) further referred a distal end of a tarsometatarsus from the Middle Eocene of Lee-on-Solent, Hampshire, England (Gosport Museum 977262, to be re-catalogued as part of the collections of the Hampshire County Council Museum Service, see Dyke & Cooper 2000: p. 280) to *P. georgei*. In the original description, the taxon was assigned to the Psittaciformes (parrots); Mourer-Chauviré (1992) also classified *Palaeopsittacus* within the Psittaciformes but included it into the new Eocene family Quercypsittidae (meanwhile, however, the specimens in the collection Daniels, she referred to on p. 171, turned out to be basal psittaciform birds not closely related to *Palaeopsittacus*, see

Mayr & Daniels, 1998).

Mayr & Daniels (1998) described additional specimens of *Palaeopsittacus georgei* from the type locality Walton-on-the-Naze. These bones come from two individuals and comprise a coracoid and a tarsometatarsus of a juvenile bird, and a distal part of a tibiotarsus and a tarsometatarsus of an adult (fig. 1). They exhibit the characteristic morphology of the corresponding elements of the holotype (e.g. coracoid with foramen nervi supracoracoidei, incisura intercondylaris of distal tibiotarsus very wide, hypotarsus with two canals). The referred tarsometatarsi clearly show that *P. georgei* is no member of the Psittaciformes since the species lacks the zygodactyl foot characteristic of all other members of the Psittaciformes, and further reveal that the referred distal end of a tarsometatarsus from Lee-on-Solent is not from *P. georgei*.

After plotting the width of the proximal ulna against the dimensions of various other bones, Dyke & Cooper (2000) concluded that the proximal end of the ulna was incorrectly referred to *P. georgei* by Harrison (1982), and that the species was «most likely based on some unassociated material». However, concerning recent birds, Dyke & Cooper (2000) made comparisons only with Psittaciformes and the results of their analysis thus merely show, that in its bone proportions *Palaeopsittacus* differs from parrots.

In this study, I describe a specimen of *Palaeopsittacus* from the Middle Eocene of Messel, Germany, which is the first articulated skeleton of this taxon and the first record outside the type locality (a survey on the fossil avifauna from Messel was given by Peters, 1988 and Mayr, 2000, general information on the site can be found in Schaal & Ziegler, 1988). *Palaeopsittacus* is yet another bird that exemplifies the great concordance between the early Eocene avifaunas of Walton-on-the-Naze and Messel (see Mayr, 1998a; Mayr, 1998b; Mayr & Daniels, 1998).

