JOURNAL OF
PALEONTOLOGY
A PUBLICATION OF THE | Paleontological SOCIETY

New late Eocene and Oligocene plotopterid fossils from Washington State (USA), with a revision of "*Tonsala*" *buchanani* (Aves, Plotopteridae)

Gerald Mayr[1]* and James L. Goedert[2]

[1]Senckenberg Research Institute and Natural History Museum Frankfurt, Ornithological Section, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany <Gerald.Mayr@senckenberg.de>
[2]Burke Museum of Natural History and Culture, University of Washington, Box 353010, Seattle, Washington 98195, USA <jamesgoedert@outlook.com>

Abstract.—We report new specimens of the Plotopteridae from Washington State (USA), an area where these flightless seabirds underwent significant diversification during the late Eocene and Oligocene. To date, five plotopterid species from western Washington have been formally named. Specimens previously assigned to *Tonsala buchanani* Dyke, Wang, and Habib, 2011 belong to at least two, but probably even three, different species. One of these, the large-sized "Whiskey Creek specimen" from late Eocene deposits mapped as the Makah Formation, is the oldest known plotopterid and is here tentatively assigned to ?*Klallamornis clarki* Mayr and Goedert, 2016. Another specimen originally referred to *T. buchanani* is also likely to belong to a different species and is among the most substantial records for North American plotopterids. We formally transfer *T. buchanani* to the taxon *Klallamornis* and show that the only unambiguously identified specimen of the species—the holotype—is currently poorly diagnosed from *Klallamornis abyssa* Mayr and Goedert, 2016, which is from coeval strata of the Pysht Formation. Although the holotype of *K. abyssa* is larger than that of *K. buchanani*, there remains a possibility that plotopterids were sexually dimorphic in size. We describe the first ungual phalanx of a plotopterid, which is referred to *K. buchanani*, and report previously unknown elements of the large ?*K. clarki* and the first records of this species from the Lincoln Creek Formation. Current data indicate that plotopterids originated in the middle or late Eocene on islands off western North America, and we hypothesize that the radiation of these birds in the North Pacific Basin may have been related to the evolution of kelp forests.

Introduction

The Plotopteridae were penguin-like, flightless seabirds that inhabited the North Pacific Basin in the late Eocene and Oligocene and possibly survived into the middle Miocene. The fossil record of these birds has significantly increased in the past years and now includes four genera (*Copepteryx*, *Hokkaidornis*, *Empeirodytes*, and *Stenornis*) with five named species from Japan and six genera (*Phocavis*, *Tonsala*, *Olympidytes*, *Klallamornis*, *Plotopterum*, and *Stemec*) with eight named species from North America (Howard, 1969; Olson, 1980; Goedert, 1988; Olson and Hasegawa, 1996; Sakurai et al., 2008; Kaiser et al., 2015; Mayr and Goedert, 2016; Ohashi and Hasegawa, 2020). *Plotopterum* and *Olympidytes* have also been tentatively recognized from rocks in Japan (Hasegawa et al., 1977; Olson and Hasegawa, 1985; Mori and Miyata, 2021). The osteology and taxonomic diversity, stratigraphic occurrence, and interrelationships of plotopterids remain, however, insufficiently known mainly because many taxa are represented by only a few bones.

Plotopterids were initially considered to be most closely related to the suliform Phalacrocoracidae (cormorants) and Anhingidae (anhingas; Howard, 1969; Olson, 1980; Olson and Hasegawa, 1996). By contrast, Mayr (2005) hypothesized

that these birds are the sister taxon of the Sphenisciformes (penguins), but subsequent analyses recovered plotopterids as the sister taxon of either the Phalacrocoracidae and Anhingidae (Smith, 2010) or a more inclusive clade including the Sulidae (gannets and boobies), Phalacrocoracidae, and Anhingidae (Mayr et al., 2015; see Mayr et al., 2021 for a more detailed discussion of the affinities of plotopterids).

In North America, plotopterid fossils were found in strata dating to the earliest Miocene in California (USA) and late Oligocene in British Columbia (Canada), which yielded the holotypes of *Plotopterum joaquinensis* Howard, 1969 and *Stemec suntokum* Kaiser, Watanabe, and Johns, 2015, respectively (Howard, 1969; Kaiser et al., 2015). The type locality for *P. joaquinensis* is in the Pyramid Hill Sand Member of the Jewett Sand and is considered to be earliest Aquitanian or earliest Miocene in age (Shimada et al., 2014; contra Kaiser et al., 2015, who assumed a late Oligocene age). One of the geochronologically earliest North American plotopterids, *Phocavis maritimus* Goedert, 1988, is from the late Eocene Keasey Formation in Oregon (Goedert, 1988). The only bones known of *P. joaquinensis* and *S. suntokum* are coracoids, whereas *P. maritimus* is represented by a tarsometatarsus.

Most North American plotopterids, however, come from deposits on the Olympic Peninsula in Washington State, USA. Intense collecting efforts by one of the authors (J.L.G.) during the past four decades have yielded comprehensive fossil material from various sites of the late Eocene or early Oligocene Lincoln

*Corresponding author

224

Table 1. Overview of the stratigraphic provenance of the published plotopterid material from western Washington State (Olson, 1980; Goedert and Cornish, 2002; Dyke et al., 2011; Mayr et al., 2015; Mayr and Goedert, 2016, 2018; this study).

	Lincoln Creek Formation	Makah Formation	Pysht Formation
Tonsala hildegardae		SMF Av 613 (tentative) SMF Av 662 (tentative)	Holotype (USNM 256518) UWBM 86873 UWBM 86874 SMF Av 599 SMF Av 600 SMF Av 601 SMF Av 645
Tonsala sp.		SMF Av 614	
Olympidytes thieli	Holotype (SMF Av 608)		
cf. *Olympidytes thieli*		SMF Av 609	
Gen. indet. sp. indet. A (cf. *Olympidytes/Klallamornis*)		UWBM 86871 SMF Av 650	
Klallamornis buchanani			Holotype (UWBM 86875) SMF Av 663
cf. gen. indet sp. indet. A and *Klallamornis buchanani*		UWBM 86870	
Klallamornis abyssa		SMF Av 611 UWBM 108400	Holotype (SMF Av 610)
?*Klallamornis clarki*	UWBM 86872 SMF Av 664	Holotype (LACM 129405) SMF Av 612 SMF Av 665	
cf. ?*Klallamornis clarki* ("Whiskey Creek specimen")		UWBM 86869	

Creek and Makah formations and the Oligocene Pysht Formation (see Goedert and Cornish, 2002 for a detailed review of the geology and stratigraphy of these formations).

Although one of the species from the Olympic Peninsula, *Tonsala hildegardae* Olson, 1980, is among the first plotopterids to be named (Olson, 1980), the diversity of plotopterids from the Lincoln Creek, Makah, and Pysht formations is still poorly understood. Goedert and Cornish (2002) reviewed the then-known fossil material and noted the presence of at least five different species. However, Dyke et al. (2011) studied the same material and recognized only two species, *T. hildegardae* and one they described as *Tonsala buchanani* Dyke, Wang, and Habib, 2011. The study by Dyke et al. (2011) suffered from various shortcomings that have confused and impeded a well-resolved taxonomy of plotopterids from western Washington. Not only did Dyke et al. (2011) choose one of the least substantial specimens available to them as the holotype of *T. buchanani*, but their diagnosis of the species did not include any characters preserved in the holotype, the dimensions of some of the fossils were incorrectly given, and most of the referred specimens clearly belong to species other than *T. buchanani*. As already detailed by Mayr et al. (2015), some of the skeletal elements were misidentified or attributed to the wrong specimen number. Other errors, such as measurements attributed to the wrong specimen in table 1 of Dyke et al. (2011) were repeated later (Mori and Miyata, 2021, p. 152, table 1). One of the aims of this paper is to clarify this confusion by formally revising the status of *T. buchanani* and various specimens assigned to that species by Dyke et al. (2011).

