A NEW SPECIES OF OWL (AVES: STRIGIFORMES) FROM THE MIDDLE EOCENE MESSEL OIL SHALE

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ABSTRACT. The postcranial skeleton of a small owl from the oil shale of Messel (Middle Eocene, Lower Geiseltalium) is described as *Palaeoglaux artophoron* new species. The family Palaeoglaucidae Mourer-Chauviré 1987 is different from all other known families of owls, but it is not possible to determine the phylogenetic relationships of the paleoglaucids because the phylogeny of owls is so poorly known. The unusual plumage structure of *P. artophoron* and its possible significance is discussed.

ZUSAMMENFASSUNG. Das postcraniale Skelett von *Palaeoglaux artophoron* n. sp., einer kleinen Eule aus dem Ölschiefer von Messel (Mittel-Eozän, Unteres Geiseltalium), wird beschrieben und mit anderen fossilen und rezenten Eulen verglichen. Die Familie Palaeoglaucidae Mourer-Chauviré 1987 weicht von allen anderen Eulen ab. Ihre genealogischen Beziehungen lassen sich zur Zeit kaum rekonstruieren, da die Phylogenie der Eulen insgesamt nur unzureichend bekannt ist. Das ungewöhnliche Gefieder von *P. artophoron* und seine mögliche Bedeutung werden kurz diskutiert.

Key words: Aves, Strigiformes, *Palaeoglaux*, Palaeoglaucidae, phylogeny, plumage, Eocene, Messel.

INTRODUCTION

The fossil record of owls begins in the Paleocene, with *Ogygoptynx* Rich and Bohaska 1981 from Colorado and *Sophiornis* Mourer-Chauviré 1987 from France. During the Eocene, at the latest, owls underwent a considerable radiation, with no less than 2 families comprising 7 genera and 11 species being described from the Phosphorites du Quercy, France, alone (Mourer-Chauviré, 1987). Additional species of Eocene owls are known from Europe and North America, although the fossil record of most species is based on only scarce, fragmentary remains. The specimen discussed herein is the first articulated skeleton of an Eocene owl to be described.

Many fossil birds have been found in the lake deposits of Grube Messel (Peters, 1988), but among these raptorial species are quite rare. Only two specimens of the order Falconiformes are known, and the specimen described herein is the only owl ever recovered from the site. It may be that raptors of the time were predominately forest birds, thereby avoiding the trap-effect of the lake (Franzen, 1985), or that they were simply still uncommon birds. General information about the Messel site was given by Hoch (1980) and Franzen (1985); for more details see Schaal and Ziegler (1988).

MATERIALS

Comparative specimens were examined from the following extant species of owls: *Phodilus badius* (Horsfield 1821), *Tyto alba alba* (Scopoli 1769), *T. a. guttata* (C.L. Brehm 1831), *T. a. glaucops* (Kaup 1852), *Otus asio* (Linnaeus 1758), *Otus bakkamoena* Pennant 1769, *Bubo bubo* (Linnaeus 1758), *Buto virginianus* (Gmelin 1788), *Nyctea scandiaca* (Linnaeus 1758), *Pulsatrix perspicillata* (Latham 1790), *Glaucidium brasilianum* (Gmelin 1788), *Glaucidium passerinum* (Linnaeus 1758), *Ninox novaeseelandiae* (Gmelin 1788), *Athene noctua* (Pontoppidan 1763), *Speotyto cunicularia* (Molina 1782), *Strix aluco* Linnaeus 1758, *Asio otus* (Linnaeus 1758), *Asio flammeus* (Pontoppidan 1763), and *Aegolius acadicus* (Gmelin 1788).

SYSTEMATICS

Order Strigiformes (Wagler 1830)

Family Palaeoglaucidae Mourer-Chauviré 1987 (n. stat.)

TYPE GENUS. *Palaeoglaux* Mourer-Chauviré 1987.

EMENDED DIAGNOSIS. Coracoideum pneumatic, with elevation of processus acrocoracoideus overhanging sulcus m. supracoracoidei; humerus with sulcus ligamentosus transversus extending proximad to tuberculum ventrale; ulna with proximal end dorsoventrally rather narrow; radius without ossified arch; tarsometatarsus resembles that in *Necrobyas* Milne-Edwards 1892, but with shaft more slender, transition between fossa m. flexoris hallucis brevis and sulcus flexorius lower, and plantar wing of trochlea metatarsi II shorter; distal tarsal phalanges with tuberculum flexorium comparatively long proximodistally and in plantar view nearly dumbbell-shaped.

