Abstract

Psittaciform birds from the Middle Eocene of Messel (Hessen, Germany) and from the Lower Eocene London Clay of Walton-on-the-Naze (Essex, England) are described (Psittacopes lepidus n. g., n. sp. and three unnamed species). These birds resemble the Recent family Psittacidae in the morphology of the tarsometatarsus, but exhibit distinct differences in other skeletal elements, especially in the rather coly-like beak and in the wing skeleton. For the first time the presence of the Quercypsittidae MOURER-CHAUVIRE 1992 in the Lower Eocene London Clay is demonstrated; this family differs distinctly from the four taxa mentioned above. Since new material of Palaeopsittacus georgei HARRISON 1982 from the type locality shows that this bird was anisodactyl (and therefore not a member of the Psittaciformes), the Quercypsittidae only contain the genus Quercypsitta MOURER-CHAUVIRE 1992.

Key words: Aves, Psittaciformes, Quercypsittidae, taxonomy, Tertiary, Eocene, Messel, Germany.

Kurzfassung


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Introduction

The parrots (Psittaciformes) are an osteologically very homogeneous order comprising only a single Recent family, the Psittacidae. For a long time, fossil psittaciform birds were unknown from deposits older than Miocene, and those found in the early Miocene of France (Archaeopsittacus verreauxi Milne-Edwards 1867-71) and Nebraska (Conuropsis fratercula Wetmore 1926) are true members of the Psittacidae, and closely resemble modern taxa.

In recent years, however, two Eocene taxa have been attributed to the Psittaciformes: Palaeopsittacus georgei Harrison (1982) from the Lower Eocene of Walton-on-the-Naze (Essex, England), and the genus Quercypsitta Mourer-Chauviré (1992) from the Upper Eocene of France. The record of both is fragmentary: P. georgei is known from 11 associated skeletal elements, and a referred incomplete distal tarso-metatarsus from the Middle Eocene of Hampshire (England); Quercypsitta has been described on the basis of few isolated elements (coracoid, proximal end of carpometacarpus, distal end of tibiotarsus, tarsometatarsus). Mourer-Chauviré (1992) included both taxa in the new Family Quercypsittidae.

Herein we describe new psittaciform birds from the Middle Eocene of Messel (Hessen, Germany) and from the London Clay of Walton-on-the-Naze, which differ considerably from Palaeopsittacus and Quercypsitta.

Material and methods

The anatomical terminology follows Baumel & Witmer (1993). The dimensions represent the maximum length of the bone along its longitudinal axis, except for the claws where the distance between the tuberculum extensorium and the apex phalangis has been measured.

Abbreviations used to indicate collections in which specimens are deposited:

- BC: private collection P. & A. Berghaahl, Driftwood Vista Avenue, Kirby-le-Soken (Essex; England)
- SMF: Forschungsinstitut Senckenberg, Frankfurt am Main
- SMNK: Staatliches Museum für Naturkunde, Karlsruhe
- WN: private collection M. Daniels, Clacton-on-Sea (Essex; England).

Acknowledgements

We would like to thank C. Mourer-Chauviré (Université Claude-Bernard, Lyon) for making the Quercypsittidae available for study during G. Mayr’s visit. We also thank P. and A. Berghaahl (Kirby-le-Soken, Essex, Great Britain), W. Munk and B. Herkner (both Staatliches Museum für Naturkunde, Karlsruhe) for the loan of specimens. B. Stephan (Museum für Naturkunde, Berlin) made Recent skeletons under his charge available for comparison. S. Tränker (Forschungsinstitut Senckenberg) took the photographs on plates 1 and 2, L. Berner (Museum für Naturkunde, Berlin) helped by preparing the x-ray photograph on plate 1. Finally we like to thank P. Daniels for always meeting us with much patience.

Systematics

Order Psittaciformes

The monophyly of the Psittaciformes (including Psittacopes lepidus n. g., n. sp., the species A-C described below, and the Psittacidae) is supported by the following characters:

1. well-developed blade-like spina externa with a dorsad projecting tip;
2. ulna distinctly longer than humerus;
3. hypotarsus with two sulci, which might be closed to form one or two foramina;
4. broad trochlea metatarsi III bearing a tubercle on its lateral side;
5. trochlea metatarsi IV turned plantad (fully zygodactyl foot);
6. Sehnenhalter separated from the trochlea metatarsi IV by a furrow.

Although these characters are likely to be derived within neognathous birds, it has to be emphasized that none of them is restricted to the Psittaciformes only, (6) is also found in the Piciformes. Amongst other features (for example the poorly developed processus supracondylaris dorsalis of the humerus and the relatively shorter tarsometatarsus), characters (1) and (2) distinguish the Psittaciformes from the Cuculiformes (cuckoos).

Within the Psittaciformes the Psittacidae form a monophyletic group because of the following derived characters, which are absent in the Eocene taxa described in this paper:

1. "parrot-like beak" (maxilla broad dorso-ventrally and with sigmoidally curved ventral margin, mandible distinctly shorter than maxilla, narial openings small, etc.);
2. quadratum with slender processus oticus;
3. coracoid with elongated processus acrocoracoideus;
4. margo caudalis of sternum with two fenestrae (two incisurae in a few species);
5. humerus with large crista deltopectoralis;
6. large trochlea metatarsi II;
7. fossa metatarsi I situated on the medial side of the tarsometatarsus;
8. proximal three phalanges of the fourth toe shorter than fourth phalanx;
9. claws long and slender.

Psittacopes n. g.

Type species: Psittacopes lepidus n. g., n. sp., only known species of the genus.
**Etymology:** The generic name has been derived from psittacus (Lat.) = parrot; pes (Lat.) = foot.