Increased preparation efforts of undescribed material yielded new insights into the diversity of plotopterids from southwest Washington State and the Olympic Peninsula and led to the description of three further species (Mayr et al., 2015; Mayr and Goedert, 2016, 2018). One of these, *Olympidytes thieli* Mayr and Goedert, 2016, is a medium-sized species with stouter limb bones than *Tonsala hildegardae* and is so far

the only named plotopterid species from the Lincoln Creek Formation. Two larger species were assigned to the taxon *Klallamornis*. The smaller of these, *K. abyssa* Mayr and Goedert, 2016, is represented by partial skeletons and isolated bones of a few individuals. The larger species was tentatively referred to *Klallamornis* and described as ?*K. clarki* Mayr and Goedert, 2016.

Herein, we report new specimens that inform the osteology and stratigraphic occurrence of some poorly known species. In addition to revising material assigned to *Tonsala buchanani*, we furthermore address the diversity of plotopterids from Washington State and present a new hypothesis concerning the evolutionary origin of these birds.

Materials and methods

Although plotopterid fossils are not uncommon in some localities on the Olympic Peninsula, they are typically preserved in very hard concretions, the preparation of which is difficult and very time consuming. In some cases, after excess rock has been mechanically removed, acid etching yields good results, but this depends on the chemistry of the concretion. Some matrices (and these can be from the same locality and rock unit) respond to dilute acetic acid; others respond only to formic acid. Other concretions are insoluble, and mechanical preparation is the only way to expose the bones, in which case extreme care must be taken.

Repositories and institutional abbreviations.—The fossils are deposited in the Natural History Museum of Los Angeles County, Los Angeles, CA, USA (LACM), the Senckenberg Research Institute, Frankfurt, Germany (SMF), the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM), and the Burke Museum of Natural History and Culture, University of Washington, Seattle, WA, USA (UWBM).

Systematic paleontology

Aves Linnaeus, 1758
Plotopteridae Howard, 1969
Tonsalinae Mayr and Goedert, 2018
Tonsala Olson, 1980

Type species.—*Tonsala hildegardae* Olson, 1980, by original designation.

cf. *Tonsala hildegardae* Olson, 1980
Figure 1.1–1.3

Holotype.—USNM 256518: partial associated skeleton. Beach west of Murdock Creek, Clallam County, Washington; Oligocene, lower part of the Pysht Formation.

Description and comparisons.—SMF Av 662 is the most complete scapula of a North American plotopterid described so far. The bone is, however, split in a transverse plane so that only internal structures are exposed. The tip of the acromion still appears to be hidden in the matrix. In its size and shape, SMF Av 662 corresponds well with the scapula of the *T. hildegardae* holotype (Fig. 1.4) and shows that the irregular margins of the scapular blade of the latter are due to postmortem damage, as already assumed in the original description (Olson, 1980).

Material.—SMF Av 662: left scapula, which is still preserved in a block of matrix (Fig. 1.1–1.3); from the Jansen Creek Member of the Makah Formation; collected by J.L.G. on 11 June 1999.

Measurement.—Length as preserved, 123.8 mm.

Remarks.—The tentative assignment of this fossil to *T. hildegardae* is based mainly on its small size. The specimen comes from the Makah Formation and is therefore somewhat older than the holotype of *T. hildegardae* from the Pysht Formation. The only other record of *T. hildegardae* from the Makah Formation is a coracoid, which was tentatively referred to the species by Mayr and Goedert (2016).

Klallamornis Mayr and Goedert, 2016

Type species.—*Klallamornis abyssa* Mayr and Goedert, 2016, by original designation.

Klallamornis buchanani (Dyke, Wang, and Habib, 2011), n. comb.
Figures 2.1, 2.2, 2.8–2.12, 2.17, 2.18, 4.9, 4.13

2011 *Tonsala buchanani* Dyke, Wang, and Habib, p. 2, fig. 2A–V.
2015 *Tonsala buchanani*; Mayr, Goedert, and Vogel, restricted to holotype UWBM 86875 only.

Figure 1. (**1–3**) cf. *Tonsala hildegardae* (SMF Av 662) left scapula compared with (**4**) a cast of the right scapula of the holotype (LACM 123791) and (**5**) the left scapula of gen. indet. sp. indet. A (UWBM 86871); in (**3**), the surrounding matrix was digitally removed. acr = acromion. Scale bars = 20 mm.

Figure 2. (**1, 2**) Left femur of the holotype of *Klallamornis buchanani* (UWBM 86875) in caudal view; in (**2**), the bone was coated with ammonium chloride and mirrored; the missing portion of the condylus medialis is indicated by the gray area. (**3–5**) Right femur of the holotype of *Klallamornis abyssa* in caudal view (SMF Av 610); in (**4**), the surrounding matrix was digitally removed, and the missing proximal end of the bone is indicated by the gray area; in (**5**), the bone was coated with ammonium chloride. (**6, 7**) Left femora (cranial view) of the extant *Phalacrocorax carbo* (Phalacrocoracidae) to illustrate the pronounced sexual size dimorphism in the length of the bone: (**6**) a female individual; (**7**) a male individual. (**8, 9**) Fragment of the proximal end of a right femur referred to *K. buchanani* (SMF Av 663): (**8**) caudal view; (**9**) medial view. (**10, 11**) Thoracic vertebra associated with SMF Av 663: (**10**) dorsal view; (**11**) cranial view. (**12**) Partial ungual phalanx associated with SMF Av 663 in lateral and plantar views; the arrow denotes an enlarged view of the bone. (**13–16**) Ungual phalanges of (**13**) *Fregata magnificens* (Fregatidae), (**14**) *Anhinga anhinga* (Anhingidae), (**15**) *Morus bassanus* (Sulidae), and (**16**) *Phalacrocorax carbo* (Phalacrocoracidae). (**17, 18**) Three thoracic vertebrae associated with the holotype of *Klallamornis buchanani* (UWBM 86875): (**17**) right lateral view; (**18**) cranial view. cdl = condylus lateralis; cdm = condylus medialis; fac = facies articularis acetabularis; fat = facies articularis antitrochanterica; flx = tuberculum flexorium; fvc = fovea costalis; psp = processus spinosus; ptv = processus transversus; pvt = processus ventralis; zcr = zygapophysis cranialis. Scale bars = 20 mm (the same scale applies for [**13–16**]).

2016 "*Tonsala*" *buchanani*; Mayr and Goedert, fig. 1D.
2018 "*Tonsala*" *buchanani*; Mayr and Goedert, p. 52, fig. 2D.

Holotype.—Partial skeleton: UWBM 98975; both femora, proximal end of a tibiotarsus, three vertebrae, ribs, and other bone fragments. Beach west of Murdock Creek, Clallam County, Washington; Oligocene, lower part of the Pysht Formation.