Genus *Palaeoglaux* Mourer-Chauviré 1987

TYPE SPECIES. *Palaeoglaux perrierensis* Mourer-Chauviré 1987.

DIAGNOSIS. As for family.

DESCRIPTION. The new species from Messel is in agreement with *Palaeoglaux* inasmuch as it has the tarsometatarsus with shaft expanded only a very little distally; trochlea metatarsi II with plantar wing comparatively short; coracoideum pneu-

Figure 1. *Palaeoglaux artophoron* n. sp. Holotype, SMF-ME 1144A, main slab. Coated with ammonium chloride. 1, Dorsal end of **left clavicle;** 2, left scapula; 3, left manus; 4, right fibula. 1.29×.

Figure 2. *Palaeoglaux artophoron* n. sp. Holotype, SMF-ME 1144B, counter-slab. Coated with ammonium chloride. During preparation (resin transfer method) the caudal part of the slab was erroneously displaced to the left compared with the cranial part. In the natural position, the big arrows should be facing each other. **1**, Right coracoideum; **2**, left coracoideum; **3**, crista sterni, cranial margin; **4**, furcula, symphysis. 1.44×.

matic; and ulna with proximal end appearing rather narrow dorsoventrally.

Palaeoglaux artophoron new species

Figures 1–8

HOLOTYPE. Slab and counter-slab with a nearly complete postcranial skeleton, Forschungsinstitut Senckenberg No. SMF-ME 1144, A, B.

DIAGNOSIS. Distinctly smaller than *Palaeoglaux perrierensis*, the only other known species of the genus.

TYPE LOCALITY. Ölschiefergrube Messel, Hessen, Germany.

TYPE STRATUM. Lower Middle Eocene, Lower Geiseltalium, Messel Formation.

ETYMOLOGY. Greek, *artophoron*, bread-basket; noun used in apposition; dedicated respectfully to Pierce Brodkorb.

DESCRIPTION. The anatomical terminology used herein is after Baumel et al. (1979), and the measurements (mm) follow those of Driesch (1976), unless otherwise indicated. Many of the measurements are estimates because all of the bones are fixed in the slabs, and most of them are more or less deformed.

Vertebrae. Only six cervical vertebrae are sufficiently preserved to permit study. Although the vertebrae fall within the morphological spectrum of strigiform cervicals, the specific and individual variation of vertebrae in owls does not permit the unequivocal identification of the fossil vertebrae to number. I consider the six cervicals tentatively as cervicals VI–XI, the alternative sequence V–X being less probable. The ventral surface of the corpora of cervicals VI–IX is flattened and cranially slightly concave, whereas in cervicals X and XI it forms a longitudinal crest with, in cervical XI, a ventral spine. The processus spinosus can be seen in cervicals VII–XI as low, blunt crests. The processus articulares caudales bear processus dorsales that are narrow and prominent in cervicals VI–VIII, but broader and less prominent in cervicals IX–XI. Measurements: Cervical VIII: medial length of lamina dorsalis arcus, 1.7; maximum breadth between lateral margins of processus articulares caudales, 6; length between cranial margin of corpus VI and caudal margin of corpus XI, 21.