**Diagnosis:** Slightly smaller than Loriculus galgulus (Psittacidae). The genus Psittacopes exhibits the synapomorphies of the Psittaciformes mentioned above, except characters (3), (4) and (6) which are not visible due to the preservation of the specimens. It can further be characterized by the following features:

1. short holohenal beak with large narial openings and short rostrum maxillae;
2. mandible with short rostrum mandibulae, large oval fenestra mandibulae and prominent processus coronoideus;
3. coracoid with shallow facies articularis scapularis and long processus procoracoideus;
4. U-shaped furcula with small apophysis furculae;
5. margo caudalis of sternum with four incisurae;
6. slender carpometacarpus with long symphysis metacarpalis distalis;
7. crista cnemialis lateralis (tibiotarsus) hooked;
8. short claws.

Psittacopes lepidus n. g., n. sp.

*Pl. 1 fig. 1; pl. 2 fig. 2; text-figs. 1-4*

**Etymology:** lepidus (Lat.) = nice, sweet.

**Holotype:** SMF-ME 1279 (pl. 1: slightly disintegrated skeleton lacking the right leg).

**Dimensions:** see tables 1 and 2.

**Type locality:** Messel (Hessen, Germany).

**Type horizon:** Geiseltalium, lower Middle Eocene.

**Referred specimen:** SMNK-Me 1089a+b (pl. 2: complete articulated skeleton).

**Diagnosis:** Only species of the genus, therefore diagnosis as for genus.

**Description and comparison**

- **Skull** (text-fig. 1A): The cranium appears to be rounded. The interorbital bridge is narrow compared with the very broad one of the Psittacidae. The processus oticus of the quadratum is broad medio-laterally (SMF-ME 1279) in contrast to the very slender processus oticus of the Psittacidae; capitulum oticum and capitulum squamosum are small, an incisura intercapitularis is absent. The bill is short, it measures less than half of the total length of the skull. Maxilla and mandible are of equal length, while the mandible is shorter than the maxilla within the Psittacidae. The exact shape of the maxilla cannot be determined with certainty (text-fig. 1A it has been reconstructed following the curvature of the mandible). The nares (visible through the reverse of the transparent slab of SMF-ME 1279) are holohenal, of oval shape and large; they reach approximately 2/3 of the length of the bill. The rami mandibulae are much more slender than those of most Psittacidae and slightly curved (within the Psittacidae we only found a comparatively slender mandible in the genus Loriculus (text-fig. 1B)). The rostrum mandibulae is short and of equal length as the rostrum maxillae. A large oval fenestra mandibulae (text-fig. 1A, 1) is present, above which a prominent processus coronoideus arises (text-fig. 1A, 2). Although the dorsal margin of the mandible of the Psittacidae also shows a large convexity (text-fig. 1C, 3), its homology with the processus coronoideus has to be checked.

- **Vertebrae:** The cervical vertebrae are short. The number of praesacral vertebrae cannot be ascertained. SMF-ME 1279 exhibits five caudal vertebrae, and in contrast to the Psittacidae the pygostyle is very small.

- **Ribs:** In SMNK-Me 1089 seven or eight vertebral ribs are visible. Six sternal ribs and three slender processus uncinati (at those vertebral ribs which articulate with the three most cranial sternal ribs) can be counted in SMF-ME 1279. The most caudal sternal rib does not reach the sternum.

- **Coracoid** (text-fig. 2A): The shaft of this bone is long and thin. The processus acrocoracoideus is shorter than that of the Psittacidae (text-fig. 2B). The facies articularis scapularis (SMF-ME 1279, visible through the reverse of the transparent slab) is very shallow and fuses with the facies articularis.

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**Tab. 1. Length of the limb bones (left/right), in mm:**

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<td>~25.0/?</td>
<td>~13.3/?</td>
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**Tab. 2. Length of the pedal phalanges, in mm:**

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<td>4.5</td>
<td>5.1</td>
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<td>~2.8</td>
<td>2.8</td>
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humeralis (like in many Piciformes and unlike the Lower Eocene species described below). The sulcus musculi supracoracoidei is shallow, and the processus procoracoideus long. The processus lateralis of the sternal end is short and rounded.

- Furcula: The furcula is U-shaped, its extremitas sternalis broader than the scapus claviculae. In contrast to the Psittacidae a small apophysis furculae is present. The extremitas omalis is not visible.

- Scapula (text-fig. 2C): The corpus scapulae is slender along its whole length, its distal part is less inflected than in the Psittacidae. The acromion is not visible in any of the specimens.

- Sternum (text-figs. 3A, B): The sternum (SMF-ME 1279) is small, approximately as long as the humerus, while it is much longer than this bone in the Psittacidae. As in the latter, the corpus sterni is longer than wide and becomes broader towards its caudal end. The processus cranii laterales are hidden by overlying bones. The carina sterni (text-fig. 3A) is lower than that of the Psittacidae, and the apex carinae situated much farther caudally. The well-developed blade-like spina externa (text-fig. 3A, 1) protrudes cranially from the carina, its tip projects dorsad. In lateral view the spina externa resembles that of Psittacus erithacus, Ara ararauna (both Psittacidae) and a few passeriform birds (with unforked spina externa). Contrary to P. lepidus, the cranial margin of the carina sterni runs in a straight vertical line within most Psittacidae, and is continuous with the cranial margin of the spina externa. The margo caudalis of the sternum of P. lepidus (text-fig. 2B) shows four incisurae, the incisurae laterales reach almost half the length of the sternum, while the incisurae mediales are much shorter. The trabeculae laterales and intermedianae are slender and bear no transverse processes at their end. Within most Psittacidae only two fenestrae laterales are present (text-fig. 3C), which can be reduced (e.g. Strigops habroptilus) or open (e.g. Ara macao, A. chloroptera).

