

An assessment of the Cenozoic avifauna of Switzerland, with a description of two fossil owls (Aves, Strigiformes)

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Abstract The fossil skeletal record of birds from the Cenozoic of Switzerland is rather poor, despite the fact that avian tracks have been described from twenty tracksites. We review the Swiss fossil skeletal avifauna with emphasis put on new material discovered in the collection of the Natural History Museum Basel. This material includes two new owls (Strigiformes), one from a Late Eocene fissure filling from the Gösgen canal, and another from the Late Oligocene of Mümliswil. The Eocene owl specimen consists of a partial, distal tarsometatarsus, and is therefore too incompletely preserved to allow for reliable hypotheses concerning its taxonomic affinities. It does, however, display features resembling members of the extinct family Palaeoglaucidae. The Oligocene specimen is tentatively attributed to the genus *Oligostrix*, and it is the youngest representative of the extinct family Protostrigidae. Based on the first complete tarsometatarsus for this family, we

erect a new species, *?Oligostrix bergeri*. These two specimens represent the first record of fossil owls from Switzerland.

Keywords Fossil birds · Protostrigidae · Avian tracks · Vertebrate ichnology · Swiss Molasse · *Oligostrix bergeri* sp. nov. · Eocene · Oligocene

Abbreviations

NMB	Naturhistorisches Museum Basel
PIMUZ	Paläontologisches Institut und Museum der Universität Zürich
MN	Mammal Neogene
MP	Mammal Palaeogene

1 Introduction

Cenozoic fossil birds from the Swiss Molasse were first mentioned by von Meyer (1839a, b). The first specimen, from the Early Oligocene of Engi (Matt Formation) in the Canton of Glarus, was described as *Protornis glarniensi* (von Meyer 1844, 1856) and sparked international interest, as during the first half of the nineteenth century mentions or publications concerning fossil birds were still extremely rare (Furrer and Leu 1998). The most recent review of the fossil avifauna of Switzerland was undertaken by Mlíkovský (1996), but significant finds of fossil bird bones were limited to only a couple of localities (i.e. Egerkingen and Engi). As detailed in Mlíkovský (1996), most publications on the Swiss avian fossil record that appeared in the last 60 years actually concern fossil footprints (review in Weidmann and Reichel 1979, but see also: Speck 1945; Bräm 1954; de Clerq and Holst 1971; Weidmann and Reichel 1979; Berger 1985).

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The majority of avian fossil remains from Switzerland—both bones and tracks—have been recovered from deposits of the northern Alpine foreland basin. Three of the four lithostratigraphic groups of the Swiss Molasse Basin yielded avian remains: the Oligocene to Miocene Lower Freshwater Molasse (USM, see Fig. 1) in fluvio-lacustrine settings, the Miocene Upper Marine Molasse (OMM, Fig. 1) in shallow marine to coastal settings, and the essentially Miocene Upper Freshwater Molasse (OSM, Fig. 1), again in a fluvio-lacustrine context (Berger 1985). Fissure fillings within Jurassic limestones, such as those of the Eocene reference locality of Egerkingen or from Moutier, have also yielded an interesting but limited number of fossil bird specimens (e.g. Schaub 1940).

Here we present an amended list of the fossil avian localities of Switzerland based on Mlíkovský (1996) and on newly discovered material from seven new localities. Unfortunately, not much progress regarding the Swiss fossil avifauna has been made in recent years and fossil bird remains from Swiss localities are still scarce. It is therefore not surprising that most avian groups remain

unrepresented. Some of the avian specimens mentioned herein are in need of a more exhaustive revision, but a thorough taxonomic classification of this material is beyond the scope of this paper. Nevertheless, we describe two owls from Swiss Palaeogene localities, which represent the first record of fossil owls from Switzerland.

Owls are cosmopolitan birds (commonly found in all continents except Antarctica; del Hoyo et al. 1999), and comprise over 200 extant species (Weick 2006). The order Strigiformes is currently represented by two extant families, Tytonidae (barn and bay owls) and Strigidae (typical owls), but five extinct families are also recognised (e.g. Kurochkin and Dyke 2011), namely Ogygoptygidae from the Palaeocene of North America, Sophiornithidae from the Palaeocene of Europe, Palaeoglaucidae from the Eocene of Europe, Protostrigidae from the Eocene and Oligocene of the Northern Hemisphere, and Heterostrigidae, from the Oligocene of Asia. The Oligocene record also includes representatives of the Tytonidae (Mourer-Chauviré 1987). Notably, the Palaeogene record of owls is restricted to the Northern Hemisphere (Mayr 2009).