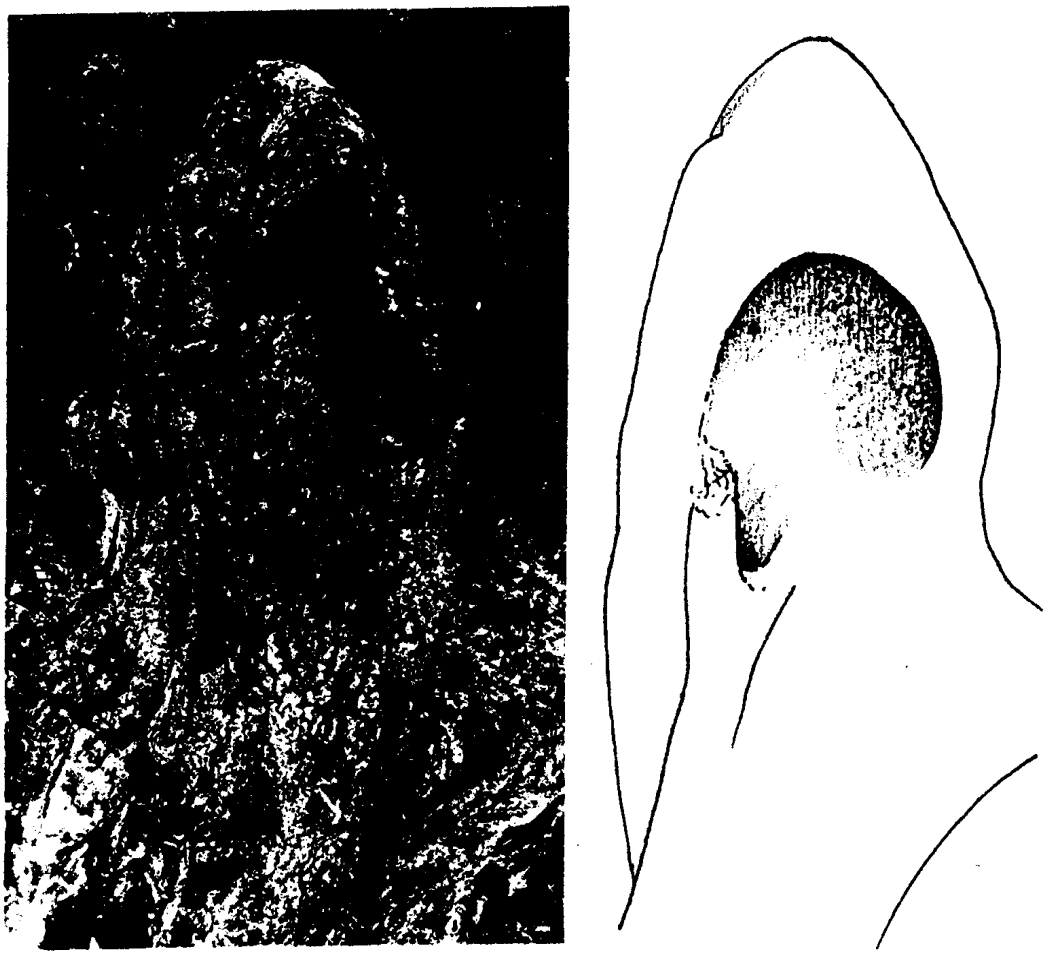

Figure 3. *Palaeoglaux artophoron* n. sp. Right coracoideum, extremitas omalis, medial view. 12.0×.

Sternum. The cranial margin of the crista sterni is preserved on the counter-slab (Fig. 2). It displays on its dorsal part two weak, rounded cristae laterales and between them a shallow sulcus divided longitudinally by a small, narrow crista mediana. The rostrum sterni and apex carinae are worn, but the remains of the apex suggest a closer similarity to the Strigidae than to the Tytonidae. Bony remnants can be seen on the main slab that might be parts of the right processus craniolateralis, but they are too fragmentary to yield any relevant information.

Furcula. The expanded dorsal end of the left clavicle and the fused sternal ends of both clavicles are preserved (Figs. 1, 2). The synostosis is drawn out into a small knob-like apophysis. The extremitas omalis is truncated at the end, approaching the condition in *Tyto* Billberg 1828. The lateral side is hidden from view so it is not known if the clavicles were pneumatic. Measurements: diameter of synostosis, including apophysis, 1; apical breadth of extremitas omalis, 3.8.

Scapula. Only parts of the left scapula are preserved (Fig. 1), and they are not particularly diagnostic. The elliptical facies articularis humeralis has a craniocaudal diameter of 3 mm and a dorsoventral diameter of 2 mm.

Coracoideum. The medial aspect of both coracoidea is exposed on the counter-slab (Fig. 2). Both coracoidea are badly crushed and both extremitates sternales are lacking, but the extremitas omalis of the right coracoideum is sufficiently preserved to reveal some important details (Fig. 3): The collum acrocoracoidei is comparatively short; an elevation of the processus acrocoracoideus overhangs the sulcus m. supracoracoidei ventrally and cranially; and a small foramen pneumaticum can be seen on one of the bony fragments of the sulcus, but more foramina may have existed. The proportions of the fragmentary shaft and procoracoid are similar to the general strigiform condition, but no further distinctions can be made. Measurements: maximum length (estimated), 18–19 mm.

