

A new short-legged landbird from the early Eocene of Wyoming and contemporaneous European sites

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Fluvioviridavis platyrhamphus, a new genus and species of short-legged landbirds from the Lower Eocene Green River Formation (Wyoming, USA) is described. The taxon is known from a single, nearly complete and slightly dissociated skeleton which was made the paratype of the putative oilbird *Prefica nivea* Olson, 1987 (Steatornithidae, Caprimulgiformes). Apart from the greatly abbreviated tarsometatarsus, *Fluvioviridavis* especially corresponds to recent oilbirds in the unusually wide proximal end of the humerus. However, in other features, e.g., the shape of its much longer beak, the Eocene taxon is clearly distinguished from the recent oilbird (*Steatornis*). In contrast, *Prefica nivea* agrees with *Steatornis* in the shape of the mandible but differs in the much narrower proximal end of the humerus. At present, no derived character convincingly supports a classification of *F. platyrhamphus* into any of the higher avian taxa. The species is here classified 'order and family *incertae sedis*'. An isolated skull from the Middle Eocene of Messel (Hessen, Germany) is tentatively assigned to ?*Fluvioviridavis* sp., and associated bones from the Lower Eocene London Clay of Walton-on-the-Naze (Essex, England) might also be related to the genus *Fluvioviridavis*.

Key words: Fossil birds, Eocene, *Fluvioviridavis*, Green River Formation, Messel, London Clay.

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Introduction

The Lower Eocene deposits of the Green River Formation (Wyoming, USA) originated in a complex lacustrine system and yielded a large number of fossil birds (Grande 1980). Taxa identified so far include frigatebirds, Galliformes, Caprimulgiformes, and members of the extinct families Lithornithidae, Foratidae, Messelornithidae, Pseudasturidae, and Sandcoleidae (Eastman 1900; Feduccia & Martin 1976; Olson 1977, 1987, 1992;

Houde 1988; Hesse 1992; Houde & Olson 1992; Mayr 1998, 2000a, and references cited therein). In general, the Green River avifauna shows a high degree of concordance to that from the early Eocene of Europe (see Mayr 1999a, 2000b).

The specimen SMNK.PAL.2368a+b was first figured by Olson (1985: p. 126) who stated that it 'can hardly be distinguished from the living genus *Eurystomus* [broad-billed rollers, Coraciiformes], at least on the basis of its photograph'. However, Olson (1987) described another skeleton from the Green River Formation as *Prefica nivea*, a putative Lower Eocene oilbird (Steatornithidae, Caprimulgiformes). He made specimen SMNK.PAL.2368a+b a paratype of *P. nivea* and its classification into the genus *Prefica* was adopted by Feduccia (1996: p. 322).

For the first time, specimen SMNK.PAL.2368a+b was examined in the course of a revision of the caprimulgiform birds from Messel by Mayr (1999a), who established that its assignment to *Prefica nivea* is incorrect since it distinctly differs from the latter species in size, limb proportions and a number of osteological features. The specimen is described in the present study.

Similar taxa have also been identified in the extensive avian record from the Middle Eocene of Messel (Hessen, Germany) and the Lower Eocene London Clay of Walton-on-the-Naze (Essex, England).

The anatomical terminology follows Baumel & Witmer (1993). Unless otherwise specified, 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. — SMNK, Staatliches Museum für Naturkunde Karlsruhe, Germany; SMF, Forschungsinstitut Senckenberg, Frankfurt a.M., Germany; WN, private collection of M. Daniels.

Systematic paleontology

Order and family *incertae sedis*

Genus *Fluviovidavis* gen. n.

Type species: *Fluviovidavis platyrhamphus* sp. n.

Etymology: The generic name has been derived from Latin words: *fluvius* – river, *viridis* – green, and *avis* – bird, and refers to the type locality.

Diagnosis. — Small anisodactyl birds with a large skull; wide and dorso-ventrally flattened beak; coracoid with deeply excavated, cup-like cotyla scapularis and foramen nervi supracoracoidei; sternum with two pairs of shallow notches; humerus with very large proximal end and short, convexly bowed crista deltopectoralis; ulna exceeding humerus in length; phalanx digiti alulae and phalanx distalis digiti majoris with claws; tarsometatarsus strongly abbreviated.