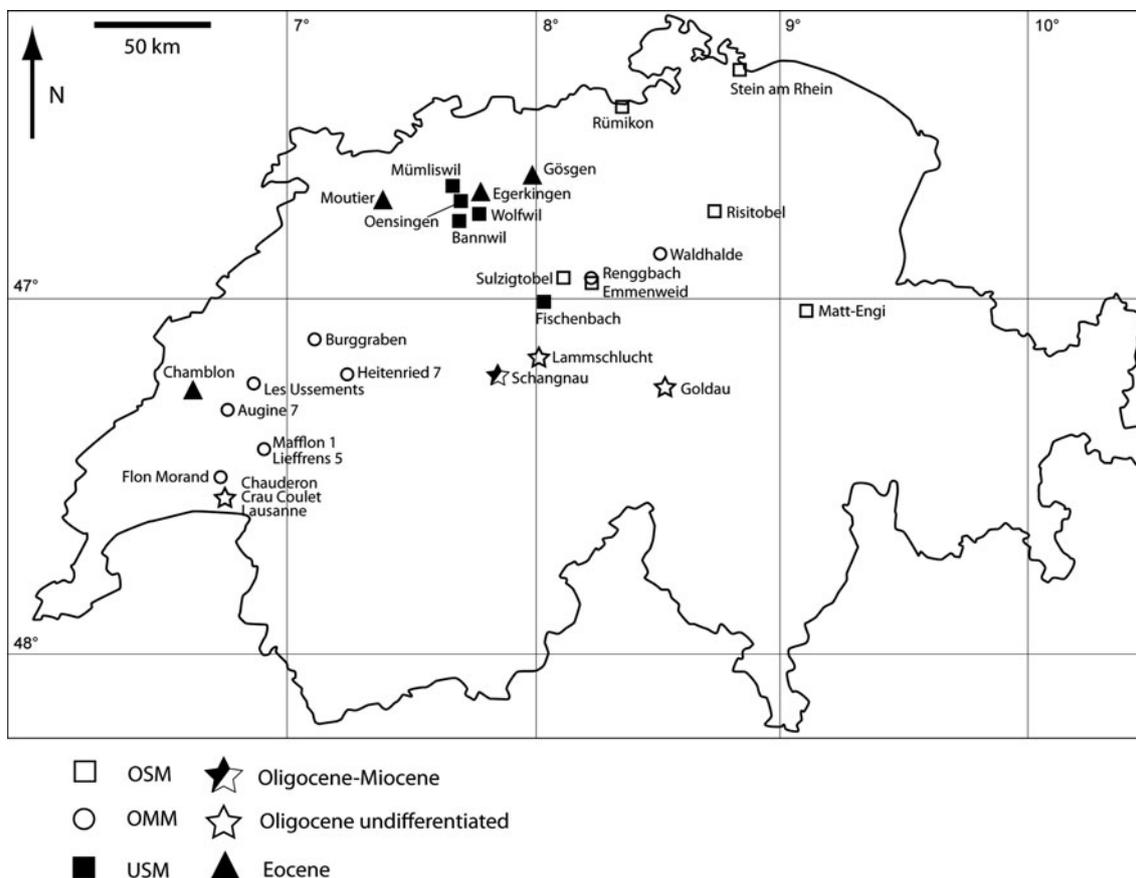


Fig. 1 Map of Switzerland showing the geographical position and age of the localities with fossil bird remains (bones, eggs, and tracks). See text and supplementary information for details

2 Materials and methods

Anatomical terminology follows Baumel and Witmer (1993). All measurements are in mm. Geological references concerning the localities mentioned herein can be found in the supplementary information.

Comparative material. The publication record for fossil Strigiformes is very extensive, and morphological descriptions, particularly for tarsometatarsi, are abundant (e.g. Mourer-Chauviré 1983, 1987, 1994; Kurochkin and Dyke 2011). For this reason we mostly refer to the literature for comparisons regarding extinct taxa of the Strigiformes. Extant representatives of Strigidae and Tytonidae housed at NMB were also used for comparisons.

3 Fossil sites with skeletal remains and eggs

3.1 Egerkingen (Canton Solothurn; Middle Eocene, MP 14)

Eleutherornis helveticus Schaub, 1940

Material. Synsacrum (NMB Eh.781 Fig. 2a1–a3), caudal portion of synsacrum (NMB Eh.782, Fig. 2b1–b3).

Aves indet.

Material. NMB Ef. 998–1001 (pedal phalanges, Fig. 2c1–f2); NMB Eg. 611 (distal right ulna, Fig. 2h); NMB Eg. 612 (distal right ulna, Fig. 2i).

Remarks. *Eleutherornis helveticus* was considered to be a palaeognathous bird by Schaub (1940), but his referral was only based on overall similarity. Comparisons with other giant flightless taxa, including gastornithids and other extinct palaeognathous birds, still need to be completed. The pedal phalanges (Fig. 2c1–f2) mentioned by Schaub (1929) were thought to be too large to correspond with those of *Eleutherornis helveticus* (Schaub 1940, see also Mayr 2009).

3.2 Moutier (Canton Bern; Middle Eocene, MP 16)

Galliformes Temminck, 1820
cf. Gallinuloididae Lucas, 1900

Material. NMB Ms.103 (distal right tibiotarsus, Fig. 2j).

Remarks. The tibiotarsus is about the size of that of the California Quail, *Callipepla californica*, and represents the first record of a bird from the Eocene locality of Moutier. It differs from *Paraortyx lorteti* (Paraortygidae) from the Late Eocene and Early Oligocene of France in that the condylus medialis is mediolaterally slightly narrower than the condylus lateralis, whereas in *P. lorteti* the condylus lateralis is much wider than the condylus medialis. In distal

view, both condyles are oriented parallel in *P. lorteti*, but they are slightly divergent in the Moutier specimen. NMB Ms.103 also differs from *Quercymegapodius brodkorbi* (Quercymegapodiidae) from Quercy, France, in that the condyles are not as flat, and the incisura intercondylaris is narrower. Overall, the Moutier specimen resembles the corresponding bone of representatives of the Gallinuloididae, particularly in the presence of a broad pons supratendineus. It bears a closer resemblance to members of the genus *Gallinuloides* than to *Paraortygoides*; in the latter both condyles are about the same size and the incisura intercondylaris is wider (Weidig 2010).

3.3 Gösigen (Canton Solothurn; Late Eocene, MP 18)

Aves indet.

Material. NMB H.R.137 (fragment of phalanx, Fig. 2g1–g2)

Strigiformes Wagler, 1830

Fam. et gen. indet.