Humerus. The humeri are wholly preserved, but they are badly crushed and only a few details are recognizable. The tuberculum dorsale is relatively strong, whereas the intumescentia and bicipital crest seem to be rather small. The distal ends are only moderately expanded. Although the proximal ends are too badly crushed to reveal details, the fragments suggest that the sulcus ligamentosus transversus extended proximal to the tuberculum ventrale, similar to the configuration found in the Strigidae. This would coincide with the fact that the foramen pneumaticum cannot be seen, because in strigid owls, and also in *Phodilus* Geoffroy Saint-Hilaire 1830, this foramen is greatly hidden by overhanging bone in ventral view and can easily be covered by fragments if the bone is crushed. The margo caudalis seems to be more pronounced than in all known owls. Measurements: maximum length of right humerus, 43; the left humerus seems to be much shorter (36) (the observed difference is certainly a result of the different distortions of the humeri; the estimated true length is 40); proximal breadth, 9.

Ulna. Both ends of the ulna are crushed or hidden from view, but most of the shaft can be seen. It is not very diagnostic,

Figure 4. *Palaeoglaux artophoron* n. sp. Radius, section of the shaft. Big marks indicate points of attachment of the supposed connective tissue arch. Small mark indicates nutrient foramen. U, ulna. 8.45×.

Figure 5. *Palaeoglaux artophoron* n. sp. Right carpometacarpus, proximal end. 1, Processus extensorius; 2, digitus alulae, proximal phalange; 3, doubtful ossicle (phalanx distalis alulae or os prominens?). 6.58×.

however. It appears that the proximal end was only slightly dorsoventrally expanded. Measurements: maximum length (estimated), 49.

Radius. The most interesting feature of this bone can be seen on the counter-slab, where the caudal aspect of the right radius is exposed (Figs. 2, 4). The osseous arch, present in most modern owls, is lacking. Nevertheless, there are two small elevations about 5 mm apart, with slightly roughened surfaces and a slightly flattened area between them. The nutrient foramen of the radius is located immediately proximal to the distal elevation. This configuration is very similar to the condition in other owls, save for the lack of the arch itself, suggesting that there might have been an unossified arch. The remaining caudal surface of the shaft is not evenly curved, but instead has the shape of a faint ridge. Measurements: maximum length (estimated), 49.

Ossa Carpi. These bones are insufficiently preserved for analysis.

Carpometacarpus. Dorsally, the os metacarpale alulare and os metacarpale majus merge into each other with almost no intervening concavity. The dorsal surface of the processus extensorius is deeply excavated (Fig. 5). The sulcus tendineus of the os metacarpale majus is comparatively broad and extends over approximately two-thirds of the length of the bone. The os metacarpale majus and os metacarpale minus are more or less parallel and of equal length distally. The spatium intermetacarpale is long and narrow. The proximal and distal synostoses seem to be rather short, but it cannot be ascertained whether or not a free processus intermetacarpalis existed. Measurements: maximum length, 24±; distal breadth, 3.

Phalanx Proximalis Digiti Majoris. The pila cranialis is divided into two blunt crests by a shallow longitudinal furrow. Both crests expand at their distal end into cranially projecting processes. The flattened caudal wing of the bone is not fenestrated. It is constricted craniocaudally just proximal to its distal end, as in *Phodilus* and genera of Strigidae. Its caudal border is curved smoothly proximally, as in *Tyto* and *Phodilus* (Ford, 1967). Measurements: maximum length, 9.5.

Phalanx Distalis Digiti Majoris. The left bone is visible craniventrally, but it offers no special information beyond that of being strigiform. Measurements: maximum length, 9.

Phalanx Digiti Minoris. The processus for the attachment of m. flexor digiti minoris is very close to the proximal articulation, as in other owls. The bone seems to be comparatively stouter than that in *Tyto*. Measurements: maximum length, 5.

Digitus Alulae. This digit is sufficiently preserved only on the right wing. The slender proximal phalanx does not display any peculiar features, but another small conical ossicle lies on the distal fragment of the carpometacarpus on the counter-slab near to the distal end of the proximal phalanx (Fig. 5). This ossicle might be a dislocated os prominens, although one cannot preclude that it is a distal phalanx. Measurements: length of proximal phalanx, 7; length of the distal ossicle, 1.5.

Pelvis. The fragments of these bones are so crushed and deformed that no unambiguous analysis is possible.

Femur. Both femora are lost, with the exception of a small distal fragment of the right femur.

Tibiotarsus. The crista cnemialis cranialis is proximodistally rather short. Its border does not curve smoothly to join the shaft but turns sharply, forming a distinct angle, thus approaching the condition in *Tyto* and *Phodilus*. The distance between the tuberositas retinaculi mm. extensorum and the proximal border of the condylus medialis approximately equals the maximal distal breadth of the bone. The crista fibularis is comparatively short. In lateral and medial view, the shape of the condyles very closely resembles that in *Phodilus* and *Necrobyas*. The condylus medialis projects caudally with its proximal border at almost right angles to the shaft, whereas the condylus lateralis is caudally more evenly curved, fusing at a very obtuse angle with the shaft. The sulcus cartilaginis tibialis is comparatively shallow and broad. Measurements: maximum length (estimated), 53; craniocaudal depth of condylus lateralis, 5.5; craniocaudal depth of condylus medialis, 6.5.