Description and comparisons.—The fragmentary proximal end of the femur of the newly referred specimen SMF Av 663 consists of the caudal half of the proximal end of the bone (Fig. 2.8, 2.9). The fossil closely corresponds to the femur of

the holotype of *Klallamornis buchanani* in size and morphology. It is smaller than the femur of the *K. abyssa* holotype (the width of which is estimated at 34–35 mm) and larger than that of the *Olympidytes thieli* holotype (which measures 28.6 mm). A referral to *K. buchanani* is also supported by the fact that the fossil is from the type locality and horizon of the species. As in *K. buchanani*, *Tonsala hildegardae*, and *O. thieli*, the distal margins of the facies articularis antitrochanterica and the facies articularis acetabularis form a distinct rim, whereas the distal portion of the facies articularis acetabularis smoothly merges into the femur shaft in *Hokkaidornis abashiriensis* Sakurai, Kimura,

and Katoh, 2008 and the species of *Copepteryx* (see also Mori and Miyata, 2021). As in other plotopterids, the fovea ligamenti capitis is very pronounced.

SMF Av 663 also includes an ungual phalanx, which lacks a part of its dorsal section and the proximal tip (Fig. 2.12). Ungual phalanges of plotopterids have not been described previously. The bone has an ovate cross section, lacks a laterally open sulcus neurovascularis, and exhibits numerous neurovascular openings on its surface. It is markedly curved and very robust, and in its overall shape is more like the ungual phalanges of the Fregatidae (Fig. 2.13) and Anhingidae (Fig. 2.14) than those of the Sulidae (Fig. 2.15) and Phalacrocoracidae (Fig. 2.16). However, unlike in the Fregatidae and Anhingidae but as in the Phalacrocoracidae and Sulidae, the tuberculum flexorium is only weakly prominent and forms a lip-like transverse ridge rather than a true tubercle.

Material.—SMF Av 663: fragment of proximal end of right femur, fragmentary thoracic vertebra, and ungual phalanx (Fig. 2.8–2.12); from the lower part of the Pysht Formation west of Murdock Creek, regarded as late early Oligocene or early late Oligocene (Barnes and Goedert, 2001), or late but not latest Oligocene (Nesbitt et al., 2010); collected by J.L.G. on 26 June 1983.

Measurement.—SMF Av 663: proximal width of femur, 32.0 mm.

Remarks.—The holotype of *Tonsala buchanani* (UWBM 86875) is a partial skeleton consisting of both femora, the proximal end of a tibiotarsus (incorrectly labeled as UWBM 86871 by Dyke et al., 2011, fig. 2T), three vertebra, ribs, and other bone fragments. Contrary to the statement of Dyke et al. (2011, p. 2), the specimen does not include the proximal end of a tarsometatarsus or a fibula; Dyke et al. (2011, fig. 2R) furthermore illustrated the right femur of *T. buchanani* without the associated head.

Tonsala buchanani was not properly diagnosed because all the characters listed by Dyke et al. (2011) pertain to the humerus, coracoid, and carpometacarpus and can therefore not be assessed in the holotype, which does not include these bones. Although the "Whiskey Creek specimen" (UWBM 86869) was only tentatively referred to *T. buchanani* by Dyke et al. (2011, p. 6), the associated carpometacarpus was considered to have characters diagnostic for *T. buchanani*. The alleged differences of this carpometacarpus and that of *T. hildegardae* furthermore appear to be based on comparisons with the os carpi ulnare of the latter species (Mayr and Goedert, 2016). The humerus and coracoid referred to and used to diagnose *T. buchanani* belong to a specimen (UWBM 86871; Fig. 3) that is discussed in the following and likely represents a different species. Whether the tarsometatarsus UWBM 86870, which was referred to *T. buchanani* by Dyke et al. (2011), belongs to this species cannot be determined for sure; Goedert and Cornish (2002) thought it was referrable to the species represented by UWBM 86871 because of its size and because it was found in the same rock unit. All of this leaves only the femora (Fig. 2.1, 2.2), proximal tibiotarsus, and thoracic vertebrae (Fig. 2.17, 2.18) of the holotype as unambiguously identified material of *T. buchanani*.

Dyke et al. (2011, table 1) gave the distal width of the holotype femur of *T. buchanani* as 25.2 mm, but this value is too small and may pertain to the width of the bone as it is preserved. The actual distal width of the complete bone is here estimated at approximately 30.5 mm. With a length of 134.2 mm (Dyke et al., 2011, table 1), the femur of *T. buchanani* is shorter than that of *Klallamornis abyssa* (Fig. 2.3–2.5), which measures about 143 mm and has a distal width of about 34 mm (Mayr and Goedert, 2016). Although the holotype of *K. abyssa* is therefore distinctly larger than that of *T. buchanani*, the magnitude of this size difference falls within the intraspecific sexual size dimorphism of extant Phalacrocoracidae, in which the males are significantly larger than the females, with their limb bones measuring up to 120% the length of those of females (Fig. 2.6, 2.7).

The holotypes of both *T. buchanani* and *K. abyssa* are from the lower part of the Pysht Formation near Murdock Creek, and at present it is not possible to reliably differentiate both species on the basis of morphological features other than size. The femur of *T. buchanani* appears to have a straighter shaft than that of *Klallamornis abyssa*, and the caudal portion of the condylus lateralis seems to have a wider medial rim. However, these differences are not reliably diagnostic, and the possibility remains that *Klallamornis abyssa* is a junior synonym of *T. buchanani*. Currently, however, we refrain from a formal synonymization and note that the preparation of two partial skeletons of similar-sized species from the Olympic Peninsula is pending, which may inform the osteology of these species. In any case, the femur of *T. hildegardae* is not as stout as that of *T. buchanani*, and we here transfer the latter species to the genus *Klallamornis*.

Gen. indet. sp. indet. A (cf. *Klallamornis* or *Olympidytes*)
Figures 1.5, 3.1–3.9, 4.1, 4.3, 4.4, 4.7, 4.8, 4.12, 5.8

2002   Plotopteridae, new species?; Goedert and Cornish, p. 67, figs. 3b, 4b, 5d.
2011   *Tonsala buchanani* (in part); Dyke, Wang, and Habib, p. 2, figs. 2G–J, 2M, 2P–Q, 2U–V.
2018   "*Tonsala*" *buchanani*; Mayr and Goedert, fig. 2D.
2021   Plotopteridae, unidentified species; Mayr et al., p. 2, fig. 3a.

Description and comparisons.—UWBM 86871 is the only plotopterid in which the humerus, coracoid, and femur of a single individual are preserved in their entire length. As such, the specimen is of significance for an assessment of the limb proportions of plotopterids, even though all three bones are broken in two or more parts that were shifted apart owing to tectonic movements during the fossilization process.

UWBM 86871 includes the cranial extremity of the left scapula, which has been freed of matrix, with a portion of the scapular blade still being appressed to the sternal end of the coracoid. The scapula was mentioned by Goedert and Cornish (2002) but not by Dyke et al. (2011), who stated that the bone is known only from the *T. hildegardae* holotype. As in other plotopterids, the scapula of UWBM 86871 has a very long acromion, which forms a sharper angle with the cranial margin of the bone than in *T. hildegardae*, in which the base of the acromion smoothly merges into the cranial margin of the scapula

Figure 3. (**1–9**) Major bones of the plotopterid specimen UWBM 86871 from the Makah Formation (gen. indet. sp. indet. A), which was previously assigned to, and in part used to diagnose (incorrectly), *Tonsala buchanani* by Dyke et al. (2011). (**1, 2**) Left coracoid: (**1**) dorsal view; (**2**) ventral view. (**3**) Cranial portion of the left scapula in lateral view. (**4–6**) Left humerus: (**4**) cranial view; (**5**) caudal view; (**6**) caudoventral view. (**7**) Proximal and distal portions of left ulna. (**8, 9**) Left femur: (**8**) caudal view; (**9**) cranial view. (**10**) Right humerus, which is here assigned to the same indeterminate species (SMF Av 650). acr = acromion; fac = facies articularis clavicularis; ppc = processus procoracoideus; scp = portion of scapular blade; tbd = tuberculum dorsale. Scale bars = 20 mm.