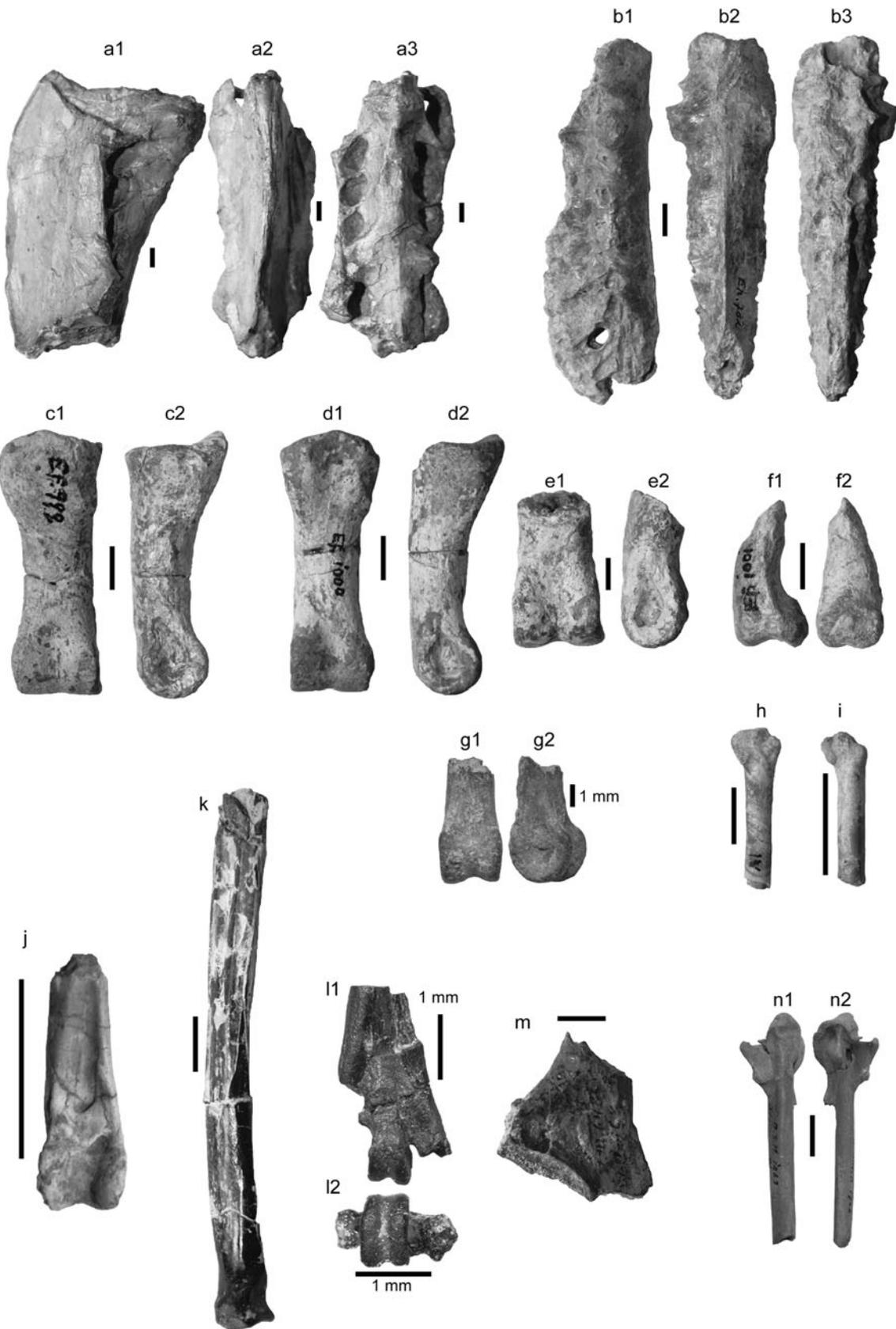
Material. NMB G.C.623 (partial distal left tarsometatarsus, Fig. 3g–i)

Measurements. width of trochlea metatarsi III: 2.6; depth of tr. met. III: 2.4; estimated distal width: 6.3.

Description and comparisons. The foramen vasculare distale is situated more proximally than in most examined fossil and extant owls, so that the area between the foramen vasculare distale and the incisura intertrochlearis is broad, a feature also described for the Late Eocene Messel owl *Palaeoglaux artophoron* Peters 1992.

The plantar projection of trochlea metatarsi II is only incompletely preserved. In distal view, it is not as broad as in members of the Sophiornithidae and Protostrigidae (see Mourer-Chauviré 1994), and resembles that of *Palaeoglaux perrierensis* (see Mourer-Chauviré 1987).

An unusual feature of this tarsometatarsus is the globular lateral projection on trochlea metatarsi III (Fig. 3i), which, as such, is absent from all other examined owls, both fossil and recent. There is, however a well-developed protuberance on the lateral side of trochlea metatarsi III in *Palaeoglaux perrierensis*, albeit this protuberance is incompletely preserved in the only known tarsometatarsus for this taxon. In species of the extinct tytonid genus *Necrobyas* there is a small bead-like process on the lateral side of trochlea metatarsi III, but it is unlike the bulge present in NMB G.C.623. In distal view, the rims of trochlea metatarsi II are symmetrical, thus resembling the condition in representatives of the Sophiornithidae, Palaeoglaucidae, and some Protostrigidae. Overall, NMB G.C.623 is most similar to *Palaeoglaux perrierensis*, albeit considerably smaller. Unfortunately more detailed comparisons with *Palaeoglaux artophoron* Peters, 1992 are not



◀ **Fig. 2** Avian remains from Swiss localities. **a1–b3** *Eleutherornis helveticus* Schaub, 1940 from the Middle Eocene of Egerkingen: **a1–a3** synsacrum (NMB Eh.781, holotype) in lateral (**a1**), dorsal (**a2**), and ventral (**a3**) views. **b1–b3** Caudal portion of synsacrum (NMB Eh.782) in lateral (**b1**), dorsal (**b2**), and ventral (**b3**) views. **c1–f2** Pedal phalanges from the Middle Eocene of Egerkingen, Aves indet.: **c1–c2** NMB Ef. 999. **d1–d2** NMB Ef. 1000. **e1–e2** NMB Ef. 998. **f1–f2** NMB Ef. 1001. **g1–g2** Fragment of pedal phalanx from the Late Eocene of Gösgen (NMB H.R.137). **h–i** Aves indet., distal right ulnae from the Middle Eocene of Egerkingen: **h** NMB Eg. 611. **i** NMB Eg. 612. **j** Cranial view of distal right tibiotarsus (NMB Ms.103) from the Middle Eocene of Moutier, Gallinuloididae indet. **k** Right radius (NMB U.M.6483) from the Late Oligocene of Wolfswil, Aves indet. **l1–l2** Distal right tarsometatarsus (NMB U.M.6484) from the Late Oligocene of Wolfswil in dorsal (**l1**) and distal (**l2**) views, Aves indet. **m** Sternal portion of right coracoid (NMB U.M.6485) from the Late Oligocene of Wolfswil in dorsal view, Aves indet. **n1–n2** Suliformes indet., left carpometacarpus (NMB O.S.M.1263) from the Middle Miocene of Stein am Rhein in dorsal (**n1**) and ventral (**n2**) views. *Scale bars* 10 mm, except in **g1–g2** and **l1–l2** (1 mm)