Differential diagnosis. — *Fluviovidavis* differs from *Prefica* Olson, 1987 in the smaller size and different limb proportions (especially the tarsometatarsus is proportionally longer, the ratio ulna : tarsometatarsus for example is 4.2 vs. 6.6 in *Prefica*), the narrower and more elongated beak, the wider interorbital part of the os frontale, the slightly narrower incisions in the caudal margin of the sternum, and the imperforated phalanx proximalis digiti majoris. Only a few other early Tertiary avian genera are known which have an equally abbreviated tarsometatarsus, i.e. the caprimulgiform genus *Paraprefica* Mayr, 1999a, and the coraciiform genus *Eocoracias* Mayr & Mourer-Chauviré, 2000. However, in none of these taxa the proximal end of the humerus is as wide as in *Fluviovidavis*

gen. n., *Paraprefica* further differs in the much shorter beak (see Mayr 1999a). *Eocoracias* is distinguished in the deeper notches in the caudal margin of the sternum.

Fluioviridavis platyrhamphus sp. n.

Figs. 1, 2.

Prefica nivea; Olson 1987: pp. 57–61.

Holotype and only known specimen: SMNK.PAL.2368a+b, nearly complete, slightly dissociated skeleton on a slab (Fig. 1; some missing parts have been painted by the preparator of the specimen, i.e. the proximal left femur, the distal left tibiotarsus, the mid-section of the left ribs, and a small part of the proximal left humerus). Counterslab with fragments of the left humerus, femur, and tibiotarsus.

Type locality: 'Tynsky Quarry', near Diamondville, Wyoming, USA.

Type horizon: Upper Lower Eocene (Fossil Butte Member of the Green River Formation).

Etymology: The specific name has been derived from Greek words: *platys* – broad and *rhamphos* – bill.

Diagnosis. — Same as for genus.

Description and comparisons. — Measurements: Skull, ~62; beak, 34.8; width of skull at nasofrontal hinge, 13.3; coracoid, ~20 (r); humerus, 50.1 (l)/49.5 (r); maximum proximal width of humerus, 16.5 (l); ulna, 56.3 (l)/56.0 (r); carpometacarpus, 27.7 (l)/27.5 (r); femur, 24.3 (l); tibiotarsus, 34.2 (r); tarsometatarsus, 13.5 (l)/13.5 (r). Pedal phalanges: dI p1, 7.5; dI p2, 4.8; dII p1, 6.4; dII p2, 5.2; dII p3, 4.4; dIII p1, 7.1; dIII p2, 5.3; dIII p3, 6.3; dIII p4, 5.1; dIV p1, 4.9; dIV p2, 4.0; dIV p3, 4.4; dIV p4, 4.4; dIV p5, 5.5.

Fluioviridavis platyrhamphus gen. et sp. n. has a similar size and, apart from the somewhat more abbreviated tarsometatarsus, also similar limb proportions like the recent Broad-billed Roller, *Eurystomus glaucurus afer* (Coraciidae).

Skull: The skull of *Fluioviridavis* is large in relation to the body (contrary to *Prefica* which has a rather small skull). The beak measures half the entire length of the skull. It is dorso-ventrally flattened, fairly wide at its basis and gradually becomes narrower towards the pointed tip. In its shape it most closely resembles the beak of some recent tyrant flycatchers (Tyrannidae, Passeriformes), e.g., *Tolmomyias* spp. and *Empidonax* spp., although these birds are much smaller. The narial openings are elongated and narrow, the ventrally adjacent part of the ossa maxillaria is dorso-ventrally high. The interorbital part of the frontal is wide, contrary to *Prefica nivea* (see Olson 1987: pl. 3). The rest of the cranium is too poorly preserved to allow the recognition of any details. A small ossicle which lies between the right humerus and the right ulna might be the left os quadratum. If this interpretation is correct, the latter bone bears a very short processus orbitalis in *Fluioviridavis*, similar to the condition in recent Caprimulgidae, Nyctibiidae, and Aegothelidae (Caprimulgiformes). An osseous bar which is situated next to the putative quadratum might be a pterygoid.

Vertebrae: The cervical vertebrae are rather short. The lacuna interzygapophysialis is deep. Six to seven free caudal vertebrae can be counted. The wide lamina pygostyli is similar to that of *Prefica nivea* and recent rollers (Coraciidae).