(Fig. 1.4, 1.5). The acromion of UWBM 86871 is less ventrally deflected than in a plotopterid from Japan (Ando and Fukata, 2018). The bone appears to be slightly larger than the scapula we refer to *T. hildegardae* in the present study (SMF Av 662; see the preceding notes).

Dyke et al. (2011, p. 2) stated that the coracoid of UWBM 86871 consists of the "cranial [sic] end […] broken at the level of the sternocoracoid impression," but the bone is completely preserved. The UWBM 86871 coracoid (Fig. 4.1) is distinctly smaller than the coracoid that was referred to *Klallamornis abyssa* (Fig. 4.2) by Mayr and Goedert (2016). The fossil differs from the coracoid of the *Tonsala hildegardae* holotype in that the facies articularis clavicularis does not form a pronounced hook. It is distinguished from the coracoid SMF Av 614, which was referred to *Tonsala* sp. by Mayr and Goedert (2016), in that the processus procoracoideus more strongly points in the omal direction. The sternal extremity of UWBM 86871 is too poorly preserved for close comparison with other plotopterids. Apart from being smaller, the coracoid of UWBM 86871 resembles that of the recently described *Stenornis kanmonensis* Ohashi and Hasegawa, 2020 from the early Oligocene of Japan (Ohashi and Hasegawa, 2020). However, since the coracoids of other similar-sized taxa, such as *Olympidytes thieli*, are unknown, it is not possible to assess the phylogenetic significance of this resemblance. Ohashi and Hasegawa (2020, p. 288) did not list measurements for the length of the *Stenornis kanmonensis* coracoid but noted that "the size is almost the same as *Copepteryx hexeris*," for which the length

of the coracoid was given as 180 mm by Olson and Hasegawa (1996). With an estimated length of ∼150 mm, the coracoid of UWBM 86871 is distinctly shorter.

The humerus of UWBM 86871 and the referred humerus SMF Av 650 are the only completely preserved humeri of plotopterids from the Olympic Peninsula discovered so far. The shaft of the bone shows a marked sigmoid curvature, which is characteristic of the plotopterid humerus. It is more slender than the humerus shaft of *Copepteryx hexeris* Olson and Hasegawa, 1996, the only other plotopterid species for which a complete humerus is known. The shaft is not as strongly bulging dorsally as it is in the *T. hildegardae* holotype, a condition that was considered of pathologic origin by Olson (1980). The distal end of the bone resembles the humerus of *T. hildegardae* in the dorsoventrally narrow process flexorius. As detailed by Goedert and Cornish (2002), however, the trochlear ridges are better developed than in the *T. hildegardae* holotype.

The ulna (Fig. 3.7) is broken in two portions and lacks the intermediate section. The proximal end of this bone was previously illustrated by Dyke et al. (2011, fig. 2M) but misidentified as the proximal radius. As far as comparisons are possible, the preserved portions of the bone resemble the ulna of *T. hildegardae* (Olson, 1980; Mayr et al., 2015).

Dyke et al. (2011, p. 2) stated that the femur of UWBM 86871 was "glued together in the UWBM collection back-to-front." However, and as noted by Mayr and Goedert (2016), the bone has merely been freed from surrounding rock and is in the same state it was in the original matrix.

Figure 4. Selected bones of specimen UWBM 86871 (gen. idet. sp. indet. A) compared with other plotopterids. (**1**) Left coracoid of UWBM 86871 in dorsal view. (**2**) Right coracoid (UWBM 108400; dorsal view), which was assigned to *Klallamornis abyssa* by Mayr and Goedert (2016). (**3, 4**) Omal extremity of the left coracoid of UWBM 86871: (**3**) dorsomedial view; (**4**) medial view. (**5**) Omal extremity of the coracoid of *Tonsala hildegardae* in dorsomedial view (cast of the holotype, LACM 123791). (**6**) Omal extremity of the coracoid of *Plotopterum joaquinensis,* earliest Miocene, California, in medial view (holotype, LACM 8927). (**7, 8**) Left femur of UWBM 86871; in (**8**) the bone was digitally brought to its presumed original length. (**9**) Left femur of *Klallamornis buchanani* (holotype, UWBM 86875). (**10**) Left femur of *Tonsala hildegardae* (UWBM 86873). (**11**) Left femur of *Olympidytes thieli* (cast of holotype, SMF Av 608; coated with ammonium chloride). (**12, 13**) Details of the proximal ends (caudal view) of the femora of (**12**) UWBM 86871 and (**13**) *K. buchanani* (holotype, UWBM 86875). hkp = hook-like projection formed by processus acrocoracoideus; pac = processus acrocoracoideus; ppc = processus procoracoideus. Scale bars = 20 mm.

Material.—UWBM 86871: partial skeleton (Fig. 3.1–3.9), including the left coracoid, left scapula, left humerus (erroneously stated to be from the right side by Dyke et al., 2011, p. 2 but correctly labeled as a left humerus by Dyke et al., 2011, fig. 2I–J; Dyke et al., 2011 also listed the distal end of a left humerus, but UWBM 86871 includes only the left humerus, which is complete), partial left ulna (erroneously identified as the radius by Dyke et al., 2011), and left femur; from the Jansen Creek Member of the Makah Formation, southeast of Bullman Creek. SMF Av 650: right humerus (Fig. 3.10); from the Jansen Creek Member of the Makah Formation, approximately 200 meters west of the mouth of Rasmussen Creek; collected by JLG on 27 December 1986. The Jansen Creek Member is an olistostrome and latest Eocene to earliest Oligocene in age.

Measurements.—UWBM 86871: humerus, length as preserved, 143.8 mm (Dyke et al., 2011, table 1), distal depth, 16.1 mm; coracoid, length as preserved, ~150 mm; femur, length as preserved, 133.0 mm (Dyke et al., 2011, table 1 erroneously listed the femur measurements for UWBM 86870, which is an isolated tarsometatarsus). SMF Av 650: humerus, maximum length along longitudinal axis, 136.0 mm; width of shaft in midsection, 20.0 mm; maximum proximal width, 33.0 mm; maximum distal width, 28.6 mm.

Remarks.—UWBM 86871 was referred to *Klallamornis buchanani* by Dyke et al. (2011) and is much more complete

than the holotype of this species. As preserved, the length of the femur of UWBM 86871 is subequal to that of the *K. buchanani* holotype (135.1 versus 133.0 mm; Fig. 4.7, 4.9), but the bone is broken in the distal section of the shaft, and the two portions are shifted apart by some distance. It was, therefore, originally shorter than the femur of the *Klallamornis buchanani* holotype (Fig. 4.8), from which it also differs in having a narrower proximal end (28.3 versus 33 mm; Fig. 4.12, 4.13). The condylus lateralis of UWBM 86871 is furthermore narrower than that of the *K. buchanani* holotype.

Apart from being larger, UWBM 86871 differs from *Tonsala hildegardae* in the shape of the processus acrocoracoideus of the coracoid, which has a bulkier tip and forms a less-pronounced hook (Fig. 4.3, 4.5); the acromion of the scapula forms a sharper angle with the cranial margin of the bone (Fig. 1.4, 1.5); the shaft of the femur is stouter than in *T. hildegardae*.