directly possible as part of the distal view is hidden in the Messel specimen, although both the Gösgen and Messel specimens may have been similar in size (Peters 1992).

3.4 Engi (Canton Glarus; Early Oligocene; Glarner Fischschiefer)

Alcediniformes sensu Mayr 1998

Protornis glarniensis von Meyer, 1844, Fig. 4a

Material. PIMUZ A/IV 37a (slab) and PIMUZ A/IV 37b (counterslab).

Remarks. von Meyer (1844) considered *Protornis glarniensis* to be a genus incertae sedis within Passeriformes. Olson (1976) assigned this specimen to the Momotidae (motmots), but failed to establish this referral with derived osteological features (Mayr 2009). As noted by Olson (1976), the proximal ends of the mandibles display marked incisions, which are derived features for both Momotidae and Todidae (todies), but *Protornis glarniensis* differs from extant motmots in several other features (Mayr and Knopf 2007). At the moment, and with the material currently available, *Protornis glarniensis* can only be confidently referred to the Alcediniformes (bee-eaters, kingfishers, motmots, and todies) based on several derived characters already listed by Mayr and Knopf (2007).

Trogoniformes

Trogonidae Lesson, 1828

gen. et sp. indet., Fig. 4b

Material. PIMUZ A/IV 39 (incomplete skeleton on slab)

Remarks. A second slab, originally attributed to *Protornis glarniensis* by Peyer (1957), was shown to represent a member of the Trogonidae (trogons and quetzals), based on the derived presence of a heterodactyl foot (Olson 1976).

3.5 Mümliswil (Canton Solothurn; Late Oligocene, MP 26)

Strigiformes Wagler, 1830

Protostrigidae Wetmore, 1933

?*Oligostrix* Fischer, 1983

?*Oligostrix bergeri*, sp. nov., Fig. 3a–f

Etymology. Species name in honour of the late Prof. Jean-Pierre Berger (1956–2012), distinguished specialist for the stratigraphy and palaeogeography of the continental Tertiary in Europe and professor for palaeontology at the University of Fribourg, Switzerland.

Holotype. Almost complete right tarsometatarsus, NMB U.M. 2528.

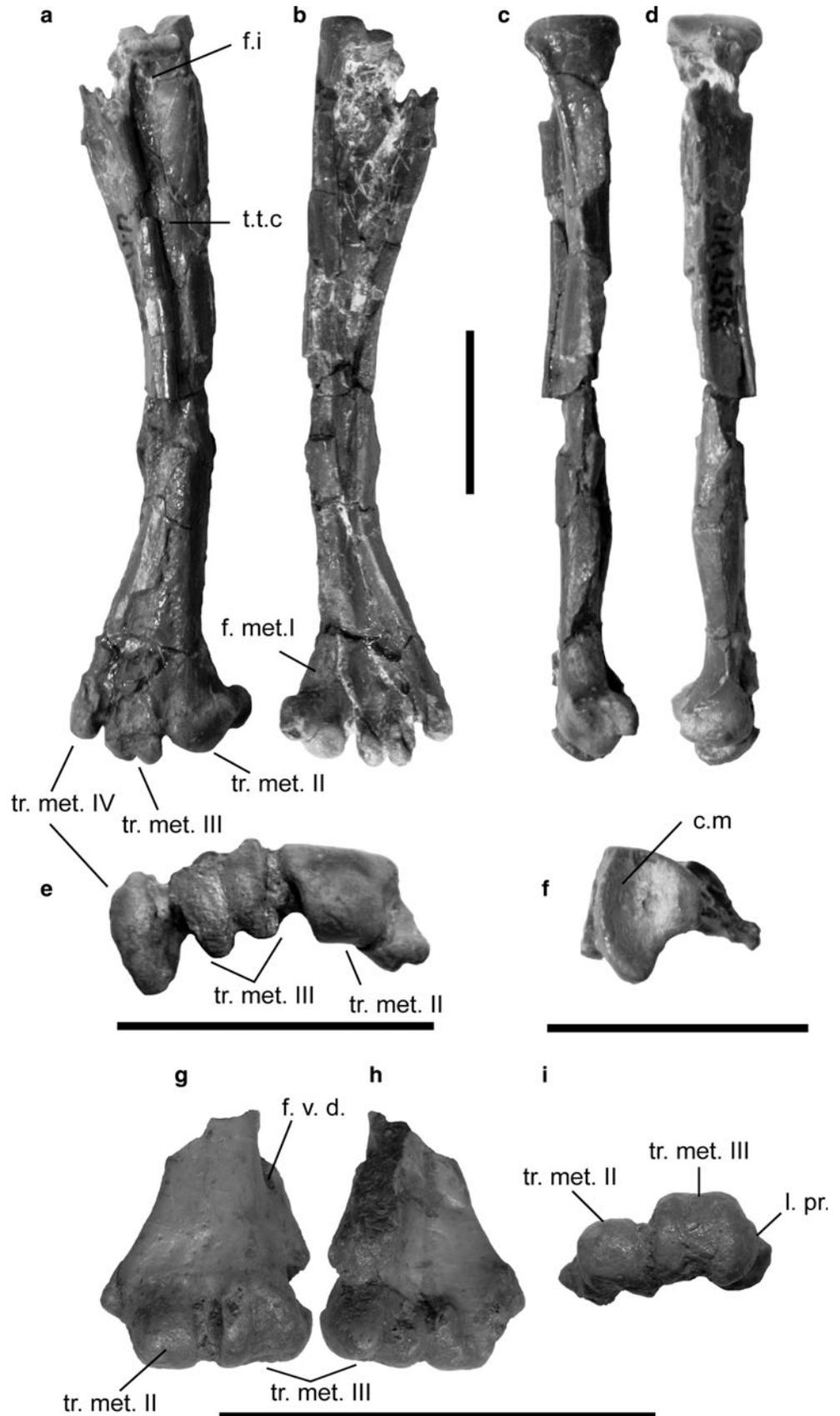
Measurements. Maximum length: 42.7; distal width: 10.3; dorsoplantar depth of cotyla medialis: 5.4; width of trochlea metatarsi II: 4.5; width of trochlea metatarsi III: 3.3, depth of trochlea metatarsi III: 3.5; depth of trochlea metatarsi IV: 1.9.