Coracoid: The coracoid (Fig. 2A) differs from that of all recent 'higher' landbirds in the combination of a small foramen nervi supracoracoidei with a deeply excavated and circular cotyla scapularis. Although the recent oilbird (*Steatornis caripensis*) exhibits a concave cotyla scapularis, this, too, is somewhat shallower and less circular than in *Fluioviridavis*; moreover, the coracoid of *Steatornis* lacks a foramen nervi supracoracoidei which among recent Caprimulgiformes only occurs in the owl-nightjars (Aegothelidae). The processus procoracoideus of *Fluioviridavis* is vestigial. The extremitas sternalis of the coracoid seems to have been similar to that of *Steatornis*. The angulus medialis is pointed and strongly protrudes medially.

Furcula: The furcula is U-shaped and has a wide extremitas omalis. The extremitas sternalis is narrow.

Scapula: The scapula is of usual shape, its distal part is slightly deflected laterally. The acromion is of average length.



Fig. 1. *Fluvioviridavis platyrhamphus*, holotype (SMNK.PAL.2368a), nearly complete, slightly dissociated skeleton in dorsal view. Scale bar 10 mm.

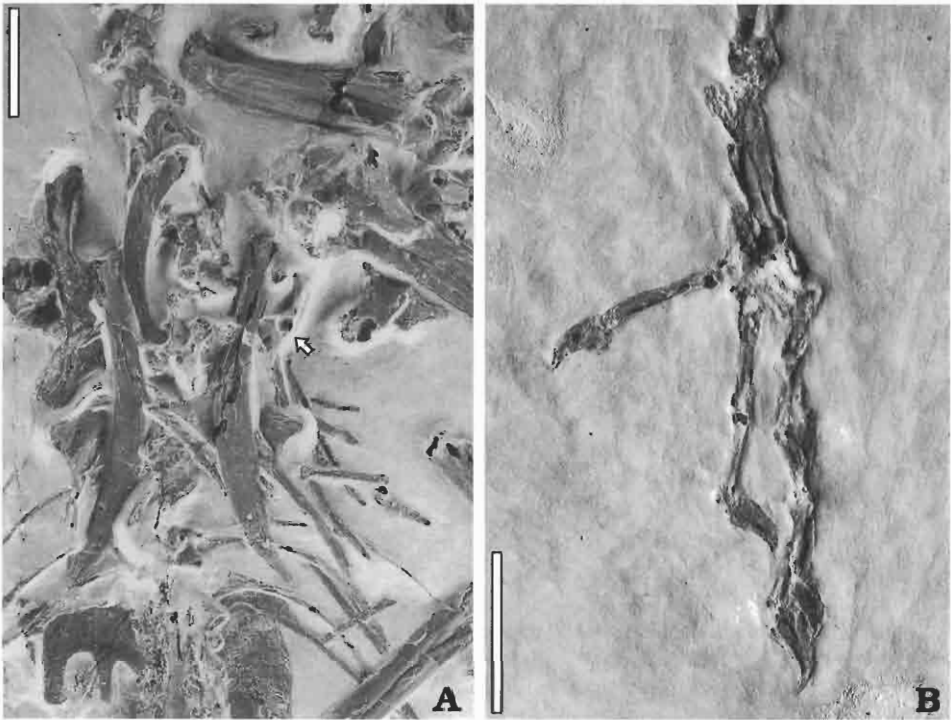


Fig. 2. *Fluvioviridavis platyrhamphus*, holotype (SMNK.PAL.2368a). A. Detail of the pectoral region, the arrow indicates the extremitas omalis of the right coracoid. B. Right foot. Scale bars 10 mm.

Sternum: As far as comparable, the sternum resembles the corresponding bone of *Prefica nivea* in having two pairs of shallow notches at its caudal margin. However, these incisions are slightly narrower than in *Prefica*. Like in the latter, all trabeculae lack transverse processes. The processes cranio-laterales are short.