Fibula. Only the corpus fibulae of the right leg is preserved. It is comparatively long, extending distad almost to the tuberositas retinaculi mm. extensorum. The distal end seems to be unfused, but a small longitudinal ridge with a proximal surface of fracture on the shaft of the tibiotarsus suggests that both bones were linked synostotically.

Tarsometatarsus. The tarsometatarsi are among the best-pre-

Figure 6. *Palaeoglaux artophoron* n. sp. Pes. 1–4, sequence of toes; 5, fossa musculi flexoris hallucis brevis. 2.96×.

served bones of the specimen (Figs. 1, 6). The overall configurations of the bone is clearly "tytonid," as exemplified by the large surface for the attachment of m. flexor hallucis brevis. Ballmann (1973:31) considers this to be one of the unmistakable features of the family Tytonidae. Unfortunately, most of the dorsal aspect is hidden from view, so nothing can be said about the presence or absence of an arcus extensorius.

Compared to a complete tarsometatarsus of *Necrobyas rossignoli* Milne-Edwards 1892, the tarsometatarsus of *Palaeoglaux artophoron* can be distinguished by the following features: Shaft somewhat shorter and distinctly more slender; crista lateralis hypotarsi posteriorly shorter and more rounded; crista medialis hypotarsi with proximal edge only a little narrower than the posterior edge and lateral face only very slightly bent laterad; transition between fossa m. flexoris hallucis brevis and sulcus flexorius very smooth and only slightly convex, thus the sulcus flexorius is proximally rather shallow, but deep distally; trochlea metatarsi II with proximal border more prominent medially and with plantar wing shorter; and fossa metatarsi I is situated more distally, i.e., closer to trochlea metatarsi II.

In contrast to the condition in *Tyto alba*, in *Palaeoglaux* and *Necrobyas* the foramen vasculare distale is situated more proximally than the dorsoproximal border of the trochlea metatarsi III. A short (5 mm) ossicle that might be the ossified part of a flexorial tendon can be seen in the sulcus flexorius of the left tarsometatarsus. Measurements: maximum length, 30.5; maximum distal breadth (estimated), 7; cranioplantar depth of the shaft laterally, 2.

Digiti Pedis. All of the toes are more or less completely preserved (Fig. 6). They differ from the toes of *Tyto* spp. by the following characters: Phalanx 1 digiti III proportionally longer; penultimate phalanges digitorum II–IV with plantar borders forming a slight convexity distal to the middle of the shaft in medial and lateral view (in *Tyto* spp. the convexity reaches proximad to about the midpoint of the shaft), and with dorsal borders of the capitula not flaring upward dorsally, but approximately forming the extension of the dorsal border of the shaft; phalanx 4 digiti IV with plantar border of capitulum semicircularly rounded in lateral view, whereas it is more or less oval in phalanx 2 digiti II and phalanx 3 digiti III; and phalanx distalis with tuberculum flexorium rather long proximodistally and in plantar view roughly dumbbell-shaped (Figs. 6, 7). Measure-

ments: maximum length: digiti I phalanx 1, 9; phalanx 2, 8; digiti II phalanx 1, 7.5; phalanx 2, 12.5; phalanx 3 (estimated), 9; digiti III phalanx 1, 5; phalanx 2, 6.5; phalanx 3, 11; phalanx 4, 9; digiti IV phalanx 1, 3±; phalanx 2, 2±; phalanx 3, 3; phalanx 4, 9.5; phalanx 5, 9.5.

Feathers. Fragments of at least eight primaries and some secondaries of the left wing are preserved as dark shadows. Shafts, barbs, and barbules can be discerned in some places, but no microstructures are recognizable. The outermost primary, lacking its tip, measures 70 mm from the tip of digitus major. Very peculiar are remnants of feathers from the trunk, most probably from the back. Numerous ribbon-like feathers are arranged there in a dense layer, partly melded into each other like a pulpy matrix (Fig. 8). These feathers are barely 1 mm wide, but at least 2 cm long, with a slender shaft. The vane appears to be membranous, without barbs, but this might be a result of diagenetic processes (see Discussion).