- Humerus (text-fig. 2D): The humerus is as long as the hand. The crista deltopectoralis is low and situated farther proximal than the larger crista deltopectoralis of the Psittacidae. The impressio coracobrachialis is a distinct semicircular elevation. The processus supracondylaris dorsalis is very short; on the cranial side of the humerus it proceeds into a small tuberosity which runs transverse to the longitudinal axis of the shaft. The condylus dorsalis resembles that of the Psittacidae. The tuberculum supracoracoideum is of average size, neither large nor small. The processus flexorius is well-developed.

- Ulna: The ulna is longer than the humerus, but no details of its morphology can be detected. Papillae remigales are not visible.
Text-fig. 3. *Psittacopes lepidus* n. g., n. sp., sternum (reconstructed after SMF-ME 1279): A) carina sterni; B) outline of the corpus sterni; C) *Melopsittacus undulatus* (Psittacidae), ventral side of sternum. – Scale = 5 mm. 1 - spina externa.

1 - Carpometacarpus (text-fig. 4A): The slender carpometacarpus of *P. lepidus* most closely resembles that of species B from the British Lower Eocene (described below), although it is relatively smaller (approximately half as long as the ulna). The os metacarpale minus runs parallel to the os metacarpale majus and becomes broader towards its proximal end (SMF-ME 1279, right side); both are of equal length, the spatium interneta carpale is narrow. The symphysis metacarpalis distalis is long (it is also wide in some Recent Psittacidae, e.g. *Conurus pertinax*, *Melopsittacus undulatus*). The os metacarpale alulare is broad proximo-distally, the processus extensorius low. A processus intermetacarpalis is absent, the sulcus tendineus is shallow.

Other elements of the wing (text-fig. 4A): The phalanx proximalis digiti majoris seems to exhibit a short processus internus indicis (SMF-ME 1279) like that of the Psittacidae (text-fig. 4B, 1), the pila cranialis is very low. The phalanx distalis digiti majoris and the phalanx digiti alulae are long. The latter bears no distal phalanx.

Pelvis: The pelvis (SMF-ME 1279) resembles that of many Psittacidae, but it is relatively smaller. The alae praeacetabulares ilii are wider and their lateral margin convex. A foramen obturatum is present, the os pubis is only slightly longer than the processus terminalis ischi.

Tibiotarsus: The crista cnemialis lateralis is hooked (pl. 1 fig. 1b). The crista tibialis measures 1/3 of the length of the tibiotarsus and is low. The distal end of the bone is slightly wider than the shaft, the incisura intercondylaralis (SMNK-Me 1089a+b) is deep. Condylus medialis and condylus lateralis have approximately the same size.

Tarsometatarsus: The tarsometatarsus is slightly shorter than the femur and dorso-ventrally flattened. It is more slender than that of most Psittacidae (except the ground living genus *Cyanoramphus*), but closely resembles the Lower Eocene species B (described below) in its proportions. The shaft becomes broader towards its distal and proximal ends which are approximately two times wider than the most narrow section of the shaft. The impressio ligamenti collateralis lateralis is large and situated near the lateral edge of the shaft. The hypotarsus is very low, like that of the Coliidae (SMNK-Me 1089a+b), fossae parahypotarsales and cristae plantares are absent.

Unfortunately, few details of the distal end of the bone are visible: The trochleametatarsi III is very broad and reaches farther distad than the trochleae metatarsi II and IV (SMNK-Me 1089a+b). The foramen vasculare distale is large (SMNK-Me 1089b, right side). The fossa metatarsi I is situated on the palmar side (SMF-ME 1279, SMNK-Me 1089a), within the Psittacidae it is shifted onto the marginal margin of the tarsometatarsus.

Toes: All toes have the usual number of phalanges. The third toe is the longest and strongest; it is approximately as long as the tarsometatarsus. In both specimens of *P. lepidus* the fourth toe is turned backwards, thus indicating a fully zygodactyl foot: in SMF-ME 1279 it lies between the second and the third toe and is visible from its dorsal side, while the latter are seen from their ventral side. In SMNK-Me 1089 (right side) the fourth toe has the same position, but exhibits its ventral side, whereas the second and third toes show their dorsal side. The phalanges of the fourth toe are of equal length (within the Psittacidae the three proximal phalanges are shorter than the fourth phalanx). While the pedal phalanges normally become shorter towards the distal end of the toe, in *P. lepidus* the second phalanx of the second toe is longer than the first (proximal) phalanx. The proximal phalanx of the far distally inserting hallux is weaker than the phalanges of the other three toes. The claws are very short and compact, unlike the long claws of the Psittacidae. The processus
articularis tarsometatarsalis of the os metatarsale I is short (SMF-ME 1279).

- Feathers: Although some small feathers are visible near the skull of SMF-ME 1279, no rectrices or remiges are preserved. The small pygostyle might indicate that the tail was short, as in Agapornis or Loriculus.

The psittaciform birds from Walton-on-the-Naze

So far three species of psittaciform birds have been found in the Lower Eocene London Clay of Walton-on-the-Naze (Essex, England) which we believe to be closely related to Psittacos. Most specimens consist of well-preserved bones, found associated, but as all are housed in private collections we did not name them.