UWBM 86871 is distinctly smaller than specimens assigned to *Klallamornis abyssa*, and the femur is longer than that of the *Olympidytes thieli* holotype (Fig. 4.11). A well-founded assignment to *Klallamornis* or *Olympidytes*, or a delimitation from either taxon is, however, not possible currently.

?*Klallamornis clarki* Mayr and Goedert, 2016
Figures 5.1–5.6, 5.9, 5.10, 6.1, 6.2, 6.8–6.11

2002   New genus and species?; Goedert and Cornish, p. 67, fig. 3c.
2009   "unnamed species"; Mayr, p. 68, fig. 7.4a.

Figure 5. New material referred to ?*Klallamornis clarki*. (**1–5**) Proximal ends of the left (**1–3**) and right (**4, 5**) humerus (SMF Av 664; ?*K. clarki*): (**1, 4**) cranial views; (**2, 5**) caudal views; (**3**) ventral view. (**6**) Shaft fragment of a right humerus (SMF Av 665; ?*K. clarki*). (**7**) Distal portion of left humerus (caudal view) of *Hokkaidornis abashiriensis*, late Oligocene, Japan (SMF, cast of holotype). (**8**) Left humerus (caudal view) of UWBM 86871 (gen. indet. sp. indet. A). (**9, 10**) Fragmentary thoracic vertebra associated with specimen SMF Av 664 (?*K. clarki*): (**9**) caudal view; (**10**) left lateral view. fac = facies articularis caudalis; fvt = foramen vertebrale; ldg = cranially protruding ledge formed by distal margin of sulcus transversus; lip = lip-like process formed by ventral rim of facies articularis caudalis; mld = tubercle for attachment of musculus latissimus dorsi, pars cranialis; stv = sulcus transversus; tbd = tuberculum dorsale; zcd = articular surface of zygapophysis caudalis. Scale bars = 20 mm.

2016   ?*Klallamornis clarki* Mayr and Goedert, p. 9, figs. 7A–F, 8A–E.

2018   ?*Klallamornis clarki*; Mayr and Goedert, p. 54, fig. 2E.

Holotype.—LACM 129405: tarsometatarsus; Jansen Creek Member of the Makah Formation, Clallam County, Washington; latest Eocene or earliest Oligocene.
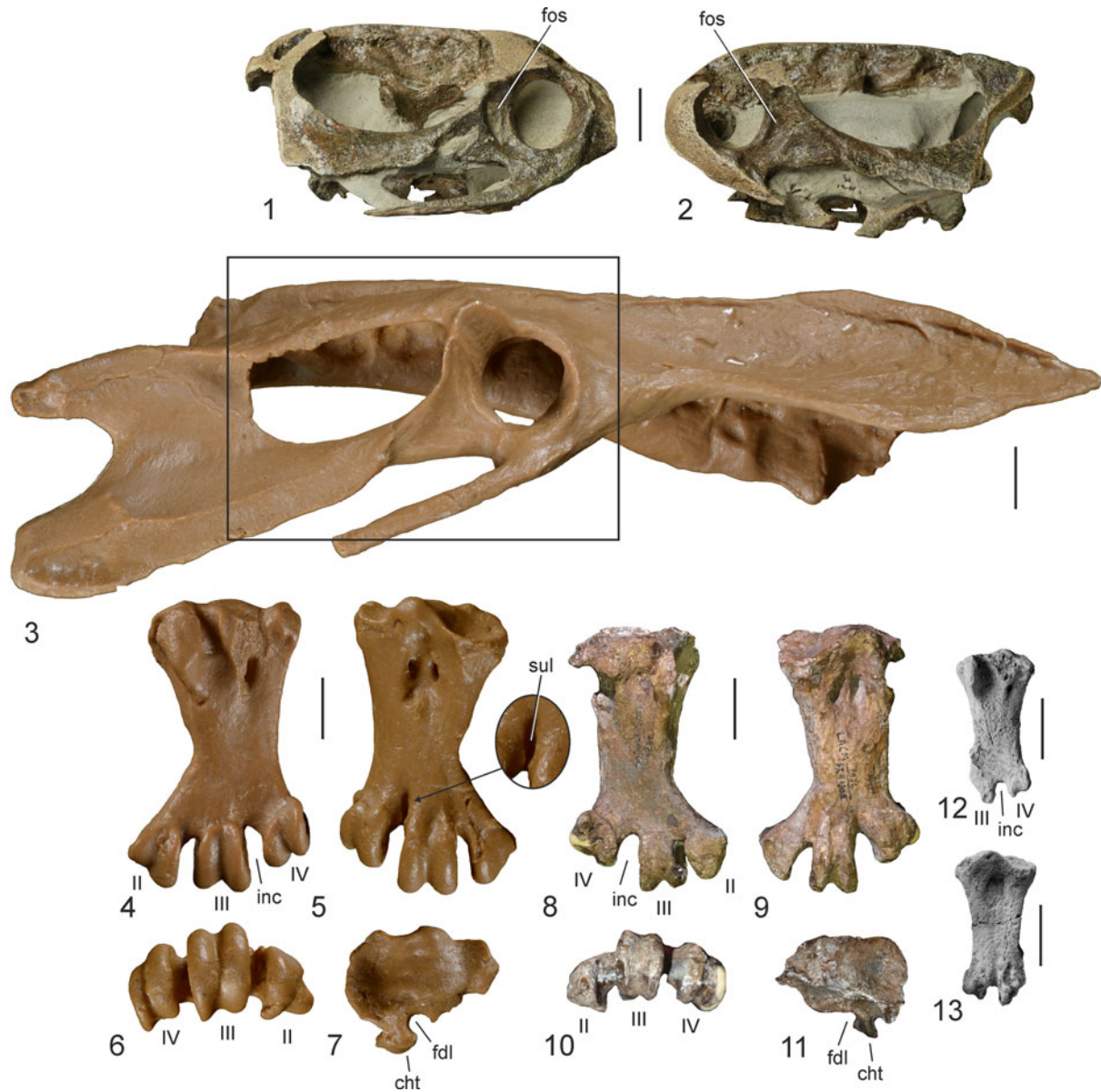
Figure 6. Comparison of selected elements of ?*Klallamornis clarki* and *Hokkaidornis abashiriensis*. (**1, 2**) Partial pelvis of ?*Klallamornis clarki* (SMF Av 612) from the Jansen Creek Member of the Makah Formation in right and left lateral views; the fossa that is situated caudal of the foramen acetabuli distinguishes the specimen from the pelvis of *Hokkaidornis abashiriensis*. (**3**) Pelvis of *H. abashiriensis* in right lateral view (SMF, cast of holotype); the frame indicates the position of the portion preserved in SMF Av 612. (**4–7**) Right tarsometatarsus of *H. abashiriensis* (SMF, cast of holotype): (**4**) plantar view; (**5**) dorsal view; (**6**) distal view; (**7**) proximal view. (**8–11**) Left tarsometatarsus (holotype, LACM 129405) of ?*K. clarki* from the Jansen Creek Member of the Makah Formation: (**8**) plantar view; (**9**) dorsal view; (**10**) distal view; (**11**) proximal view. (**12, 13**) Partial right tarsometatarsus from the Jansen Creek Member of the Makah Formation (SMF Av 609), which was tentatively referred to *Olympidytes thieli* by Mayr and Goedert (2016): (**12**) plantar view; (**13**) dorsal view; coated with ammonium chloride. In (**4, 6, 8, 10, 12**), the tarsometatarsal trochleae are numbered. cht = crista hypotarsi; fdl = sulcus for tendon of musculus flexor digitorum longus; fos = fossa caudal of foramen acetabuli; inc = incisura intertrochlearis lateralis; sul = sulcus between trochlea metatarsi III and IV. Scale bars = 20 mm.