Humerus: The proximal end of the humerus is very large and, except for the less strongly protruding tuberculum ventrale, resembles the proximal humerus of the recent oilbird, *Steatornis caripensis* (Steatornithidae). Olson (1987: p. 61) stated that the humerus of *Prefica nivea* 'is not substantially different from that of rollers or primitive Caprimulgiformes such as the Podargidae', but this certainly is not true for SMNK.PAL.2368. In its relative size, the proximal end of the humerus of *Fluvioviridavis platyrhamphus* is more than 1.5 times wider than that of *Prefica nivea* (the length of the humerus is 50.4 in *Fluvioviridavis* vs. ca. 63 in *Prefica*, the proximal width is 16.5 in *Fluvioviridavis* vs. ca. 13 in *Prefica*). In specimen SMNK.PAL.2368 a cleft separates the dorsal part of the left humerus from the ventral part; this cleft has been filled up with plaster by the preparator of the specimen who painted the missing part incorrectly – at first sight, the proximal left humerus thus appears much narrower than it actually is. Like in recent Caprimulgiformes but contrary to recent Coraciiformes, the caput humeri is oriented obliquely to the longitudinal axis of the bone and is separated from the tuberculum ventrale by a wide incisura capitis humeri. The crus dorsale fossae is wide at the level of the tuberculum ventrale. The crista deltopectoralis (only visible at the left humerus) is rather short but strongly protruding as in *Steatornis caripensis*, like in the latter its margin is convexly bowed. The crista bicipitalis is small. The preservation of the distal end of the humerus does not allow the recognition of details.

Ulna: The ulna is longer than the humerus. About ten papillae remigales can be discerned. Its proximal end is wide and appears to have similar proportions like the proximal ulna of recent Podargidae (Caprimulgiformes). The olecranon is short (more elongated in recent Coraciidae).

Carpometacarpus: The carpometacarpus is relatively shorter than in *Prefica*. The os metacarpale minus runs parallel to the os metacarpale majus. A very small processus intermetacarpalis is present. The trochlea carpalis is large. The processus pisiformis is shifted slightly cranially.

Other elements of the wing: Both the phalanx digiti alulae and the phalanx distalis digiti majoris bear a claw (see Mayr 1999a: fig. 5). Especially the claw on the phalanx distalis digiti majoris is present in only a few recent avian taxa and consistently absent in adults of all 'higher' landbirds (a survey on the occurrence of claws in recent birds was given by Stephan 1992). The phalanx proximalis digiti majoris is not perforated (contrary to that of *Prefica*) and bears a short processus internus indicis (terminology after Stegmann 1963). The phalanx distalis digiti majoris exhibits a small projection on its caudal margin.

Pelvis: The pelvis is fairly wide and except for the slightly wider alae praeacetabulares ilii resembles the pelvis of the recent *Eurystomus glaucurus* (Coraciidae) in its proportions. The praeacetabular part of the ossa ilia is slightly shorter than the postacetabular part. The alae praeacetabulares ilii are wider than in recent Caprimulgiformes and Coraciidae. The synsacrum is not fused with the ossa ilia and exhibits many foramina intertransversaria. There is a pair of distinct spinae dorso-laterales ilii as, for example, in recent *Eurystomus glaucurus* (Coraciidae) and *Batrachostomus septimus* (Podargidae). The foramina obturata are caudally open. Like in *Batrachostomus*, the narrow processus terminales ischii taper to a point and do not meet the long ossa pubes (in *Eurystomus* these processes are shorter and stouter).

Femur: The femur is straight and rather short. Due to preservation, no details of its proximal and distal ends can be discerned.

Tibiotarsus: The tibiotarsus is short and stout. The cristae cnemiales apparently were small. The condylus lateralis is small and round in lateral view, like in *Steatornis caripensis* and *Batrachostomus septimus* it hardly protrudes cranially.

Tarsometatarsus: The tarsometatarsus (Fig. 2B) is very short but proportionally somewhat longer than that of *Prefica nivea* (see Mayr 1999a). Due to preservation, not many osteological details can be discerned. The hypotarsus appears to have been complex. The trochlea metatarsi III is small and obviously reaches not farther distally than the other trochleae metatarsorum. At least in its proportions the bone is similar to a tarsometatarsus from the Lower Eocene of Virginia figured by Olson (1999: fig. 7), who assigned that specimen to the Aegialornithidae. However, contrary to the unnamed species from Virginia, the distal tarsometatarsus of *Fluvioviridavis* apparently was hardly curved on the level of the trochleae metatarsorum.