Species A
Pl. 3 figs. 3-4; pl. 4 fig. 9; pl. 5 figs. 15a, 15c, 16a, 18b; text-figs. 5B, 5D, 5H, 5K, 5L, 6D

Referred specimens: WN 80282A (tarsometatarsus); WN 85506 (pl. 3 fig. 4: several vertebrae, furcula, coracoid, scapula, proximal end of humerus, tarsometatarsus, pedal phalanges); WN 89627A (pl. 5 fig. 16a: tarsometatarsus); WN 90642A (tarsometatarsus); WN 91171 (pl. 3 fig. 3: skull, some vertebrae, coracoid, proximal and distal end of humerus, proximal end of ulna, radius, carpometacarpus, pelvis, tabitarsus, tarsometatarsus, pedal phalanges, claws).

Dimensions (in mm):
WN 85506: tarsometatarsus - 19.1;
WN 91171: coracoid - 21.2; radius - 31.0; carpometacarpus - 18.2; tabitarsus - 36.

Remarks: This is the largest species, which differs from species B in the following features:
(1) processus procoracoideus shorter (text-figs. 5A, B);
(2) os metacarpale minus more bowed;
(3) ridge from os metacarpale minus to processus pisiformis (text-fig. 5D, 4);
(4) hypotarsus with two sulci (text-fig. 5K - one sulcus closed to a foramen in species B);
(5) shaft of tarsometatarsus broader.

Species B
Pl. 3 fig. 6; pl. 4 figs. 10h, 11b, 12b; text-figs. 5A, 5C, 5J, 7B, 7D

Referred specimens: WN 86540 (pl. 3 fig. 6: several vertebrae including the atlas, furcula, coracoid, proximal and distal end of the humerus, distal end of the ulna, tarsometatarsus, pedal phalanges); WN 96926 (tarsometatarsus lacking the distal end, distal end of tibiotarsus).

Dimensions (in mm):
WN 86540: coracoid - 17.0; carpometacarpus - 13.2; phalanx proximalis digitii majoris - 6.5; phalanx distalis digitii majoris - 5.3; tarsometatarsus - 13.7.

Remarks: Of the three species described in this section, this one most closely resembles Psittacos lepidus. However, these similarities might well be plesiomorphic (e.g. the straight os metacarpale minus, the configuration of the proximal carpo-

metacarpus and the slender tarsometatarsus). Although the long symphysis metatarsalis distalis is probably derived within neognathous birds, its status within the Psittacidae is uncertain. The main differences to P. lepidus are restricted on the elements of the wing, which are relatively longer in species B.

Species C
Pl. 5 fig. 18a; text-figs. 5L, 5M, 9A

Referred specimen: WN 96949 (text-fig. 9A, pl. 5 fig. 18a: several vertebrae, scapula, proximal and distal end of humerus, proximal and distal end of carpometacarpus, tarsometatarsus lacking the proximal end).

Remarks: The record of this species, which is approximately the same size as species B, is very scatty and all bones are incomplete. Species C clearly differs from species B in the broader shaft of the tarsometatarsus.

Specimens of uncertain affinity

Referred specimens: WN 94811 (pl. 4 fig. 13: coracoid, humerus, distal end of ulna); BC 8917A (pl. 3 fig. 5: skull, some vertebrae, coracoid, scapula, furcula, cranial end of sternum, humerus, ulna, incomplete carpometacarpus, femur).

Dimensions (in mm):
WN 94811: coracoid - 17.2; humerus - 21.6;

Remarks: Since the two specimens lack the tarsometatarsus, the diagnostic element distinguishing species B from species C, they cannot be assigned to one of these two species with certainty.

Description and comparison

- Skull: The skull is preserved in BC 8917A (pl. 4, figs. 7-8) and WN 91711 (species A, pl. 4 fig. 9). As in Psittacos lepidus, the quadratum lacks an incisura intercapitularis (BC 8917A, pl. 3 fig. 5B). The slightly curved bill resembles that of P. lepidus in its proportions, although the rostrum maxillae is shorter and the narial openings larger. The dorsal bar of the os nasale becomes broader towards its proximal end (WN 91171). The rami mandibulae are slender, their pars symphysialis very short (BC 8917A, pl. 3 fig. 5a) - even shorter than in P. lepidus. A fenestra mandibulare, which is more elongate than that of Psittacos lepidus, is visible in WN 91171 (in the other specimens that part of the mandible is not preserved). In contrast to P. lepidus, an enlarged processus coronoides is absent in WN 91171.

- Vertebrae: The corpus atlantis of the atlas exhibits an incisura fossae (pl. 3 fig. 5c), the axis resembles that of the Psittacidae.

- Coracoid: The coracoid is slender. The processus procoracoideus of species B is long, while it is decidedly shorter in species A (see text-figs. 5A, B). The facies articularis claviculares is well-developed and overhangs the sulcus musculi supracoracoidei. The facies articularis scapularis is shallow in all three species, contrary to that of Quercypsitta. A foramen nervi supracoracoidei is absent.
Text-fig. 5. A) WN 86540 (species B), proximal end of left coracoid; B) WN 91711 (species A), proximal end of left coracoid; C) WN 86540 (species B), proximal end of right carpometacarpus; D) WN 91711 (species A), proximal end of right carpometacarpus; E) BC 8917A (species B or C), distal end of left humerus; F) BC 8917A (species B or C), proximal end of left ulna; G) BC 8917A (species B or C), distal end of radius; H) WN 91711 and WN 89627A (both species A), distal end of left tarsometatarsus; I) WN 96949 (species C), distal end of left tarsometatarsus; J) WN 96926 (species B), proximal end of right tarsometatarsus; K) WN 91711 (species A), proximal end of right tarsometatarsus; L) WN 91711 (species A), proximal end of right tarsometatarsus; M) WN 96949 (species C), distal end of left tarsometatarsus, plantar side. – Scale = 2 mm.