Description and comparisons.—Apart from being much larger, the humerus shows a close similarity to the proximal humerus of *Tonsala hildegardae* (Olson, 1980; Goedert and Cornish, 2002) and to that of UWBM 86871. It also resembles the proximal humerus of *Copepteryx hexeris* (only a small fragment of the proximal humerus of *Hokkaidornis abashiriensis* is known). The globose caput humeri protrudes slightly farther ventrally than the tuberculum ventrale (the latter is, however, damaged in both humeri of SMF Av 664). The tuberculum dorsale is proximodistally long, but its distal end does not reach farther distally than

the crista bicipitalis. The distal margin of the sulcus transversus forms a cranially protruding ledge. On the caudal surface, distal of the fossa pneumotricipitalis, is a marked tubercle for the attachment of musculus latissimus dorsi, pars cranialis (Fig. 5.5).

The ventral rim of the facies articularis caudalis of the thoracic vertebra preserved in SMF Av 664 forms a distinct, caudally directed lip-like process (Fig. 5.10). We also refer to ?*K. clarki* a thoracic vertebra also from the lower part of the Lincoln Creek Formation along the middle fork of the Satsop River, which was figured by Goedert and Cornish (2002, fig. 5a, b).

Material.—SMF Av 664: proximal ends of left and right humeri as well as a fragmentary thoracic vertebra (Fig. 5.1–5.5, 5.9, 5.10); float concretion from the lower part of the Lincoln Creek Formation (late Eocene or earliest Oligocene), gravel bar on west side of the middle fork of the Satsop River; collected by J.L.G. on 30 June 2017. SMF Av 665: shaft section of right humerus (Fig. 5.6); from the Jansen Creek Member of the Makah Formation, float from terrace approximately 1,100 m southeast of Bullman Creek; collected by J.L.G. on 11 May 2012. UWBM 86872: thoracic vertebra; from the Lincoln Creek Formation, collected by J.L.G.

Measurements.—Humerus (SMF Av 664), maximum proximal width, 56.2 mm; estimated total length, ~210–220 mm.

Remarks.—?*Klallamornis clarki* is the largest plotopterid species from the Olympic Peninsula and approaches the size of the very large Oligocene species *Copepteryx hexeris* and *Hokkaidornis abashiriensis* from Japan (Fig. 6). Its large size clearly distinguishes ?*K. clarki* from all other plotopterids from North America. Its genus-level assignment, however, is uncertain, because the known specimens have no skeletal elements in common with the fossils assigned to *K. abyssa* and *K. buchanani.*

The previously known material of ?*K. clarki* consisted of only the holotype, a tarsometatarsus (LACM 129405; Fig. 6.8–6.11), and a partial pelvis (Fig. 6.1, 6.2), which were described by Mayr and Goedert (2016).

<div style="text-align:center">

cf. ?*Klallamornis clarki*
("Whiskey Creek specimen")
Figures 7.1–7.5, 7.8, 7.9, 7.13, 7.15, 7.16

</div>

2002 New genus and species(?), the Whiskey Creek specimen; Goedert and Cornish, p. 68, figs. 4c, 5c.
2009 "Whiskey Creek specimen"; Mayr, p. 68, fig. 7.4b.
2011 *Tonsala buchanani* (in part); Dyke, Wang, and Habib, p. 2, figs. 2A, B, F, K, L, N, O.
2021 cf. *Klallamornis*; Mayr et al., p. 2, figs. 1a, 1h, 3m.

Description and comparisons.—Mandible (Fig. 7.1, 7.2) and pterygoid (Fig. 7.3) of UWBM 86869 were already described and compared with stem group Sphenisciformes and extant Suliformes by Mayr et al. (2021). As detailed by Mayr et al. (2015), an alleged pterygoid figured by Dyke et al. (2011, fig. 2A) is a vertebra.

Of the coracoid, only the portion around the cotyla scapularis is visible, which is still unprepared and partly embedded in matrix (Fig. 7.5). The processus procoracoideus appears to be proportionally longer than in specimens referred to *Klallamornis abyssa* (Mayr and Goedert, 2016).

Of the furcula, the right extremitas omalis is preserved and was listed by Goedert and Cornish (2002) but not mentioned by Dyke et al. (2011). The bone exhibits a large articular facet for the coracoid and a long but narrow processus acromialis (Fig. 7.4).

UWBM 86869 includes the distal end of the left humerus, which closely resembles the distal humerus of *Copepteryx hexeris* in its morphology. Unlike in *T. hildegardae* and UWBM 86871, the ventrodistal portion of the bone is broadly rounded (Fig. 7.8, 7.9). As already noted by Goedert and Cornish (2002), the trochlear ridges are furthermore better developed than in *Tonsala hildegardae*. The dorsal trochlear ridge, which borders the sulcus humerotricipitalis, forms a ventrally directed projection. In distal view, however (Fig. 7.13, 7.14), the intermediate trochlear ridge of UWBM 86869 is less prominent than in UWBM 86871 and is directed toward the ventral trochlear ridge, rather than being positioned parallel to it as in UWBM 86871, *C. hexeris,* and *H. abashiriensis.*

Although Dyke et al. (2011, p. 6) stated the carpometacarpus of UWBM 86869 was an incomplete proximal portion, the bone is nearly complete (Goedert and Cornish, 2002, fig. 5c; Dyke et al., 2011, fig. 2N, O; herein Fig. 7.15, 7.16). The specimen closely resembles the carpometacarpi of *Hokkaidornis abashiriensis* (Fig. 7.17) and *Copepteryx hexeris* in its proportions. However, it exhibits a better-developed processus pisiformis than the carpometacarpus of *H. abashiriensis,* and the os metacarpale alulare is proportionally shorter than in *H. abashiriensis* and *C. hexeris,* with its proximal margin being more clearly offset from the carpal trochlea.

Material.—UWBM 86869: caudal portion of left mandibular ramus, right pterygoid, right extremitas omalis of furcula, distal end of left humerus, left carpometacarpus (Fig. 7), and a vertebra; from late Eocene (35.3–34 Ma) strata of the Makah Formation west of Whiskey Creek (see Goedert and Cornish, 2002).

Measurements.—Carpometacarpus, length, 67.0 mm (Dyke et al., 2011, table 1).

Remarks.—As detailed by Goedert and Cornish (2002), this specimen is from rocks mapped as the Makah Formation west of Whiskey Creek (mapped in error as the Pysht Formation by Nesbitt et al., 2010; E.A. Nesbitt, personal communication, 2011) and is possibly the oldest North American plotopterid; *Phocavis maritimus* is from strata nearly the same age. The Whiskey Creek specimen was tentatively referred to *Klallamornis* ("*Tonsala*") *buchanani* by Dyke et al. (2011, p. 6), but it clearly represents a species that had a much larger size than *K. buchanani.*

As detailed by Goedert and Cornish (2002), UWBM 86869 distinctly differs in the shape of the distal end of the humerus from UWBM 86871, another specimen originally referred to and used in part to diagnose *Klallamornis* ("*Tonsala*") *buchanani* by Dyke et al. (2011). Apart from differences in the size and orientation of the trochlear ridges (see Goedert and Cornish, 2002: fig. 4 [the specimen in fig. 4e is the holotype of *H. abashiriensis*]), UWBM 86869 has a less-protruding and more-rounded processus flexorius than UWBM 86871 (Fig. 7.8, 7.9, 7.12). UWBM 86869 is also clearly distinguished from *Tonsala hildegardae* and *Hokkaidornis abashiriensis* in the morphology of the distal end of the humerus. The carpometacarpus of UWBM 86869 furthermore differs from that of *Copepteryx* and *Hokkaidornis* in the better-developed processus pisiformis (Fig. 7.15, 7.17).