Remarks. This tarsometatarsus represents the youngest record for protostrigid owls. The extinct family Protostrigidae includes three genera: *Eostrix* from the Early Eocene of North America (e.g. Wetmore 1938; Martin and Black 1972), Asia (Kurochkin and Dyke 2011), and Europe (Harrison 1980), *Minerva* from the Middle and Late Eocene of North America (e.g. Schufeldt 1913), and *Oligostrix* from the Early Oligocene of Europe (Fischer 1983). The Protostrigidae are thus the only extinct owl family to be represented in more than one continent. Their fossil record is based primarily on limb elements, particularly tarsometatarsi, and so far no complete tarsometatarsus attributable to this family has been recovered.

Differential Diagnosis. ?*Oligostrix bergeri* sp. nov. is within the size range known for members of the Protostrigidae. The tarsometatarsus can be referred to this family based on the combination of the following features: (1) wide cotyla medialis; (2) narrow shaft with gradual widening of the ends (distal and proximal); (3) in distal view, mediolaterally wide trochlea metatarsi II, not plantarly oriented; (4) all three trochleae oriented parallel to each other in distal view; (5) proportionally short trochlea metatarsi II; (6) trochlea metatarsi III projecting considerably further distally than trochlea metatarsi II or IV; (7) trochlea metatarsi IV more distally positioned in comparison with trochlea metatarsi III (ending at about the mid-section of trochlea metatarsi III). It agrees with representatives of the genus *Minerva* in: (8) plantarly symmetrical rims of trochlea metatarsi III.

Character 2 is shared with the protostrigid genus *Eostrix*; character 3 is shared to some degree with Sophiornithidae; character 5 is also present in Heterostrigidae. ?*Oligostrix*

Fig. 3 Tarsometatarsi of *?Oligostrix bergeri* sp. nov. (NMB U.M.2528, holotype) from the Late Oligocene of Mümliswil, Switzerland, and *Strigiformes*, fam. et gen. indet. (NMB G.C.623) from the Late Eocene of Gösgen, Switzerland. **a–f** Holotype of *?Oligostrix bergeri* sp. nov. in dorsal (**a**), plantar (**b**), medial (**c**), lateral (**d**), distal (**e**), and proximal (**f**) views. **g–i** NMB G.C.623 in dorsal (**g**), plantar (**h**), and distal (**i**) views. Abbreviations: *c.m.* cotyla medialis, *f.i.* fossa infracotylaris, *f.met.I.* fossa metatarsi I, *f.v.d.* foramen vasculare distale; *l.pr.* lateral protuberance on trochlea metatarsi III, *tr. met.* trochlea metatarsi, *t.t.c.* tuberositas m. tibialis cranialis. Scale bars 10 mm