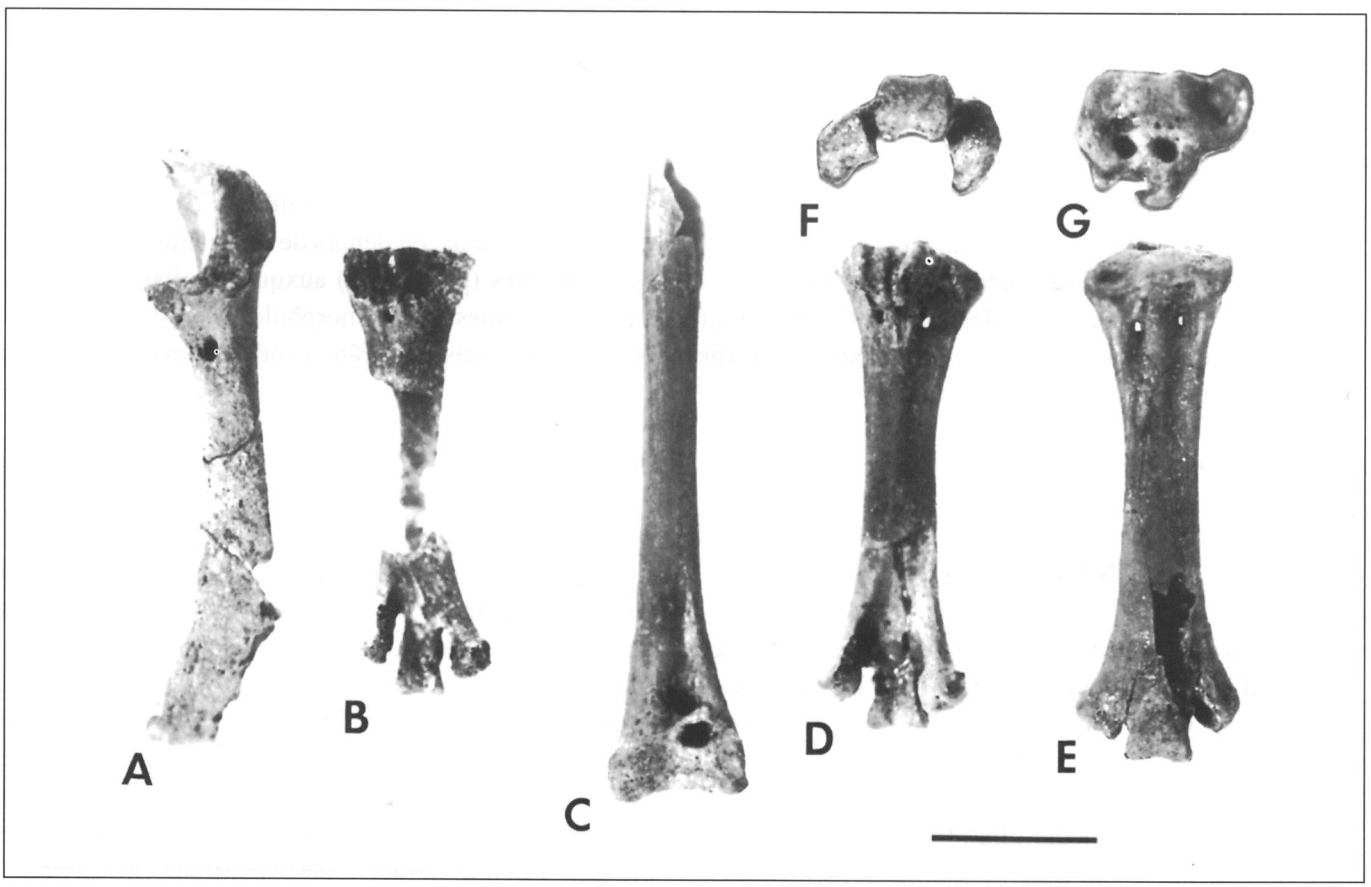

Fig. 1. *Palaeopsittacus georgei*, referred specimens from the Lower Eocene London Clay of Walton-on-the-Naze (England). WN 94838B (juvenile specimen), A: right coracoid, B: left tarsometatarsus. WN 91682 (adult specimen), C: right tibiotarsus, D-G: left tarsometatarsus in plantar (D), dorsal (E), distal (F), and proximal (G) view. From Mayr & Daniels (1998), photographs by M. Daniels. Scale bar equals 5 mm.

The anatomical terminology follows Baumel & Witmer (1993). The dimensions are in millimeters and represent the maximum length of the bone along its longitudinal axis. Regarding the claws, the distance between the tuberculum extensorium and the apex phalangis has been measured. Institutional abbreviations: BMNH - The Natural History Museum, London; SMF - Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; SMNK - Staatliches Museum für Naturkunde Karlsruhe, Germany; WN - collection of M. Daniels, Holland-on-Sea, Essex, England.

SYSTEMATIC PALEONTOLOGY

Order and family incertae sedis
***Palaeopsittacus* Harrison, 1982**
***Palaeopsittacus* cf. *georgei* Harrison, 1982**
Figs. 1-5

Referred specimen : SMNK.PAL.3834a+b (nearly complete postcranial skeleton on two slabs, figs. 2, 3).

Dimensions : Coracoid, ~ 23.1 (l)/23.1 (r); humerus, 45.0 (l)/~45.0 (r); ulna, 47.7 (l)/~47.0 (r); carpometacarpus, 24.4 (l)/24.5 (r); femur, ~28 (l)/~27.5 (r); tibiotarsus, ~31.8 (l)/~31.8 (r); tarsometatarsus, 15.3 (l)/~15.7 (r). Pedal phalanges: dI p1, 8.8; dI p2, 5.1; dII p1, 6.1; dII p2, 5.5; dII p3, ~5.4; dIII p1, 7.0; dIII p2, ~6.5; dIII p3, 7.4; dIII p4, 6.0; dIV p1, 3.5; dIV p2, 3.2; dIV p4, ~5.5; dIV p5, 5.0.