Our tentative assignment of UWBM 86869 to ?*K. clarki* is based on the very large size of the fossil. There are, however, no skeletal elements in common between UWBM 86869 and

Figure 7. The Whiskey Creek specimen UWBM 86869 (cf. ?*Klallamornis clarki*). (**1, 2**) Caudal portion of left mandible of UWBM 86869: (**1**) dorsal view; (**2**) dorsomedial view. (**3**) Right pterygoid of UWBM 86869. (**4**) Right extremitas omalis of furcula of UWBM 86869. (**5**) Fragmentary portion of the omal extremity of the left coracoid of UWBM 86869 in dorsal view. (**6**) Omal extremity of left coracoid of UWBM 86871 (gen. indet. sp. indet. A) in dorsal view. (**7**) Omal extremity of a right coracoid referred to *K. abyssa* (UWBM 108400; dorsal view). (**8, 9**) Distal end of the left humerus of UWBM 86869: (**8**) cranial view; (**9**) caudal view. (**10, 11**) Distal end of the left humerus of *Hokkaidornis abashiriensis* (SMF cast of holotype): (**10**) cranial view; (**11**) caudal view. (**12**) Distal end of the left humerus of UWBM 86871 (gen. indet. sp. indet. A) in caudal view. (**13, 14**) Distal ends (distal view) of the left humeri: (**13**) UWBM 86869; (**14**) UWBM 86871 (gen. indet. sp. indet. A). (**15, 16**) Left carpometacarpus of UWBM 86869: (**15**) ventral view; (**16**) dorsal view. (**17**) Right carpometacarpus (ventral view) of *H. abashiriensis* (SMF cast of holotype). cdd = condylus dorsalis; cdv = condylus ventralis; csc = cotyla scapularis; dtr = dorsal trochlear ridge; faa = facies articularis acrocoracoidea; flx = processus flexorius; htp = sulcus humerotricipitalis; itr = intermediate trochlear ridge; oma = os metacarpale alulare; pac = processus acromialis; pis = processus pisiformis; pmd = processus medialis; ppc = processus procoracoideus; stp = sulcus scapulotricipitalis; vtr = ventral trochlear ridge. Scale bars = 20 mm.

definitive specimens of ?*K. clarki*. Compared with the holotype of *Hokkaidornis abashiriensis*, definitive ?*K. clarki* specimens are only slightly smaller, and UWBM 86869 is also slightly smaller than what would be expected for the sizes of the carpometacarpus and distal humerus of ?*K. clarki*. Whether this size difference is due to sexual dimorphism or the older geological age of the fossil, or whether it is indicative of species-level differences, cannot be said.

Discussion

So far, five species of plotopterids from western Washington State, including the Olympic Peninsula, have been formally named: *Tonsala hildegardae* Olson, 1980, *Olympidytes thieli*

Mayr and Goedert, 2016, *Klallamornis buchanani* (Dyke, Wang, and Habib, 2011), *K. abyssa* Mayr and Goedert, 2016, and ?*K. clarki* Mayr and Goedert, 2016. The smallest and the largest of these—*T. hildegardae* and ?*K. clarki*—are readily separated by their sizes and morphological characters (Mayr and Goedert, 2016, 2018). These two species are also represented by multiple specimens, which include several diagnostic limb elements. *Klallamornis buchanani* and *K. abyssa*, however, are less well known and more difficult to distinguish, and as detailed in the preceding sections, there remains a possibility that these two species represent different size classes of a species that was sexually dimorphic in size (if so, the Japanese species *Copepteryx hexeris* and the larger *C. titan* Olson and Hasegawa, 1996 may likewise represent males and females of the same

species; compare Fig. 2.6, 2.7 with Olson and Hasegawa, 1996, fig. 8).

The tarsometatarsus of *Phocavis maritimus*—which is the holotype and only known skeletal element of the species—differs from that of other plotopterids in plesiomorphic features (Goedert, 1988; Goedert and Cornish, 2002; Mayr and Goedert, 2016, 2018), and all plotopterids except *Phocavis*, *Plotopterum*, and *Stemec* were united in the new taxon Tonsalinae by Mayr and Goedert (2018). In particular, the *Phocavis* tarsometatarsus has a fully enclosed foramen vasculare distale, and the hypotarsus exhibits a distinct sulcus for the tendon of musculus flexor hallucis longus (Mayr et al., 2021, fig. 4g). The reduction of the foramen vasculare distale characterizes the Tonsalinae (Mayr and Goedert, 2018), whereas a sulcus for the tendon of musculus flexor hallucis longus is also present in an undescribed smaller tonsaline plotopterid from early Oligocene rocks in Japan (Mayr et al., 2021, fig. 4i). The tarsometatarsi of the early Miocene *Plotopterum* and the late Oligocene *Stemec* are unknown, but these two taxa exhibit a more plesiomorphic coracoid morphology than tonsaline plotopterids (Mayr and Goedert, 2016, 2018; also compare Fig. 4.4 and 4.6).

Whereas an early divergence of *Phocavis* is well supported, the interrelationships of tonsaline plotopterids are poorly resolved. Of particular interest are the affinities between the North American and Japanese taxa (i.e., the questions as to whether the very large-sized species ?*Klallamornis clarki*, *Hokkaidornis abashiriensis*, *Copepteryx hexeris*, and *C. titan* form a clade and how often giant size evolved in the Plotopteridae).

If the largest plotopterid from the Olympic Peninsula, ?*Klallamornis clarki*, indeed belongs to the taxon *Klallamornis*, very large size would have evolved independently in plotopterids from North America and Japan because *K. buchanani* and *K. abyssa* are both distinctly smaller than ?*K. clarki* and the giant species from Japan. Evolution of large body size in plotopterids may have been triggered by oceanic cooling. The tarsometatarsus of ?*K. clarki* agrees with smaller tarsometatarsi from the Olympic Peninsula, which were assigned to *Olympidytes thieli* (Mayr and Goedert, 2016; Fig. 6.12, 6.13) and *K. buchanani* (UWBM 86870; Dyke et al., 2011), in that the crista hypotarsi is mediolaterally narrow, the incisura lateralis very wide, and the trochlea metatarsi IV shorter than in the equally large-sized taxa *Copepteryx* and *Hokkaidornis* from Japan (Fig. 6.4–6.11). The tarsometatarsus of ?*K. clarki* is furthermore distinguished from that of *Copepteryx* and *Hokkaidornis* in that there is no dorsally open sulcus between the trochleae metatarsorum III and IV. However, these differences between the tarsometatarsus of ?*K. clarki* and the large taxa from Japan may be due to the retention of plesiomorphic features in the North American plotopterids, and at present no unambiguously derived characters are known that support a clade including *K. buchanani*, *K. abyssa*, and ?*K. clarki*.