DISCUSSION

OTHER GENERA OF FOSSIL OWLS

Only a few genera belonging to the families Ogygoptyngidae Rich and Bohaska 1981, Sophiornithidae Mourer-Chauviré 1987, and Protostrigidae Wetmore 1933 are of the same age or older than the new Messel owl. *Ogygoptynx* Rich and Bohaska 1976 is known only from a single tarsometatarsus, which differs from that of *Palaeoglaux* in that its plantar metatarsal groove is very shallow, in that it lacks a lateral wall near the proximal end (in *Palaeoglaux* the medial wall is more flattened), and by having the crista lateralis hypotarsi directed laterally.

Palaeoglaux is easily distinguished from *Sophiornis* Mourer-Chauviré 1987 by its tarsometatarsus, which has a sulcus extensorius and is more slender.

Among the Protostrigidae, *Oligostrix rupelensis* Fischer 1983 is similar in size to *Palaeoglaux artophoron*, but these owls can be distinguished by the following features. In *Oligostrix* Fischer 1983, as in all genera of Protostrigidae, the condylus medialis tibiotarsi is very broad lateromedially and much broader than the condylus lateralis, particularly in caudal view. In *Palaeoglaux*, the condylus medialis is much narrower and in caudal view only somewhat broader than the condylus lateralis. The tuberositas retinaculi musculi fibularis on the condylus lateralis is very strong and prominent in *Oligostrix* but hardly detectable in *Palaeoglaux*. The genus *Minerva* Shufeldt 1915 is also distinguished from *Palaeoglaux* by the specialized phalanx 2 of digitus I (Mourer-Chauviré, 1983, 1987). *Eoglaucidium pallas* Fischer 1987 from Geiseltal, known only from the humerus, was classified with the Strigidae. In *Palaeoglaux artophoron*, the humerus is straighter and more slender; it has a more prominent tuberculum ventrale and margo dorsalis. Distal to the crista bicipitalis, the shaft is smoothly rounded, whereas in *Eoglaucidium* it is slightly ridged. Mlíkovský (this volume) may be right in assuming that *Eoglaucidium* is not an owl.

According to Mourer-Chauviré (1987), the family Tytonidae comprises eight genera in five subfamilies: Tytoninae (*Tyto* Billberg 1828), Phodilinae (*Phodilus* Geoffroy Saint-Hilaire 1830), Necrobyinae (*Necrobyas* Milne-Edwards 1892, *Nocturnavis* Mourer-Chauviré 1987, *Palaeobyas* Mourer-Chauviré 1987, *Palaeotyto* Mourer-Chauviré 1987), Selenornithinae (*Selenornis* Mourer-Chauviré 1987), and Palaeoglaucinae (*Palaeoglaux* Mourer-Chauviré 1987).

The new Messel owl differs from *Tyto*, *Phodilus*, *Necrobyas*, and *Palaeotyto* by the pneumatic coracoideum and many other features. *Palaeobyas* is known only from the tarsometatarsus, which is large and stout, very different from that of *Palaeoglaux*. *Nocturnavis* is known from the humerus, which has a tytonid character and is similar to that of *Necrobyas*. The humerus of the new owl differs from *Nocturnavis* in the overall configuration of its proximal end (see description) and by having the distal end only moderately expanded dorsoventrally. *Selenornis* is known from the distal end of the tibiotarsus, which has very different proportions from that of *Palaeoglaux*.

Figure 7. *Palaeoglaux artophoron* n. sp. Tuberculum flexorium phalangis distalis digiti II of the left pes. 16.65×.

Palaeoglaux is exceptional in the combination of its characters, in that it has a tarsometatarsus similar to that in *Necrobyas* but is very different in other respects. The most striking features of *Palaeoglaux* are the pneumatic coracoideum and the narrow proximal end of the ulna, the latter being described by Mourer-Chauviré (1987:114) as "... un peu comme celle des Galliformes ..."

THE STATUS OF *PALAEOGLAUX*

In her excellent paper on the owls of the Phosphorites du Quercy, Mourer-Chauviré (1987) placed the genus *Palaeoglaux* in its own subfamily Palaeoglaucinae and considered this group to be the sister-group of the remaining members of the Tytonidae. The definition of this subfamily was based mainly on characters of the coracoideum, which according to Mourer-Chauviré (1987: 114) approach those of the Strigidae. The osteology of *Palaeoglaux* does indeed display a combination of tytonid and strigid characters in addition to autapomorphies. Tytonid characters are associated mainly with the tibiotarsus and tarsometatarsus, whereas strigid characters are displayed by the sternum, coracoideum, and the forelimbs (see description).