1 - see text; 2 - distal end of cotyla ventralis; 3 - process on extremitas distalis of radius; 4 - ridge from os metacarpale minus to processus pisiformis; 5 - tubercle below processus pisiformis.

– Furcula: The furcula (WN 85506, WN 86540) is U-shaped. A small apophysis furculae is present, and the extremitas omalis is slender in contrast to the wider one of the Psittacidae.

– Scapula: Like the other elements of the wing, the scapula (pl. 3 figs. 2a, 3e, 4a) is relatively longer than that of *Psittacopes lepidus*. In BC 8917A (pl. 3 fig. 5e) it is as long as the ulna, while it is distinctly shorter than this bone in *P. lepidus* (pl. 2). Its shaft is slender, the distal end only slightly inflected. The acromion is very long (pl. 3 fig. 5g) and bears no process for an articulation with the furcula.

– Sternum: The cranial part of the sternum is preserved in BC 8917A and differs from that of *Psittacopes lepidus* in the apex carinae reaching farther cranial, in the higher carina sterni and in the more concave cranial margin of the carina sterni. As in *P. lepidus*, the spina externa is well-developed and blade-like. The processus cranio-laterales are long. Unfortunately the margo caudalis is not preserved in any of the specimens.

– Humerus: The humerus (WN 94811, pl. 4 fig. 13) resembles that of *Psittacopes lepidus*, its shaft is slightly curved. The crista deltopectoralis is low, the crista bicipitalis short. The fossa pneumotricipitalis is single, a foramen pneumaticum absent. The processus supracondylaris dorsalis is short and, as in *P. lepidus*, proceeds into a low tuberosity on the cranial side of the shaft (text-fig. 5F, 1). The condylus dorsalis is small, the condylus ventralis elongate and the fossa musculi brachialis shallow. The processus flexorius reaches farther distally than the condylus ventralis and the condylus dorsalis.

– Ulna: The ulna (pl. 3 figs. 3e, 5j) is longer than the humerus, papillae remigales are absent. The tuberculum ligamenti collateralis ventralis is small, the olecranon short. The cotyla dorsalis is large, yet it does not reach much farther distally than the cotyla ventralis. The distal end of the shallow cotyla ventralis tapers to a point (text-fig. 5F, 2).

– Radius: The extremitas distalis bears a hooked process (WN 91711, BC 8917A, text-fig. 5G, 3).

– Carpometacarpus: The carpometacarpus is relatively longer than that of *Psittacopes lepidus*. The processus pisiformis is centrally positioned. The carpometacarpus of species B (pl. 3 fig. 6g) differs from that of species A (pl. 3 fig. 3f) and closely resembles that of *P. lepidus*: in the straighter os metacarpale minus, the longer symphysis metacarpalis distalis, the absence of the low ridge from the os metacarpale minus to the processus pisiformis (text-fig. 5D, 4), the absence of a tubercle below the processus pisiformis (text-fig. 5D, 5), and in the ventral margin of the trochlea carpalis being more in line with the os metacarpale minus. The carpometacarpus is too poorly preserved in the only known specimen of species C to allow comparisons. In species A and species C a small processus
intermetacarpalis is present. The carpometacarpus of the Lower Eocene parrots differs from that referred by Mourer-Chauviré (1992) to Quercypsitta in the larger fossa infratrochlearis and the more shallow fovea carpalis cranialis.

- Other elements of the wing: The phalanx proximalis digiti majoris (pl. 3 fig. 6f) bears a very short processus internus indicis. The phalanx distalis digiti majoris (pl. 3 fig. 6e) is long.

- Tibiotarsus: Unfortunately the proximal end of the tibiotarsus is not preserved completely in any of the specimens, so it cannot be said if the crista cnemialis lateralis was hooked as in Psittacopes lepidus. The condylus medialis of the distal end is slightly larger than the condylus lateralis (pl. 3 fig. 4f). The incisura intercondylaris is deep, and a pons supratendineus present. A large tubercle is situated on the medial side of the sulcus extensorius (text-fig. 7B).

- Tarsometatarsus: The tarsometatarsus is slender (especially in species B). The hypotarsus (text-fig. 5L) is low with two sulci (probably for the tendons of the musculus flexor digitorum longus and the m. flexor hallucis longus) in species A (text-fig. 5K, pl. 5 fig. 15c), but one sulcus and a closed foramen are present in species B (text-fig. 5J). The number of foramina within the hypotarsus varies in the Psittacidae - most species possess two (which can be fused to become one in some species), in Neophema splendida two sulci are found. The foramina vascularia proximalia are on the same level (in contrast to Quercypsitta). The distal end of the tarsometatarsus (text-figs. 5H, I, M) closely resembles that of some Psittacidae (e.g. N. splendida, pl. 4 fig. 11a), except that the trochlea metatarsi II is smaller and bears a projection in a plantar direction. The trochlea metatarsi II and especially the trochlea metatarsi IV are distinctly shorter than the trochlea metatarsi III. The latter is broad and bears a tubercle on its lateral side. The trochlea metatarsi IV is inclined plantarily (pl. 5 fig. 15a) and exhibits a well-developed Sehnenhalter which is separated from the trochlea by a furrow. Concerning the proportions, the tarsometatarsus of species B most closely resembles that of P. lepidus.

- Toes: The claws are short as in P. lepidus (text-fig. 6D, pl. 3 figs. 4e, 5n).

A record of the Quercypsittidae Mourer-Chauviré 1992 from Walton-on-the-Naze

Referred specimen: WN 87563 (text-fig. 6, pl. 5 figs. 16b-c, 18c: femur, tibiotarsus, tarsometatarsus, pedal phalanges, claws).