Toes: The feet are anisodactyl. The third toe is the longest, the second is shorter than the fourth. The hallux is long and nearly reaches the length of the tarsometatarsus. The claws are bilaterally compressed and of average length, neither very long nor very short; the tubercula flexoria are small.

?*Fluvioviridavis* sp.

Fig. 3.

Tentatively referred specimen: SMF-ME 10783a+b, isolated skull from the Middle Eocene of Messel (Hessen, Germany) (Fig. 3).

Description. — Measurements: Length of skull, 50.3; length of mandible, 35.

Specimen SMF-ME 10783 is smaller than the skull of *Fluvioviridavis platyrhamphus*, but in the shape of the dorso-ventrally flattened beak it is very similar to the North American species. The interorbital width of the os frontale appears to have been slightly narrower than in *F. platyrhamphus*. As far as can be discerned, the ossa palatina seem to have been narrow and separated by a wide gap, thus the palate obviously was not heavily ossified as, for example, in recent Podargidae. The ossa pterygoidea are long and slender, processus basipterygoidei apparently are absent. The rami mandibulae are moderately high. The pars symphyialis is narrow but wider than in *Prefica* and most recent Caprimulgiformes (it measures ca. 5.5 mm). Fenestrae mandibulae cannot be discerned. The proximal end of the mandible bears fairly long processus mediales mandibulae. In the specimen not only the apparatus hyobranchialis is preserved but also parts of the larynx.

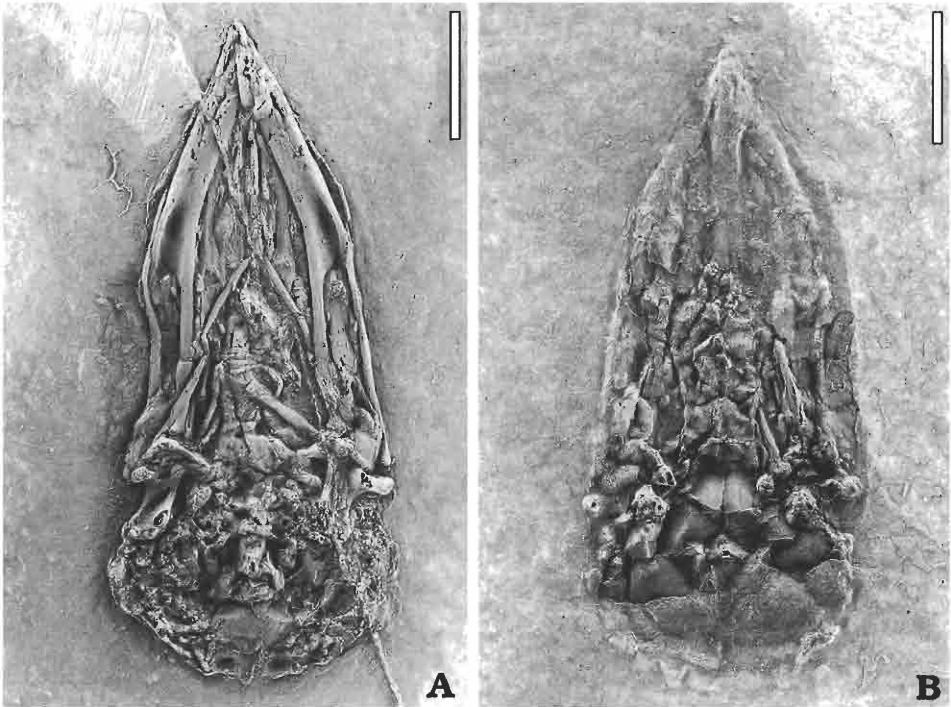


Fig. 3. ?*Fluviovidavis* sp., tentatively referred isolated skull from the Middle Eocene of Messel (Hessen, Germany) (SMF-ME 10783a+b) in ventral (A) and dorsal (B) views. Coated with ammonium chloride to enhance contrast. Scale bars 10 mm.

Because it is based on an isolated skull only, the assignment of SMF-ME 10783 to *Fluviovidavis* is tentative.