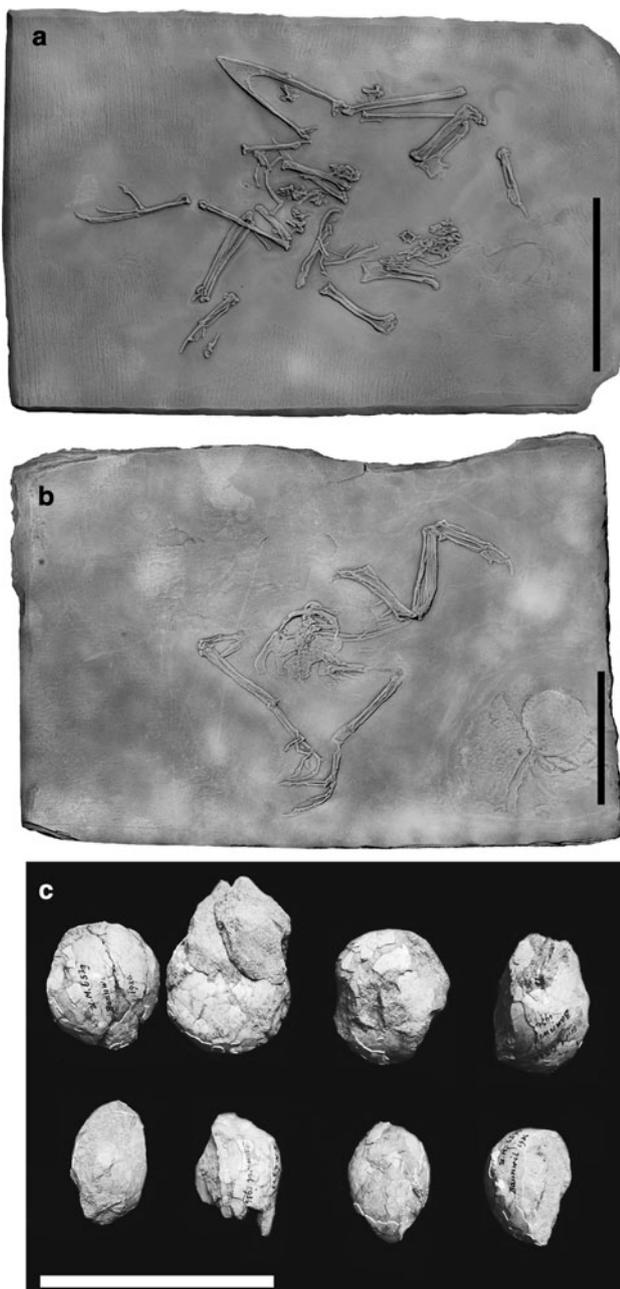


Fig. 4 a, b Birds from the Early Oligocene of the Glarner Fischschiefer, Engi, Switzerland. a Holotype of *Protornis glarniensis* von Meyer, 1844 (PIMUZ A/IV 37a). b Trogoniformes indet. (PIMUZ A/IV 39). c Remains of bird eggs (NMB U.M. 6538–45) from the Late Oligocene of Bannwil, Canton Berne. Scale bars 5 cm

bergeri differs from Ogygoptyngidae, Heterostrigidae, Strigidae and Tytonidae in character 4; differs from Ogygoptyngidae, Sophiornithidae, Palaeoglaucidae, Tytonidae, and Strigidae in characters 5–8; and from Heterostrigidae in characters 6–8. Specifically, it differs from:

- Ogygoptyngidae in: trochlea metatarsi III projecting further distally than trochlea metatarsi II; trochlea

metatarsi IV with mediolaterally narrow articular surface in distal view.

- Sophiornithidae in: smaller size; long and slender; presence of a well-marked sulcus extensorius.
- Palaeoglaucidae in: trochlea metatarsi II wider than trochlea metatarsi III (of about the same width in Palaeoglaucidae).
- Tytonidae (including *Necrobyas* and *Selenornis*): well-marked sulcus flexorius; symmetrical rims of trochlea metatarsi III; tarsometatarsus not strongly curved in distal view; differs from extant *Tyto* in: proximal end of shaft in medial view dorsoplantarily broad.
- Strigidae and Heterostrigidae in: absence of ossified arcus extensorius; fossa infracotylaris dorsalis not as deep; tarsometatarsus slender.
- Heterostrigidae in: better developed eminentia intercotylaris.
- *Eostrix* (Protostrigidae) in: cotyla medialis not shallow; deeper fossa infracotylaris; plantarly symmetrical rims of trochlea metatarsi III (as in *Minerva*).
- *Minerva* (Protostrigidae) in: trochlea metatarsi III mediolaterally wider; trochlea metatarsi IV not as proximally situated, i.e. reaching mid-length of trochlea metatarsi III (as in *Eostrix*).
- *Eostrix* and *Minerva* in: trochlea metatarsi II mediolaterally wider.

?Oligostrix bergeri sp. nov. is characterized by: (1) mediolaterally very wide trochlea metatarsi II; (2) well-marked groove on trochlea metatarsi III; (3) rims of trochlea metatarsi III narrowing dorsoplantarily towards the midline; (4) tarsometatarsus proportionally long and slender (as in Ogygoptyngidae).

Description and comparisons. The shaft of the tarsometatarsus is badly crushed; the unusual medial curvature is interpreted as distortion that occurred during fossilization. Similarly, in distal view, the position of trochlea metatarsi IV of *?Oligostrix bergeri* sp. nov. appears to have been modified (see description) as a result of taphonomical processes. Rather than creating a new genus, we tentatively refer this specimen to *Oligostrix*, a genus erected by Fischer (1983) to accommodate a small tibiotarsus of a strigiform from the Early Oligocene of Germany (MP 23–24; Mlíkovský 2002). Although direct comparisons with *Oligostrix rupelensis* are not possible, we base our referral on the similar age (Late Oligocene, MP 26, Chattian) and geographic proximity of specimen NMB U.M. 2528 and *O. rupelensis*, as well as on Fischer's familial attribution (Protostrigidae). *Oligostrix rupelensis* appears to have been only slightly smaller than *?Oligostrix bergeri*. We note however, that a more reliable generic placement will require more and better preserved material. Although NMB U.M. 2528 is superficially similar to representatives

of the genus *Minerva* (Middle–Late Eocene), the large temporal and geographical gap between them—*Minerva* is only known from North American deposits—render it unlikely for the Swiss specimen to belong in this genus.

?*Oligostrix bergeri* sp. nov. is comparable in size to extant *Asio flammeus* (Short-eared Owl), and is smaller than most representatives of the Protostrigidae, with the exception of *Eostrix tsaganica* Kurochkin and Dyke, 2011, and *Oligostrix rupelensis* Fischer, 1983. It resembles *Ogygoptynx wetmorei* Rich and Bohaska, 1976 in proportions. NMB U.M. 2528 represents the first, almost complete tarsometatarsus known for the family. The bone is however rather poorly preserved, particularly at its shaft (Fig. 3a–d). Nonetheless, a reliable comparison with other strigiforms is possible mainly based on features of the proximal and distal ends.

At the proximal end, the cotyla medialis (Fig. 3f) is dorsoplantarly elongated and wide, as seen in some representatives of the genus *Eostrix* (e.g. Kurochkin and Dyke 2011). This is due to the condylus medialis of the tibiotarsus being greatly widened in Protostrigidae (Mourer-Chauviré 1983; Mayr 2009). Contrary to the condition in members of the Strigidae, an ossified arcus extensorius is absent. Because of the distortion of the shaft, it is not possible to assess the position of the tubercle for m. tibialis anticus (tuberositas m. tibialis cranialis), which is more medially situated in representatives of the Protostrigidae (Mourer-Chauviré 1983). The scar is however elongated and well-marked (Fig. 3a).