Dimensions (in mm, in brackets the dimensions of Quercypsitta sudrei as given by Mourer-Chauviré 1992):
- tibiotarsus - 43.6 (width of distal end - 5.1 [5.0]); tarsometatarsus - 18.5 [17.5-18.4] (width of proximal end - 5.9 [5.1]; width of distal end - 6.2 [5.7-6.0]).

Remarks: WN 87563 is the earliest record of the Quercypsittidae and the only one from outside the type locality. The tarsometatarsus of this specimen differs from Q. sudrei in the presence of a canalis interosseus distalis (text-fig. 6B, 1) and in the slightly larger size. The distal end of the tarsometatarsus of WN 87563 is comparable with that referred by Mourer-Chauviré (1992) to Q. sudrei except that the trochlea cartilaginis tibialis is lower. The claws of WN 87563 (which have not previously been known from the Quercypsittidae) are long and resemble those of birds of prey (text-fig. 6C). Unfortunately no elements of the wing are preserved in WN 87563, so the assignment of the other bones referred by Mourer-Chauviré to the Quercypsittidae could not be confirmed.

The Quercypsittidae differ distinctly from the species A-C in:
- (1) foramina vascularia proximalia (tarsometatarsus) not on same level;
- (2) tarsometatarsus shorter and more compact;
- (3) Sehnenhalter only slightly separated from the trochlea metatarsi IV;
- (4) trochlea metatarsi II larger;
- (5) claws longer.

Palaeopsittacus georgei Harrison 1982 from Walton-on-the-Naze

Holotype: 11 incomplete bones found associated at Walton-on-the-Naze including a coracoid, both ends of the ulna, the proximal end of the scapula, the distal end of the carpometacarpus, the distal end of the tibiotarsus and the proximal end of the tarsometatarsus.

Referred specimens: WN 91682 (text-fig. 7A, C, pl. 5 figs. 14c-d, 18d: distal end of tibiotarsus, tarsometatarsus; WN 94838B (pl. 5 figs. 14a-b: coracoid, tarsometatarsus).

Dimensions (in mm, in brackets the dimensions of the holotype as measured by Harrison 1982):
- WN 91682: tarsometatarsus - 15.6 (width of proximal end - 5.0); tibiotarsus (width of distal end - 4.5 [4.6]);
- WN 94838B: coracoid - 20.3; tarsometatarsus - 15.0 (this is a juvenile specimen, therefore the bones are shorter).

Remarks: The nearly complete tarsometatarsus of WN 91682 clearly demonstrates that Palaeopsittacus georgei was anisosycty or at best facultatively zygodactyl and therefore no
A member of the Psittaciformes. Moreover, it shows that the incomplete distal end of the tarsometatarsus referred by HARRISON (1982) to *Palaeopsittacus* does not belong to this genus (it most closely resembles the Quercypsittidae).

Apart from the distal tarsometatarsus P. georgei differs from the species A-C in:

1. coracoid with foramen nervi supracoracoidei;
2. ulna: cotyla dorsalis reaching farther distally than cotyla ventralis;
3. cotyla dorsalis (ulna) round (not tapering to a point);
4. tibiotarsus: sulcus intercondylaris wider and shallower;
5. hypotarsus larger and with two closed foramina.

**Discussion**

Although the true phylogenetic affinities of this species remain obscure, the new material clearly shows that *Palaeopsittacus georgei* does not belong to the Quercypsittidae nor is it a psittaciform bird at all. Hence the Quercypsittidae only contains the genus *Quercypsitta*. In the light of the new findings the assignment of the Quercypsittidae to the Psittaciformes needs reinvestigation. So much the more, if MOURER-CHAUVIRE's assignment of the coracoid is correct, which is distinguished from that of all other known psittaciform birds by the cup-like facies articularis scapularis. The Quercypsittidae share the following two characters with the Psittaciformes:

1. foot zygodactyl with well-developed Sehnenhalter;
2. hypotarsus with two sulci.

Since the Sehnenhalter is only slightly separated from the trochlea metatarsi IV, the Quercypsittidae would most likely be the sister group of the taxon including the species A-C, *Psittacopes* and the Psittacidae (see text-fig. 8). However, at present the fossil record of this family seems to be too fragmentary to allow a definitive phylogenetic assignment. Characters (1) and (2) listed above are also typical of the Cuculiformes and other zygodactyl birds (e.g. the Sandcoki-formes HOUDE & OLSON 1992).

Two characters might support a monophyly of the psittaciform birds described herein (*Psittacopes lepidus* n. g., n. sp. and the species A-C):

1. ulna: distal end of cotyla ventralis tapering to a point (see text-fig. 5F, 2);
2. distal end of radius bearing a hook-like process (see text-fig. 5G, 3).

As both of these features are not visible in *P. lepidus* and the species C (due to the preservation of the specimens), we did not name a separate taxon (i.e. a new family).

Based on their modern distribution, CRACRAFT (1973: 508) assumed that the Psittaciformes originated in the Southern

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Tab. 3. Proportions of the limb bones of *Psittacopes lepidus* in comparison with psittaciform and cuculiform birds (n = number of individuals, value in parentheses = standard deviation).
Text-fig. 8. The relationship of the Eocene psittaci-form birds described in this paper. Characterization of the nodes 1 and 2 is described in the beginning of the systematic part.

Text-fig. 9. Left tarsometatarsus of A) WN 96949 (species C); B) Neophema splendida (Psittacidae); C) Trichoglossus ornatus (Psittacidae).