Discussion

Apparently, *Fluviovidavis platyrhamphus* gen. et sp. n. belongs to an extinct group of birds that had a wide distribution on the Northern Hemisphere in the early Eocene. Apart from the specimen from Messel described above, birds having a similar osteology are known from the London Clay of Walton-on-the-Naze (Essex, England), where around ten examples have been found. The principle specimen (Fig. 4) consists of several isolated bones which were found associated, and it resembles *Fluviovidavis* in particular in the morphology of the coracoid (both a cup-like cotyla scapularis and a foramen nervi supracoracoidei are present) and the carpometacarpus. It is of somewhat smaller size than *Fluviovidavis platyrhamphus* (radius 43.5 mm, carpometacarpus 23.4 mm), from which it further differs in several osteological features, e.g. the longer processus procoracoideus, the smaller proximal end of the humerus, the more strongly developed olecranon of the ulna, and the perforated phalanx proximalis digiti majoris. The humerus exhibits a small processus supracondylaris dorsalis which also seems to be absent in *Fluviovidavis*. Future specimens, especially in which the tarsometatarsus is preserved, are needed to show whether the London Clay species is indeed related to *Fluviovidavis platyrhamphus*.

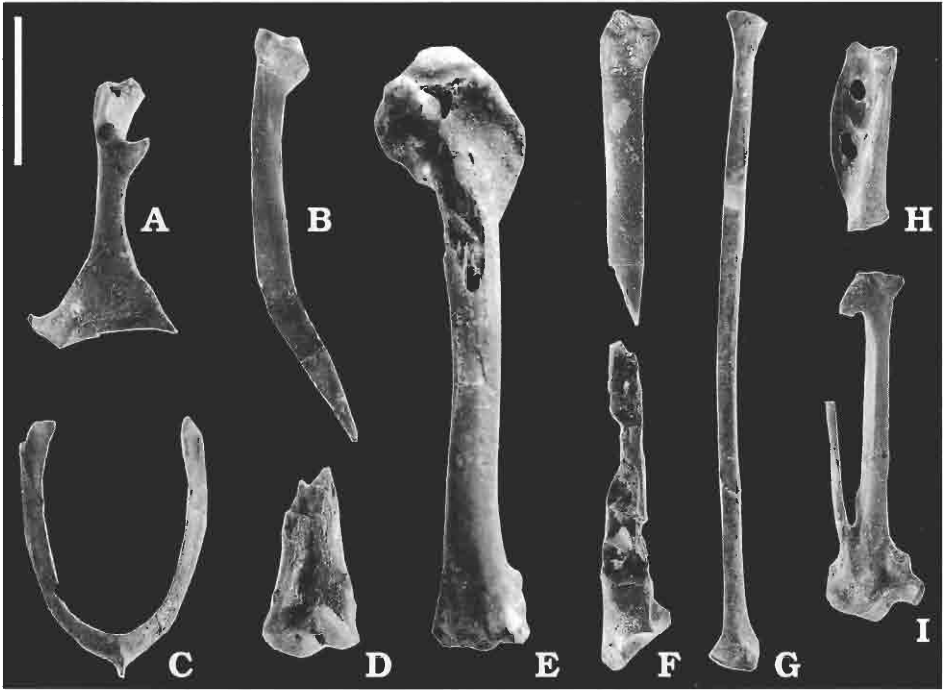


Fig. 4. cf. *Fluvioviridavis* sp., referred specimen from the Lower Eocene London Clay of Walton-on-the-Naze (Essex, England) (WN 88588). Several associated bones of a single individual, including a left coracoid (A), a left scapula (B), the furcula (C), a distal end of the left humerus (D), a complete right humerus (E), the right ulna (F), the right radius (G), a phalanx proximalis digiti majoris (H), and the right carpometacarpus (I). Scale bar 10 mm.