In medial view, the proximal end of the shaft of ?*Oligostrix bergeri* is dorsoplantarly broad, a condition observed in most Strigiformes (extant *Tyto* being an exception). This feature also distinguishes strigiforms from diurnal birds of prey (e.g. Accipitridae and Falconidae). A well-marked and symmetrical sulcus extensorius is present, contrary to members of the Strigidae, in which the sulcus extensorius is much deeper medially. In plantar view, a deep sulcus flexorius is discernable.

The distal end of ?*Oligostrix bergeri* resembles that of other protostrigid owls, however the position of trochlea metatarsi IV in relation to the other trochleae (Fig. 3e) is affected by a certain degree of (taphonomical) distortion, as it appears more dorsally situated (see below). ?*O. bergeri* agrees with other representatives of the Protostrigidae, in that all three trochleae are positioned parallel to each other, i.e. aligned, in distal view (Kurochkin and Dyke 2011).

Fossa metatarsi I is well marked (Fig. 3b). Trochlea metatarsi II is mediolaterally very wide (Fig. 3e), a condition also observed in representatives of the Sophiornithidae (see Mourer-Chauviré 1994), and absent in other protostrigid owls. ?*Oligostrix bergeri* does however agree with representatives of the Protostrigidae in that trochlea metatarsi II is much shorter than trochlea metatarsi III (e.g. Mourer-Chauviré 1983).

As already noted by Mourer-Chauviré (1983), in plantar view, the lateral rim of trochlea metatarsi III is better developed than the medial one, a condition present in extant owls as well as in representatives of the protostrigid genus *Eostrix*. In ?*Oligostrix bergeri* as well as in species of *Minerva* (e.g. *M. antiqua* and *M. leptosteus*, see Rich 1982 and Mourer-Chauviré 1983) however, the articular rims of trochlea metatarsi III are symmetrical (Fig. 3e). The medial and lateral articulation facets of trochlea metatarsi III are not positioned parallel to each other, as they narrow plantarly (Fig. 3e). Trochlea metatarsi III is mediolaterally wider than in *Minerva leptosteus*, particularly dorsally. As in extant owls, in Heterostrigidae the dorsal side of trochlea metatarsi III lies in the same plane as the dorsal side of the shaft (Kurochkin and Dyke 2011). Whether this is also true for ?*O. bergeri* cannot be assessed as the dorsal side of trochlea metatarsi III is crushed.

As in other protostrigids, trochlea metatarsi IV is dorsoplantarly long, its plantar projection however is not preserved. The position of trochlea metatarsi IV is unusual in that in distal view, it is dorsally situated in comparison to trochleae II and III. This condition is unknown for Strigiformes, and we thus hypothesise that this has resulted from taphonomical processes during fossilization. In dorsal view and compared to the other trochleae, trochlea metatarsi IV is not as proximally situated as in other Strigiformes; this condition resembles the one present in *Eostrix tsaganica* (see Kurochkin and Dyke 2011), in which trochlea metatarsi IV lies only slightly more proximally than trochlea metatarsi III (see Plate 12, Fig. 3 in Kurochkin and Dyke 2011).

3.6 Wolfswil (Canton Solothurn; Late Oligocene, MP 27)

Aves indet.

Material. NMB U.M.6483 (incomplete right radius, Fig. 2k); NMB U.M.6484 (distal right tarsometatarsus, Fig. 2l–12); NMB U.M.6485 (sternal portion of right coracoid, Fig. 2m).

Remarks. All of these remains are too fragmentary to allow for an unambiguous taxonomic placement. Radius NMB U.M.6483 belongs to a large bird, the size of the Sarus Crane, *Grus antigone*.

3.7 Bannwil (Canton Bern; Late Oligocene, MP 30)

Material. Eggs (NMB U.M. 6538–45; Fig. 4c).

Remarks. These remains comprise eight compacted eggs that were clustered together and may have been part of a single clutch.

3.8 Rümikon (Canton Zürich; Middle Miocene, MN 6)

Aves indet.

Material. Indeterminate bird remains (NMB OSM 941-3).

3.9 Stein am Rhein (Canton Schaffhausen; Middle Miocene, MN 6)

Von Meyer (1839b) mentioned the presence of galliform-like bone fragments from the Middle Miocene sandstones of Stein am Rhein, but the whereabouts of the material are presently unknown.

cf. Suliformes sensu Chesser et al. (2010)

Material. NMB O.S.M.1263 (left carpometacarpus with distal end missing, Fig. 2n1–n2).

4 Tracksites

Swiss bird tracksites have already been reviewed by Weidmann and Reichel (1979) and Mlíkovský (1996), and a list of these fossil sites is provided in the supplementary information. Twenty sites are known spanning the Late Oligocene to the Middle Miocene, with fossil bird tracks occurring in the Lower Freshwater Molasse (Chattian, Aquitanian), the Upper Marine Molasse (Burdigalian), and the Upper Freshwater Molasse (Tortonian) (see Fig. 1). The most significant discoveries were described and discussed by Speck (1945), Bräm (1954), De Clercq and Holst (1971), Weidmann and Reichel (1979), and Berger (1985).

Because the majority of the localities that yielded bird tracks occur in marls, siltstones, or fine sandstones that were deposited in fluvial, lacustrine, or tidal settings, Weidmann and Reichel (1979) hypothesised that most footprints were produced by shore or marsh birds, and indeed they attributed footprints to members of the Charadriiformes (shorebirds and allies), as morphological characteristics also pointed to affinities with these birds. The tracks they attributed to plovers, snipes and sandpipers were placed in the ichnogenus *Charadriipeda*. Further tracks were assigned to Anseriformes, “Gruiformes”, and Passeriformes (waterfowl; cranes, rails, and allies; and perching birds; see also Lockley and Meyer 2000). Although reliable identification of the tracemaker is complicated by the fact that footprint preservation depends on several parameters, such as sediment consistency (Marty et al. 2009) and foot morphology and kinematics (e.g., Falkingham 2010), it has not been unusual for these studies to produce faunal lists (see Weidmann and Reichel 1979, summarized in supplementary information). Nonetheless, Weidmann and Reichel’s contribution (1979) remains the most complete account of bird track types in their

geological context to have been given so far for Switzerland. In 2011, a new Late Oligocene—Early Miocene site was discovered near Schangnau (Canton Bern). The material consists of an isolated large sandstone block with casts of several bird tracks of two different size classes and morphotypes (Marty and Menkveld-Gfeller 2012).