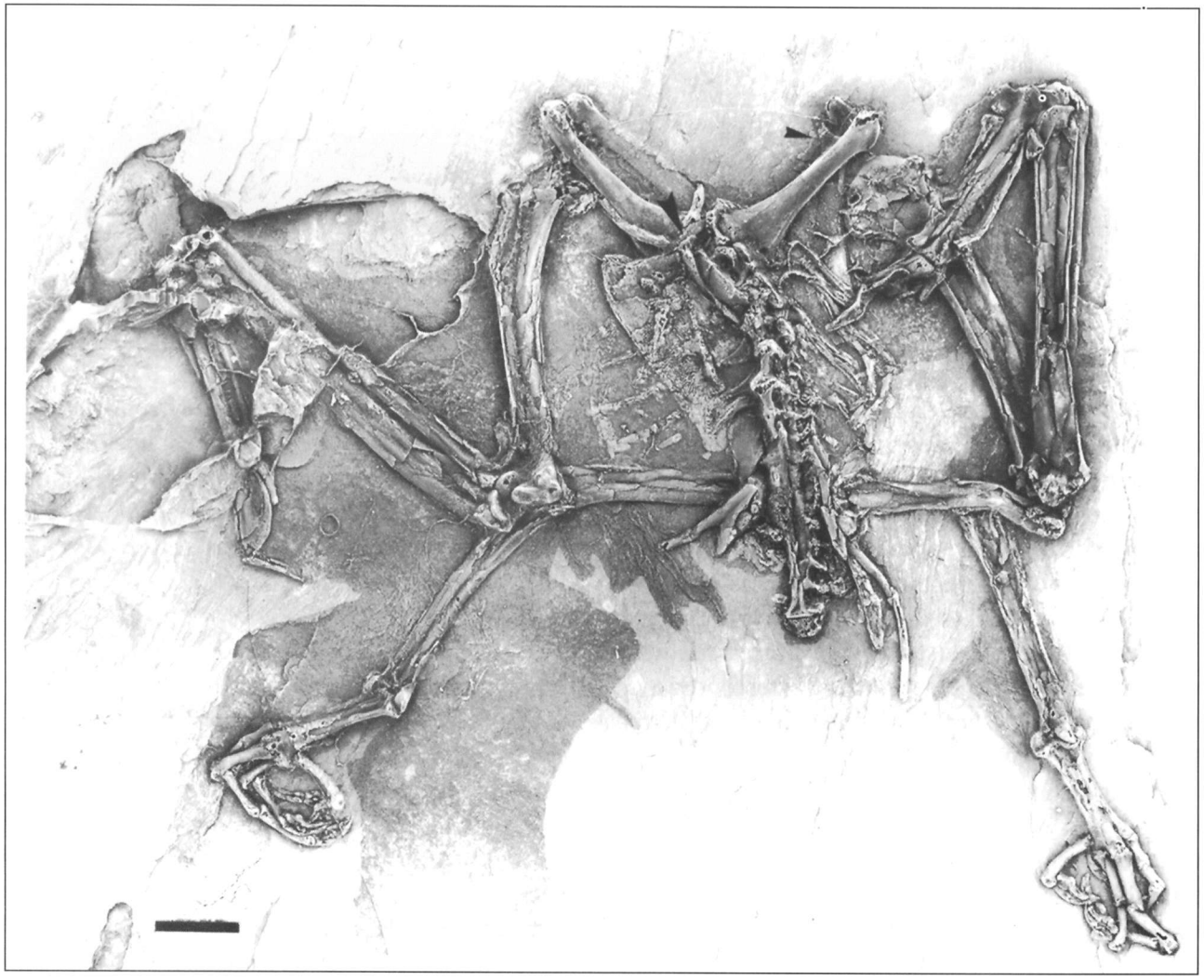

Fig. 2. *Palaeopsittacus* cf. *georgei*, referred specimen from the Middle Eocene of Messel (Germany); SMNK.PAL.3834a. The large arrow indicates the spina externa of the sternum, the small arrow points to the processus procoracoideus of the coracoid. Coated with ammonium chloride to enhance contrast, scale bar equals 10 mm.