It is very tempting to regard *Palaeoglaux* as an early genus of the Strigidae. The families Tytonidae and Strigidae are usually considered to be sister-groups, this implying that they are of the same age. This assumption is still not supported by the fossil

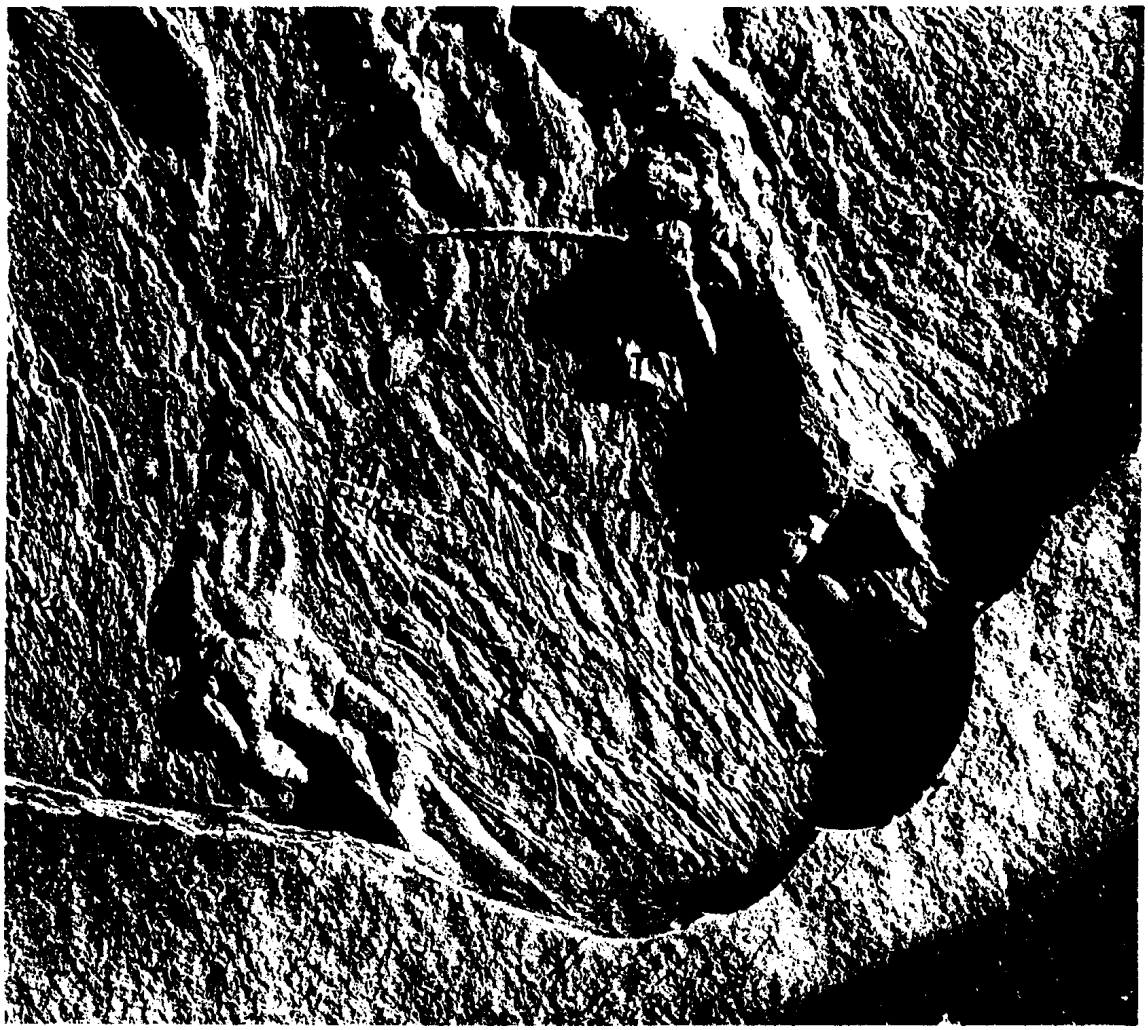

Figure 8. *Palaeoglaux artophoron* n. sp. Dense layer of narrow ribbon-like feathers. T, proximal end left tibiotarsus. 2.79×.

record because the earliest tytonids are known from the Eocene and the supposed earliest strigids are found as late as the Miocene (Mourer-Chauviré, 1987). It is possible, therefore, that *Palaeoglaux* represents the first evidence of Eocene strigids, as predicted by the sister-group hypothesis.