Text-fig. 9. Left tarsometatarsus of A) WN 96949 (species C); B) Neophema splendida (Psittacidae); C) Trichoglossus ornatus (Psittacidae).

Text-fig. 9. Left tarsometatarsus of A) WN 96949 (species C); B) Neophema splendida (Psittacidae); C) Trichoglossus ornatus (Psittacidae).

- Scale = 2 mm.

Text-fig. 9. Left tarsometatarsus of A) WN 96949 (species C); B) Neophema splendida (Psittacidae); C) Trichoglossus ornatus (Psittacidae).

- Scale = 2 mm.

Hemisphere and that the new world parrots have been separated from the old world species since the Cretaceous, which implies a Cretaceous origin for the Psittacidae. This is not supported by the fossil record, which suggests an emergence of the Psittacidae in the old world between the Late Eocene and the early Miocene (see introduction). The whole Order Psittaciformes might of course be much older, and knowing that it branched off before the Early Eocene is important for calibrating phylogenetic investigations based on molecular data (e.g. DNA-DNA hybridization). The fact that the earliest known psittaciiform birds are comparatively small reflects an evolutionary trend, which is confirmed by other fossil avian taxa, e.g. the hoopoe-like birds from Messel (MAYR, in press).

The characteristic bill of the Psittacidae is very massive, adapted for hard food (tubers, shells of large seeds, etc.) and autapomorphic for this family. The coly-like bill of the Eocene parrots indicates a predominantly vegetable diet, too, but the large narial openings and the slender mandible make it likely that their food did not include very hard ingredients. This is in concordance with the investigations of GÖRTZ (1981: 471): "The evidence presented strongly suggests that the ancestors of recent parrots were forest-living birds with an unspecialized granivorous diet".

The early Tertiary parrots also differ in the wing proportions from the Psittacidae (tab. 3). The carpometacarpus especially is much shorter than that of the Recent parrots (pl. 4 fig. 10). Together with the differences in the sternum and in the pectoral girdle mentioned in the description, this probably indicates different flight characteristics.

Some attempts have been made to analyze the relationships within the Psittacidae, and the proposed classifications vary considerably in the arrangement of the taxa (see SIBLEY & AHLQUIST 1990 for a review). SMITH (1975) subdivided them into four subfamilies, which he considered to be monophyletic:

- Platycercinae (Platycercini, Cacatuini, Nestorini, Strigopini);
- Loriinae (Loriini, Psittichasini, Psittaculini, Micropsittini, Psittaculirostrini);
- Arinae (Arini);
- Psittacinae (Psittacini).

While the 11 tribes might reflect natural units, the monophyly of the first two subfamilies can hardly be corroborated. The characters listed by SMITH in order to support a monophyly of the Platycercinae are either likely to be plesiomorphic (type A-1 of carotid arteries, sexual monomorphism) or absent in several taxa within the Platycercinae, or respectively present in some of the other subfamilies too (closed orbital ring).

Generally it is very difficult to decide whether characters are derived or primitive within a specific taxon. For example, the Psittacidae show a great variation in the relative length of their tarsometatarsus (see text-fig. 9). It is comparatively slender in the Platycercini (e.g. Cyanoramphus, Neophema, Melopsittacus), but short and compact within the Cacatuini, Loriinae, Arinae and Psittacinae. Although comparison with the Eocene psittaciiform birds indicates that a rather slender tarsometatarsus is primitive within the Psittaciformes, Archaeopsittacus veereuxi, one of the earliest known members of the Psittacidae, exhibits a stout tarsometatarsus like the modern genus Psittacus.

Obviously plesiomorphic features within the Psittaciiformes are the presence of a fenestra mandibulae (which certainly has been reduced independently more than once within the Psittacidae) and the absence of a deep furrow in the trochlea metatarsi III (which has been interpreted as a climbing adaptation by BALLMANN 1969).

The phylogenetic affinities of the whole Order Psitaciiformes remain enigmatic. Among the living birds mainly the Columbiformes (e.g. FÜHRINGER 1888), respectively the Cuculiformes (e.g. GADOW 1893, who included the Psittaciidae together with the Musophagidae and Cuculidae in this order), have been thought to be their closest relatives. Indeed, the
humeri of Recent doves (Columbidae) and Recent parrots are very similar (see WEITMORE 1926), but this resemblance is most likely due to convergence, as shown by the humeri of the fossil parrots, which differ from both Columbidae and Psittacidae. We did not find any derived osteological character supporting a monophyly of the taxon (Columbiformes + Psittaciformes), including the Eocene parrots. Like their Recent relatives, the Eocene parrots described herein differ distinctly from the Cuculidae in their proportions (tab. 3). Although this might be of minor phylogenetic importance, a monophyly of the taxon (Cuculiformes [Cuculidae] + Psittaciformes) can only be established with the zygodactyl foot. This feature alone is not very convincing, as in recent years some new fossil taxa with fully zygodactyl feet have been described, which are apparently neither closely related to the Cuculiformes nor to the Psittaciformes (Sandcoleiformes HOUDE & OLSON 1992, "Primobucco" olsoni FEDUCIA & MARTIN 1976). Birds closely related to "P" olsoni (which is not congeneric with the anisodactyl bird Primobucco mcgregori, see HOUDE & OLSON 1989) are also represented in the Eocene avifauna of Walton-on-the-Naze (pl. 5 figs. 17, 18c) and clearly differ from the psittaciform birds (e.g. coracoid with foramen nervi supracoracoidei, humerus more elongate, hypotarsus larger, taxometatarsus with sulci hypotarsi, Sehnenhalter not separated from the trochlea metatarsi IV).