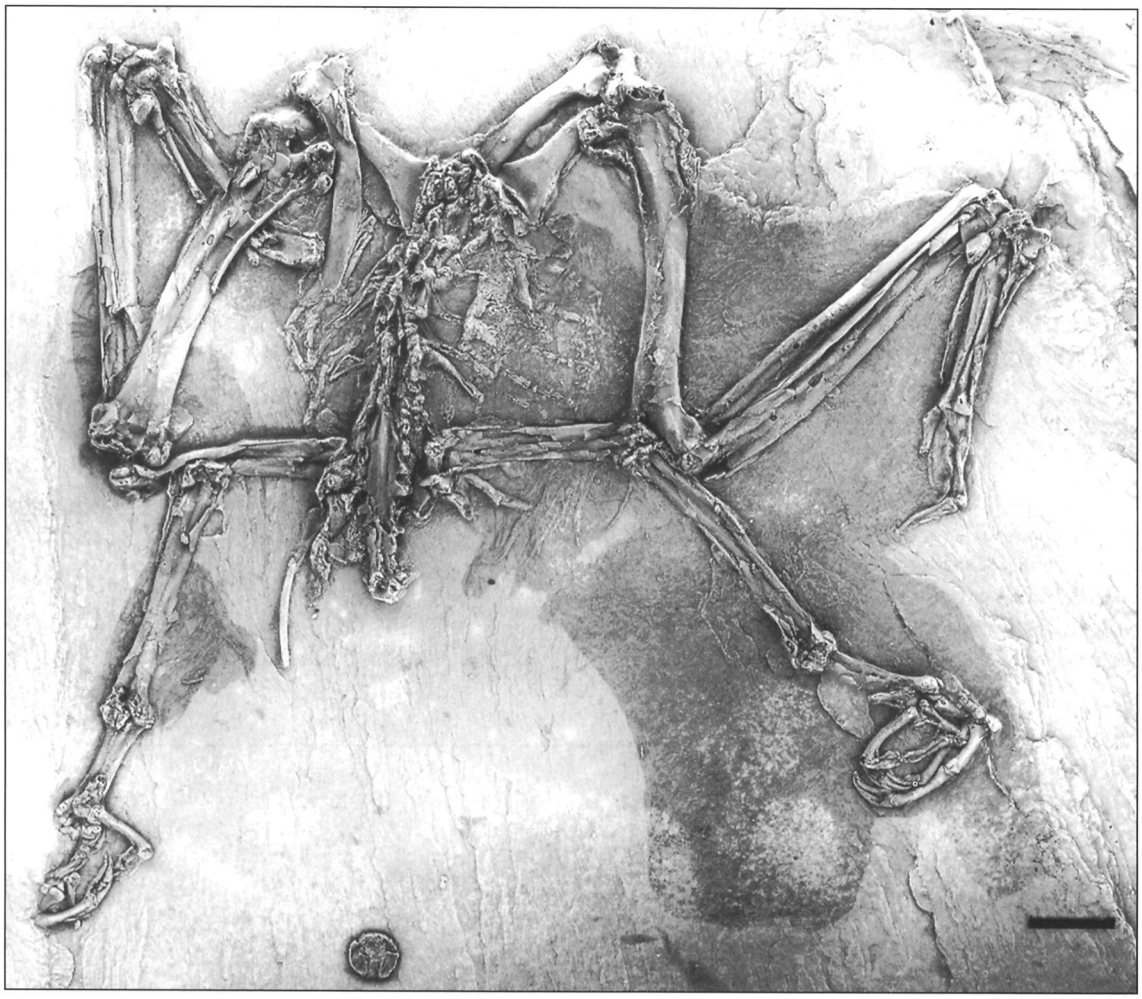

Fig. 3. *Palaeopsittacus* cf. *georgei*, referred specimen from the Middle Eocene of Messel (Germany); SMNK.PAL.3834b. Coated with ammonium chloride to enhance contrast, scale bar equals 10 mm.

Remarks : Both, in size and morphology, the skeleton from Messel closely resembles the specimens of *Palaeopsittacus* from Walton-on-the Naze in all skeletal elements, which are known from the latter. It especially corresponds to the London Clay specimens in the following features: (1) processus procoracoideus (coracoid) of triangular shape, with pointed tip and wide base; (2) distal end of tibiotarsus with low condyli and very wide incisura intercondylaris; (3) tarsometatarsus short and dorsoventrally flattened, with wide proximal and distal ends and without distinct crista medianoplantaris; (4) hypotarsus block-like and with sulcus on the medial part of its plantar surface; (5) trochleae metatarsorum splayed, and trochlea metatarsi IV with a plantarly directing wing-like projection. The combination of these features is characteristic for *Palaeopsittacus*.