Like some previously described early Eocene avian taxa (e.g., Mayr 1998, 1999b, 2000a), *Fluvioviridavis platyrhamphus* cannot be assigned to any of the known recent or fossil avian orders with certainty. Although the new taxon superficially resembles some recent Coraciiformes and Caprimulgiformes in overall morphology, no derived character convincingly supports its assignment to either of these orders. Similarities to the short-legged coraciiform genus *Eurystomsus* (broad-billed rollers) are only superficial and mainly concern the limb proportions. Apart from the greatly abbreviated tarsometatarsus, *Fluvioviridavis* especially corresponds to the caprimulgiform genus *Steatornis* (oilbirds) in the morphology of the unusually wide proximal end of the humerus. In other features, however, e.g. the shape of its much longer beak, the Eocene taxon is clearly distinguished from *Steatornis*. In contrast, *Prefica nivea*, the putative steatornithid described by Olson (1987) (see Introduction), agrees with *Steatornis* in the shape of the mandible (the upper beak is not preserved in the specimen) but – among other features – differs in the much smaller proximal end of the humerus. In its hindlimb proportions *Fluvioviridavis* corresponds better to *Steatornis* than does *Prefica*, in which the tarsometatarsus is even more abbreviated (Mayr 1999: tab. 1).

Fluvioviridavis exhibits some characters that are absent in most ‘higher’ (sensu Olson 1985) landbirds and probably are primitive among neognathous birds. This is especially true for the circular, distinctly cup-like cotyla scapularis of the coracoid (see

Mourer-Chauviré 1992; Mayr 2000b) and for the presence of a claw on both the phalanx digiti alulae and the phalanx distalis digiti majoris. If future evidence confirms an assignment of *Fluvioviridavis* to the Caprimulgiformes, the fossil genus certainly occupied a very basal position within that order.

As already noted above, the large and dorso-ventrally flattened beak of *Fluvioviridavis* somewhat resembles that of some recent tyrant flycatchers, and according to its bill-shape the Eocene taxon probably mainly fed on insects and other small invertebrates. *F. platyrhamphus* certainly was well capable of perching, although the strongly developed wing skeleton and the short tarsometatarsus might suggest that the Eocene species was adapted to a fairly aerial way of living.

The various birds in this study provide insight concerning an important avian group that lived during the Eocene. The Green River specimen together with those from the contemporary London Clay formation and from the Middle Eocene of Messel, constitute an excellent suite of phylogenetically linked fossils each offering complementary insights. The Karlsruhe specimen provides detailed overall appreciation of the general configuration, whilst those preserved in-the-round from the London Clay enable finer determination where various aspects of the American skeleton are pressure distorted. The Messel skull shows the revealing shape of this element and adds knowledge not otherwise available from the Lower Eocene individuals.

Here yet again we find strong evidence of the mosaic nature of early Palaeogene birds. These must represent stem occurrences which may give unique opportunity to determine the form of some long extinct avian group or, alternatively, track the origins of birds now fully differentiated in modern categories of the class Aves.

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Nowy krótkonogi ptak z wczesnego eocenu stanu Wyoming i równoległych stanowisk europejskich

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Streszczenie

W pracy opisano nowy rodzaj i gatunek krótkonogiego ptaka lądowego nazwanego *Fluvioviridavis platyrhamphus*, z wczesnoeocenijskiej formacji Green River (Wyoming, USA). Takson ten jest znany z jednego prawie kompletnego i nieco rozproszonego szkieletu, ustanowionego jako paratyp domniemanego kopalnego tłuszczaka *Prefica nivea* Olson, 1987 (Steatornithidae, Caprimulgiformes). Oprócz silnie skróconych kości skoku, *Fluvioviridavis* nawiązuje do współczesnych tłuszczaków bardzo szeroką nasadą kości ramiennej. Jednak pod innymi względami, np. kształtem znacznie bardziej wydłużonego dzioba, eocenijski takson wyraźnie różni się od współczesnego tłuszczaka (*Steatornis*), natomiast *Prefica nivea* ma kształt szczęki podobny jak *Steatornis*, ale różni się odeń o wyraźnie węższą nasadą kości ramiennej. Obecnie nie można wskazać żadnej apomorfii przekonująco wiążącej *F. platyrhamphus* z jakimkolwiek taksonem wyższej rangi, toteż rodzaj i gatunek ten uznano w niniejszej pracy za reprezentujący „rodzinę i rząd *incertae sedis*”. Pojedyncza czaszka ze środkowego eocenu Messel (Hesja, Niemcy) została prowizorycznie zaliczona do *?Fluvioviridavis* sp.; do rodzaju *Fluvioviridavis* mogą też należeć kości z wczesnoeocenijskich ilów londyńskich (London Clay) z Walton-on-the-Naze (Essex, Anglia).