Avian fossil tracks are not rare worldwide, and discoveries have been prompted by research on non-avian dinosaur tracks, as well as by current research concerning divergence time between avian and non-avian theropods (Melchor et al. 2002), which has led to a fairly extensive record of Mesozoic avian tracks (Lockley et al. 1992; Falk 2011). Cenozoic bird tracks are also well represented worldwide, and have been reported from almost all over the world. Well-known records include North and South America, Europe, Africa, Asia, Antarctica, and New Zealand (e.g., Lockley and Hunt 1995; Sarjeant and Reynolds 2001; Mustoe 2002; McDonald et al. 2007; Díaz-Martínez et al. 2012)

5 Discussion and concluding remarks

5.1 Fossil owls

The fossil record of the Protostrigidae extends as far back as the Early Eocene (e.g. Kurochkin and Dyke 2011). With three genera and 12 species already described, the Protostrigidae are among the most diverse families of extinct owls. The diversity of protostrigid owls seems to have been greater during the Eocene, with ten species reported from three continents, namely North America, Asia, and Europe (Kurochkin and Dyke 2011). Oligocene protostrigids are however only known from Central Europe, and are only represented by two species, *Oligostrix rupelensis* from the Early Oligocene of Germany (Fischer 1983), and *?O. bergeri* sp. nov. from the Late Oligocene of Switzerland.

The specimen referred to *?Oligostrix bergeri* represents the first, almost complete tarsometatarsus known for the Protostrigidae, indicating that in all likelihood the tarsometatarsus of representatives of this family was proportionally long and slender, as in the extinct family Ogygoptyngidae. Despite displaying features only known for members of the Protostrigidae (such as a trochlea metatarsi III that projects distally considerably beyond trochlea metatarsi II, see Diagnosis), *?Oligostrix bergeri* differs from members of the other protostrigid genera, namely *Eostrix* and *Minerva*, in the presence of a medio-laterally much wider trochlea metatarsi II. This feature is also evident in the Sophiornithidae, and it appears to be related to a strong development of the second digit. It has been hypothesized that the evolution of the foot towards a more semizygodactyl morphology within Strigiformes may

also have resulted in trochlea metatarsi II becoming smaller, as seen in Tytonidae—both extant and extinct—and Strigidae (Mourer-Chauviré 1994). This adaptation has been regarded as a progression towards potentially more pronounced perching habits, i.e. grasping capability of the foot (Mourer-Chauviré 1994), but ascertaining whether a wide trochlea metatarsi II in *?Oligostrix bergeri* is indeed linked to a more terrestrial mode of life is still speculative. Nonetheless, Kurochkin and Dyke (2011) mention some features present in members of the protostrigid genus *Eostrix*, such as the symmetrical structure of the metatarsal trochleae (also in *?Oligostrix bergeri*), as possibly being linked to poor grasping abilities in their feet.

NMB G.C.623, from the Late Eocene fissure filling of Gösigen, resembles the tarsometatarsus of the coeval *Palaeoglaux perrierensis*, from Late Eocene deposits of Quercy (Mourer-Chauviré 1987): they both display a well-developed protuberance on the lateral side of trochlea metatarsi III, symmetrical rims of trochlea metatarsi III, a trochlea metatarsi II with an articular surface not wider than trochlea metatarsi III, and a relatively broad area between the foramen vasculare distale and the incisura intertrochlearis lateralis. The latter feature was also reported for *Palaeoglaux artophoron* Peters, 1992 from Messel. The tarsometatarsus from Gösigen is significantly smaller than that of *Palaeoglaux perrierensis*, but may be similar in size to *P. artophoron* (Peters 1992). Given the fragmentary nature of the Gösigen specimen however, an unambiguous referral to the Palaeoglaucidae is not possible.

5.2 Swiss avian fossil record

The Cenozoic avian fossil record from Switzerland was last reviewed by Mlíkovský (1996), but the records on which this assessment was based were primarily concerned with publications on avian fossil tracks, and indeed very few records pertained to skeletal remains. After examination of fossil material housed in the Natural History Museum Basel, we were able to expand the list of avian fossil skeletal remains from two certain records to nine. Six of these localities are from the Swiss Molasse Basin, and three are from fissure fillings in the Jura Mountains. Bird remains have also been reported from the Middle Eocene locality of Chamblon, in the Canton of Vaud (Thenius 1959; Mlíkovský 1996). These remains are however unspecified and their whereabouts unknown.

The Swiss avian fossil record also includes remains of eggs and egg clutches (Bachmann 1878) from the Upper Freshwater Molasse of Bannwil (Canton Bern) and Emmenweid (Canton Luzern), respectively, but specimens described in the latter record are probably lost. Two specimens of fossil bird pellets with bone fragments and a

rodent incisor from the Upper Freshwater Molasse at Immenberg, Canton Thurgau, were interpreted as owl pellets (Bolliger 1999), and a similar fossil from the Upper Freshwater Molasse of Le Locle (Canton Neuchâtel) has been reported by Kälin (1993).

With 20 tracksites, the Swiss bird track record is comparatively rich, and new tracksites are currently being investigated. An updated field-based review of these localities would certainly prove to be a valuable contribution towards a thorough revision of the Swiss fossil record.

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