The Messel specimen differs from the type of *Palaeopsittacus georgei* in the somewhat shorter acromion of the scapula and possibly belongs to a different species. Without additional material, however, I prefer a classification as *Palaeopsittacus* cf. *georgei* against naming a new taxon.

Description and comparison :

Vertebrae : Taxonomically relevant details of the vertebrae cannot be discerned. Except for one, all tail vertebrae, including the pygostyle, have been lost.

Coracoid : The coracoid of the Messel specimen has about the same length as in the holotype of *P. georgei* (tab. 1). The processus acrocoracoideus is not very prominent, the shaft of the bone is slender. The processus procoracoideus is distinct and of triangular

shape, with a pointed tip and a wide base. It closely resembles the processus procoracoideus of the juvenile specimen of *P. georgei* from Walton-on-the-Naze (fig. 1A); in the holotype this process is broken. Due to preservation, the foramen nervi supracoracoidei cannot be discerned in the Messel specimen. The processus lateralis of the extremitas sternalis appears to have been short.

Furcula : The furcula is U-shaped, the scapi claviculae are slender in their sternal part. An apophysis furculae was either absent or small.

Scapula : The acromion is well-developed but somewhat smaller than in *P. georgei* where it is very long and pointed. There is a small tuberculum coracoideum which indicates that the facies articularis scapularis of the coracoid was concave as in the referred coracoid of *P. georgei* from Walton-on-the-Naze (fig. 1A).

Sternum : The carina sterni is of average height as, for example, in the recent *Coracias garrulus* (Coraciiformes, Coraciidae). There is a spina externa which is similar in shape to that of recent Psittaciformes, though it is relatively smaller. Details of the margo caudalis are not visible.

Humerus : Apart from being somewhat stouter, the humerus resembles that of recent *Podargus* (Caprimulgiformes, Podargidae) in its shape. It is fairly long and slender, the shaft is curved, and the crista deltopectoralis appears to have been rather short and not very prominent, similar to *Podargus* or *Coracias*. The tuberculum ventrale appears to have been somewhat protruding, though not as strongly as, for example, in most recent caprimulgiform birds. In its proportions, the distal end of the bone resembles the distal humerus of *Coracias garrulus*. The condylus ventralis is elongated and bears a shallow furrow on its cranial surface. The sulcus humerotricipitalis is wide.

Ulna : The ulna is the longest limb element and exceeds the humerus in length. The olecranon is short and stout. The cotyla ventralis is large; the tuberculum ligamenti collateralis ventralis is low.

Carpometacarpus : The carpometacarpus has similar proportions to that of the recent genus *Caprimulgus* (Caprimulgidae, Caprimulgiformes). The processus extensorius is well-developed; the processus pisiformis is shifted slightly towards the cranial side of the bone. The os metacarpale minus hardly exceeds the os metacarpale majus in length.

Other elements of the wing: The phalanx proximalis digiti majoris bears a fossa ventralis and is not fenestrated.

Pelvis: The pelvis resembles that of recent Psittaciformes in its proportions. The praeacetabular part is somewhat shorter than the postacetabular part, foramina intertransversaria are present. The alae praeacetabulares ilii are well-developed, similar in shape to those of many recent Psittaciformes (e.g. *Brotogeris*) and Columbiformes (e.g. *Columba*); within most recent Coraciiformes and Caprimulgiformes (except *Podargus* and *Nyctibius*), they are distinctly narrower. The ossa pubes are long, reaching well beyond the processus terminales ischii.

Femur: Taxonomically relevant details of the femora cannot be discerned.

Tibiotarsus: The tibiotarsus is short with small cristae cnemiales. Compared to recent birds, the distal end of the bone resembles the distal tibiotarsus of the Madagascan Cuckoo-roller, *Leptosomus discolor*. The condyli are low and the incisura intercondylaris is wide, as in the type specimen and in the referred specimen from Walton-on-the-Naze. The distal width of the bone is larger in the Messel specimen (tab. 1), but the difference might well be due to the flattening of the bones.