Unfortunately, the anagenetic polarity of the characters in question is unknown. This means that classifying *Palaeoglaux* with the Strigidae or the Tytonidae would anticipate the phylogenetic evaluation of the characters. Classifying *Palaeoglaux* with the Tytonidae implies that the characters shared by *Palaeoglaux* with the Strigidae are symplesiomorphies, and vice versa. Therefore, I prefer, in accordance with the predominantly typological classification of owls, to place *Palaeoglaux* in a separate family, the Palaeoglaucidae. The phylogenetic relationships of owls are clearly unsettled and present a challenge for further research.

As far as I can determine, only three osteological features can be interpreted as autapomorphies in *Palaeoglaux*. These are the peculiar shape of the proximal end of the ulna and the tuberculum flexorium of the ungual phalanges, and the relatively strong margo caudalis humeri. The conditions of these features are unknown for the families Ogygoptyngidae and Sophiornithidae because the requisite bones have not yet been found.

The peculiar feathers from the body plumage of *Palaeoglaux* may also be an autapomorphy, but because nothing is known of the plumage of other fossil owls this is pure speculation. Nonetheless, the feathers deserve attention. Remnants of soft body parts are preserved in Messel as "bacterial copies." Wuttke (1983, 1988) described the chemical aspect of these processes, where vast numbers of minute petrified bacterial bodies are left in place of histological details. Sometimes the space between the fossilized bacteria is infiltrated with organic matter to such a degree that the original structures become more or less blurred. The latter may have happened to the feathers in question, giving them a membraneous or "melded" appearance. There are only some very faint traces of a texture that suggests that the vanes consisted of barbs. Narrow, elongated contour feathers are known from species of several families, e.g., Phasianidae, Cotingidae, Paradisaeidae, and in all cases they play a role in visual display. However, ornamental plumes would have been very unusual in a nocturnal bird. Perhaps these early owls were more diurnal in habits than their modern counterparts.

Finally, although the reevaluation of characters defining families and subfamilies of owls is beyond the scope of the present work, at least two features should be discussed briefly.

The osseous arch of the radius seems to be a unique character of owls. Bock and McEvey (1969) supposed that it exists in all modern species of owls, but there are some exceptions. A. Kar-

khu (pers. comm.) did not find an osseous arch in *Glaucidium passerinum*, *G. siju*, or *Surnia ulula*. K. Campbell (pers. comm.) found "that the spp. of *Glaucidium* often did not have an osseous arch." In a spirit specimen of *G. brasilianum*, I found the arch made of soft connective tissue. Also, the consistency of the arch seems to vary in the Bay Owl, *Phodilus badius*, of which only a few skeletons exist in collections. Two of these were examined. One specimen (Museum of Vertebrate Zoology, Berkeley, MVZ 154170) displayed "slight bony crests on each radius which may have supported such an arch . . ." that "may have been broken off during specimen preparation (D.A. Bell, pers. comm.)." The second specimen (National Museum of Natural History, Washington, D.C.) has a "slight ridge or crest" that is "really evident only on the right radius and not on the left" (S.L. Olson, pers. comm.). My later examination of this specimen confirmed that the left radius did not have any trace of a bony arch. The arch seems to be lacking also in many prepared specimens of other species. However, in all such specimens that I examined, marks of excessive "cleaning" could be found. In some cases, the arches were cut away with a scalpel.

We do not know whether or not the bony arch existed in the fossil groups previously mentioned because the proximal part of the radius is not preserved in those owls.

On the basis of the evidence at hand, the arch as such seems to be a synapomorphic character of owls. Its ossification, or the secondary loss of ossification, may, however, have happened several times independently.

The os prominens is lacking in the family Tytonidae, but it occurs as an apparent apomorphy of the family Strigidae. Thus, if the small ossicle of the manus of *Palaeoglaux artophoron* was an os prominens, it would strongly support the hypothesis that *Palaeoglaux* pertains to the Strigidae. If the small ossicle is instead a distal phalanx, then it would be a plesiomorphy and it would not indicate any special phylogenetic relationship.

SUMMARY

The Eocene owl *Palaeoglaux artophoron* new species from the oil shales of Messel provides further evidence that the genus *Palaeoglaux* displays a mixture of tytonid and strigid characters. Pending further discoveries, placing the genus into its own family, the Palaeoglaucidae, appears to be the most appropriate action.

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