Apparently the parrots are a very ancient taxon, which might have branched off in the Paleocene or even earlier. Searching for a single Recent sister taxon might therefore be doomed to failure from the beginning, since it is likely that the Psittaciformes are in a sister group relationship with more than one extant order.

References


Fig. 1. *Psittacopes lepidus* n. g., n. sp.
*Holotype* (SMF-ME 1279).

a) covered with ammonium chloride;

b) x-ray photograph.
G. MAUR & M. DANIELS: Eocene parrots from Messel (Hessen, Germany) and the London Clay of Walton-on-the-Naze (Essex, England)
Fig. 2. *Psittacopes lepidus* n. g., n. sp.
Covered with ammonium chloride.

a) SMNK-Me 1089b;
b) SMNK-Me 1089a.
G. Mayr & M. Daniels: Eocene parrots from Messel (Hessen, Germany) and the London Clay of Walton-on-the-Naze (Essex, England)
Plate 3

Fig. 3. WN 91711 (species A)
Scale = 5 mm.

a) left coracoid;
b) proximal end of left humerus;
c) distal end of left humerus;
d) left radius;
e) left ulna;
f) right carpometacarpus;
g) right tarsometatarsus.

Fig. 4. WN 85506 (species A)
Scale = 5 mm.

a) right scapula;
b) proximal end of right humerus;
c) distal radius;
d) proximal radius;
e) claws;
f) distal end of left tibiotarsus;
g) left tarsometatarsus.

Fig. 5. BC 8917A (species B or C)
Scale = 5 mm.

a) mandible;
b) right quadratum;
c) atlas;
d) cervical vertebra;
e) scapula;
f) right coracoid;
g) proximal end of scapula;
h) proximal end of right humerus;
i) distal end of left humerus;
j) left ulna;
k) distal end of radius;
l) proximal end of left carpometacarpus (in matrix);
m) proximal end of tibiotarsus;
n) claws.

Fig. 6. WN 86540 (species B)
Scale = 5 mm.

a) right scapula;
b) left coracoid;
c) proximal end of left humerus;
d) distal end of right humerus;
e) phalanx distalis digiti majoris;
f) phalanx proximalis digiti majoris;
g) right carpometacarpus;
h) right tarsometatarsus.
G. Mayr & M. Daniels: Eocene parrots from Messel (Hessen, Germany) and the London Clay of Walton-on-the-Naze (Essex, England)
Plate 4

Fig. 7.  
a) BC 8917A (species B or C), lateral view of skull. – Scale = 5 mm.
b) *Neophema splendida* (Psittacidae), skull. – Scale = 5 mm.

Fig. 8.  
BC 8917A (species B or C), dorsal view of skull. – Scale = 5 mm.

Fig. 9.  
WN 91711 (species A), skull and part of mandible in matrix. – Scale = 5 mm.

Fig. 10.  
a) *Neophema splendida* (Psittacidae), left carpometacarpus. – Scale = 5 mm.
b) WN 86540 (species B), left carpometacarpus. – Scale = 5 mm.

Fig. 11.  
a) *Neophema splendida* (Psittacidae), left tarsometatarsus. – Scale = 5 mm.
b) WN 86540 (species B), right tarsometatarsus. – Scale = 5 mm.

Fig. 12.  
a) *Neophema splendida* (Psittacidae), left coracoid. – Scale = 5 mm.
b) WN 86540 (species B), left coracoid. – Scale = 5 mm.

Fig. 13.  
WN 94811 (species B or C), left humerus. – Scale = 5 mm.
G. MAYR & M. DANIELS: Eocene parrots from Messel (Hessen, Germany) and the London Clay of Walton-on-the-Naze (Essex, England)
Plate 5

Fig. 14. *Palaeopsittacus georgei* HARRISON 1982
Scale = 5 mm.

a) WN 94838B (juvenile specimen), right coracoid;
b) WN 94838B (juvenile specimen), left tarsometatarsus;
c) WN 91682, right tibiotarsus;
d) WN 91682, left tarsometatarsus.

Fig. 15. a) WN 89627A (species A), distal end of right tarsometatarsus. – Scale = 5 mm.
b) WN 91682 (*Palaeopsittacus georgei*), distal end of left tarsometatarsus. – Scale = 5 mm.
c) WN 89627A (species A), proximal end of right tarsometatarsus. – Scale = 5 mm.
d) WN 91682 (*Palaeopsittacus georgei*), proximal end of left tarsometatarsus. – Scale = 5 mm.

Fig. 16. a) WN 89627A (species A), right tarsometatarsus. – Scale = 5 mm.
b) WN 87563 (*Quercypsittidae* indet.), right tarsometatarsus. – Scale = 5 mm.
c) WN 87563 (*Quercypsittidae* indet.), right tibiotarsus. – Scale = 5 mm.

Fig. 17. WN 85508 (cf. *"Primobucco" olsoni* FEDUCCIA & MARTIN 1976)
Scale = 5 mm.

a) scapula;
b) right coracoid;
c) proximal end of right humerus;
d) distal end of right humerus;
e) left ulna;
f) right carpometacarpus;
g) left femur;
h) right tibiotarsus;
i) left tarsometatarsus.

Fig. 18. Tarsometatarsi in comparison
Scale = 5 mm.

a) WN 96949 (species C), left tarsometatarsus;
b) WN 89627A (species A), right tarsometatarsus;
c) WN 87563 (*Quercypsittidae* indet.), right tarsometatarsus;
d) WN 91682 (*Palaeopsittacus georgei*), left tarsometatarsus;
e) WN 85508 (cf. *"Primobucco" olsoni*), left tarsometatarsus.