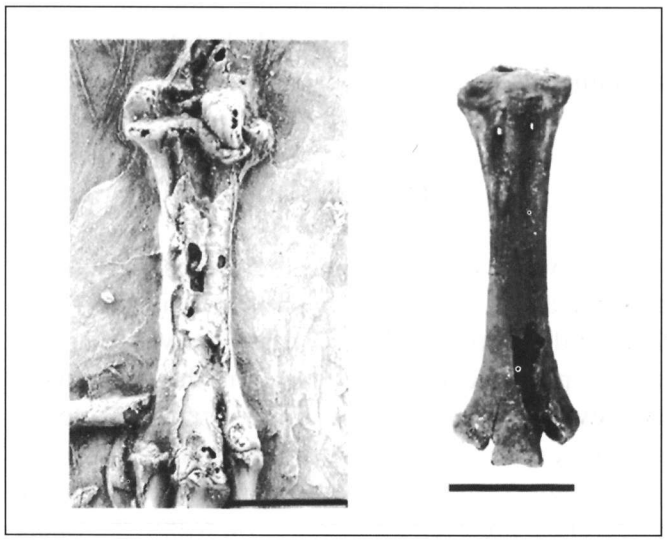

Fig. 4. Left tarsometatarsus in comparison. WN 91682 (left, from Mayr & Daniels, 1998); SMNK.PAL.3834a (right, coated with ammonium chloride to enhance contrast), scale bars equal 5 mm.

Tarsometatarsus: The tarsometatarsus (fig. 4) is a short and rather stout bone which measures about 2/3 of the length of the carpometacarpus and widens towards its proximal and distal ends. In specimen SMNK.PAL.3834 it has the same length as in the referred specimen from Walton-on-the-Naze (tab. 1). In its proportions, the bone is most similar to the tarsometatarsus of *Podargus strigoides*. The shaft is dorso-ventrally flattened and lacks a crista medianoplantaris, which for example is present in most coraciiform birds. The hypotarsus is block-like and bears a sulcus on its medial part (the isolated bones from Walton-on-the-Naze show that it further encloses two canals, as in *P. strigoides*). The foramen vasculare distale is small. The trochlea metatarsi III is rather short and wider than long; it reaches farther distally than the other two trochleae. The trochleae metatarsorum II and IV are splayed and as in the referred specimens from Walton-on-the-Naze, the trochlea metatarsi IV of the Messel skeleton bears a plantarly directing flange, which is also present in *P. strigoides*.

Toes : The feet are preserved in an anisodactyl position. The hallux is long, the third toe is the strongest and distinctly exceeds the tarsometatarsus in length. The claws are fairly long and exhibit distinct sulci neurovasculares. The os metatarsale I bears a processus articularis tarsometatarsalis of average length.

Feathers : Few remains of the wing and contour feathers are preserved on the slab, but do not allow a meaningful description.

DISCUSSION

In overall osteology and the morphology of the tarsometatarsus, *Palaeopsittacus* is similar to recent Podargidae (frogmouths); a shared derived character is the presence of two canals in the hypotarsus. However, *Palaeopsittacus* differs from all recent caprimulgiform birds in the presence of a spina externa (sternum), and since neither its assignment to the Podargidae nor even a classification within the Caprimulgiformes can be convincingly supported with derived characters, the Eocene genus has been classified order and family incertae sedis in this study.

Masillapodargus longipes, which also comes from the Middle Eocene of Messel and which I consider an Eocene representative of the Podargidae (Mayr, 1999), distinctly differs from *Palaeopsittacus* in the longer and more slender tarsometatarsus, the shorter hindtoe, and the smaller claws. Unfortunately, the few known skeletons of *Masillapodargus* are too poorly preserved for more detailed comparisons. *Palaeopsittacus* agrees with the genus *Quercypodargus*, which Mourer-Chauviré (1989) described from the Upper Eocene to Upper Oligocene deposits of the Quercy (France) in the wide incisura intercondylaris of the tibiotarsus. However, with regard to this feature, both *Palaeopsittacus* and *Quercypodargus* are distinguished from recent Podargidae.

Compared to other early Tertiary birds, in limb proportions and overall osteology *Palaeopsittacus* resembles a bird from the Lower Eocene Green River Formation of Wyoming, which is figured in Olson (1985: p. 126) and Feduccia (1996: p. 322). This bird (with the collection number SMNK.PAL.2368a+b) is represented by a complete articulated skeleton and was incorrectly referred to the putative Lower Eocene oilbird *Prefica nivea* by Olson (1987) (see Mayr, 1999). It was recently restudied by Mayr & Daniels (2001) who considered its higher systematic position uncertain and described it as a new taxon, *Fluvioviridavis platyrhamphus*. As in *Palaeopsittacus*, the coracoid of *F. platyrhamphus* exhibits a foramen nervi supracoracoidei (see Mayr, 1999).

Since both the Messel specimen and the skeleton from the Green River Formation are preserved as more or less crushed, flattened skeletons on slabs, detailed comparisons of the bones are limited. However, the following differences between *Palaeopsittacus* and the yet undescribed genus from the Green River Formation at least warrant the maintenance of two different genera: The proximal end of the humerus of the Green River specimen is wider than in *Palaeopsittacus*, the tarsometatarsus of *Palaeopsittacus* is relatively longer (~15.5 vs. 13.5 mm, whereas the other limb bones are shorter in *Palaeopsittacus* - the humerus for example measures 45 vs. ~50 mm), the scapi claviculae are much narrower in *Palaeopsittacus*, and the coracoid of *Palaeopsittacus* bears a larger processus procoracoideus.

Fluvioviridavis platyrhamphus has a very characteristic bill shape, and there is an isolated skull from Messel with a similar dorso-ventrally flattened

beak, which Mayr & Daniels (2001) tentatively referred to *Fluvioviridavis* (fig. 5). It now seems possible that this skull (SMF-ME 10783), which measures 50.3 mm, belongs to *Palaeopsittacus*. The bill-shape of SMF-ME 10783 would be in concordance with the limb proportions of the postcranial skeleton described in this study, which indicate that *Palaeopsittacus* was fairly aerial and might have caught its prey on the wing. If the skull in fig. 5 indeed belongs to *Palaeopsittacus*, the very wide and dorso-ventrally flattened bill would be another feature in which the Eocene genus corresponds to recent Podargidae (though in *Masillapodargus* and recent Podargidae the beak is wider and has a less pointed tip).

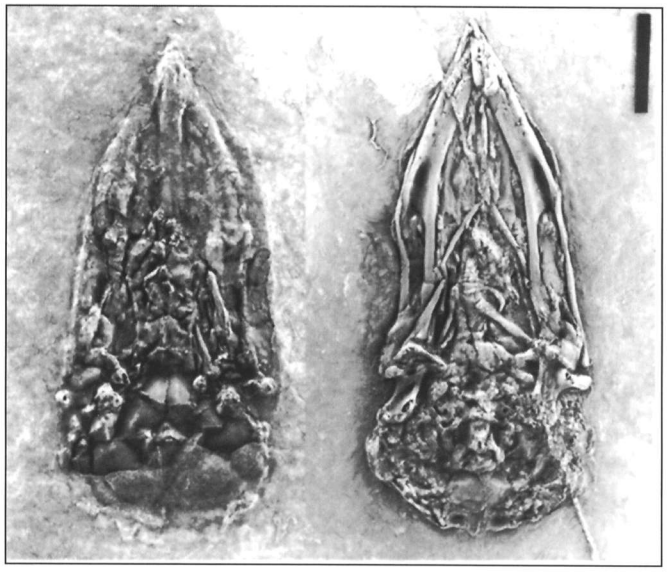

Fig. 5. Isolated skull from the Middle Eocene of Messel (Hessen, Germany) (SMF-ME 10783a+b), dorsal view (left), ventral view (right). Coated with ammonium chloride to enhance contrast, scale bar equals 10 mm.

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Tables

Table 1: Dimensions of the referred bones of *Palaeopsittacus georgei* from Walton-on-the-Naze, in comparison with those of the skeleton from Messel.

	coracoid	tibiotarsus	tarsometatarsus	
	length	distal width	length	prox. width
holotype[1]	23.5	4.6		
WN 91682[2]		4.5	15.6	5.0
WN 94838B (juv.)[2]	~20.3		15.0	
SMNK.PAL.3834	23.1	5.8[3]	15.3/~15.7	5.8[3]

[1]after Harrison (1982)
[2]after Mayr & Daniels (1998)
[3]differences probably due to flattening of Messel specimens