The "Whiskey Creek specimen" UWBM 86869 is distinguished from the smaller plotopterids from the Olympic Peninsula for which the humerus is known (*T. hildegardae* and UWBM 86871) in that the ventrodistal portion of the bone is broadly rounded. This morphology is shared with *Copepteryx* (the corresponding portion of the humerus of *Hokkaidornis* is damaged). If UWBM 86869 indeed belongs to ?*Klallamornis clarki*, this species is clearly different from smaller plotopterids

from the Olympic Peninsula. The carpometacarpus of the Whiskey Creek specimen also exhibits a more plesiomorphic morphology than that of the giant taxa from Japan, *Copepteryx* and *Hokkaidornis*, in that the processus pisiformis is better developed and the os metacarpale alulare proportionally shorter, with its proximal margin being more clearly offset from the carpal trochlea (Fig. 7.15–7.17).

Irrespective of its exact affinities, the Whiskey Creek specimen, as possibly the oldest known plotopterid (Goedert and Cornish, 2002), shows that very large size was achieved early in the evolution of the Plotopteridae, as it also was in stem group Sphenisciformes (Mayr et al., 2017). Very large-sized plotopterids, that is, specimens of ?*Klallamornis clarki*, are as yet unknown from the later Oligocene rocks of the Pysht Formation (Table 1). The absence of this very large species in the geochronologically youngest plotopterid-bearing strata of the Olympic Peninsula may be of evolutionary significance, but well-based conclusions can be drawn only when more-robust data on the stratigraphic distribution of the plotopterids from the Olympic Peninsula are available.

The femora of *Klallamornis* and *Olympidytes* have a similar shape, whereas the shaft of the femur of *Tonsala hildegardae* is more slender. Although these differences in the proportions of the bone may be functionally related to the different sizes of the involved species, a slender femur and small size are likely to represent the plesiomorphic conditions within tonsaline plotopterids (Mayr and Goedert, 2018). With *Phocavis* being the sister taxon of tonsaline plotopterids (to which all currently known species from Japan belong) and *Tonsala* being the sister taxon of other tonsaline plotopterids of which the femur is known, the interrelationships of plotopterids suggest a North American origin of the clade.

The high diversity of plotopterids in the late Eocene and Oligocene of the North Pacific Basin is notable, and their geographic restriction to the North Pacific calls for an explanation. The fossil record indicates that plotopterids underwent a rapid radiation in the late Eocene. This coincides with profound climatic, environmental, and ecological changes in marine ecosystems in the North Pacific Ocean. Paleogeographic reconstructions of what is today western Oregon and Washington show, due to subduction-related volcanism, the emergence of a succession of mostly small to moderately large volcanic islands far off the coast starting possibly in the late Paleocene and continuing throughout most of the Eocene (e.g., Snavely and Wagner, 1963; Wells and Coe, 1985; Snavely and Wells, 1996). During the Oligocene, most of this offshore volcanism had ceased; islands were eroding, and relatively rapid subduction formed broad offshore basins; and the oceans were cooling. By the early Miocene, the islands were gone, as were most of the plotopterids. Offshore islands and rocks, free of potential terrestrial mammalian predators that were diverse on the North American continent, would have been essential for the evolution and continued survival of flightless birds such as plotopterids (Warheit and Lindberg, 1988). The situation was different on the western side of the Pacific Ocean, with the islands of Japan being separated from Asia comparatively late in the Cenozoic (e.g., Maruyama et al., 1997). Despite this, there were still places where plotopterids were able to breed and nest because plotopterids are known from at least the latest Eocene in Japan.

The origin of highly productive marine biotas in the North Pacific Ocean has been attributed to cooling events during the late Eocene and Oligocene (Vermeij, 2018; Vermeij et al., 2019), but recent molecular analyses also date the radiation of kelp forests in the North Pacific to the Eocene/Oligocene boundary (Starko et al., 2019; Vermeij et al., 2019). Here we hypothesize that the evolution and diversification of plotopterids may have been causally linked to these events. According to Starko et al. (2019), complex kelps originated in the northeast Pacific Ocean, where the earliest and phylogenetically most basal plotopterids evolved. However, whether the diversification of both kelp and plotopterids was related to an increased productivity in marine biotas of this area or whether either was triggered by the other in a coevolutionary process needs to be addressed in future studies. An understanding of plotopterid evolution would be fostered by an improved knowledge of the temporal sequence of the evolution of these birds and by a better-resolved phylogeny, which we aim to analyze in more detail once critical new fossil material has been prepared.

Acknowledgments

References

Ando, T., and Fukata, K., 2018, A well-preserved partial scapula from Japan and the reconstruction of the triosseal canal of plotopterids: PeerJ, v. 6, e5391, https://doi.org/10.7717/peerj.5391

Barnes, L.G., and Goedert, J.L., 2001, Stratigraphy and paleoecology of Oligocene and Miocene desmostylian occurrences in western Washington State, USA: Bulletin of Ashoro Museum of Paleontology, v. 2, p. 7–22.

Dyke, G.J., Wang, X., and Habib, M.B., 2011, Fossil plotopterid seabirds from the Eo-Oligocene of the Olympic Peninsula (Washington State, USA): Descriptions and functional morphology: PLoS ONE, v. 6, n. 25672, https://doi.org/10.1371/journal.pone.0025672

Goedert, J.L., 1988, A new late Eocene species of Plotopteridae (Aves: Pelecaniformes) from northwestern Oregon: Proceedings of the California Academy of Sciences, v. 45, p. 97–102.

Goedert, J.L., and Cornish, J., 2002, A preliminary report on the diversity and stratigraphic distribution of the Plotopteridae (Pelecaniformes) in Paleogene rocks of Washington State, USA, *in* Zhou, Z., and Zhang, F., eds., Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution, Beijing, 1–4 June 2000: Beijing, Science Press, p. 63–76.

Hasegawa, Y., Okumura, Y., and Okazaki, Y., 1977, A Miocene bird fossil from Mizunami, central Japan: Bulletin of the Mizunami Fossil Museum, v. 4, p. 169–171.

Howard, H., 1969, A new avian fossil from Kern County, California: Condor, v. 71, p. 68–69.

Kaiser, G., Watanabe, J., and Johns, M., 2015, A new member of the family Plotopteridae (Aves) from the late Oligocene of British Columbia, Canada: Palaeontologia Electronica, 18.3.52A, 18 p.

Linnaeus, C., 1758, Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis (tenth edition): Holmiae, Laurentius Salvius, 824 p.

Maruyama, S., Isozaki, Y., Kimura, G., and Terabayashi, M., 1997, Paleogeographic maps of the Japanese Islands: plate tectonic synthesis from 750 Ma to the present: The Island Arc, v. 6, p. 121–142.

Mayr, G., 2005, Tertiary plotopterids (Aves, Plotopteridae) and a novel hypothesis on the phylogenetic relationships of penguins (Spheniscidae): Journal of Zoological Systematics and Evolutionary Research, v. 43, p. 61–71.

Mayr, G., 2009, Paleogene Fossil Birds: Heidelberg, Springer, 262 p.

Mayr, G., and Goedert, J.L., 2016, New late Eocene and Oligocene remains of the flightless, penguin-like plotopterids (Aves, Plotopteridae) from western Washington State, USA: Journal of Vertebrate Paleontology, v. 36, e1163573, https://doi.org/10.1080/02724634.2016.1163573

Mayr, G., and Goedert, J.L., 2018, First record of a tarsometatarsus of *Tonsala hildegardae* (Plotopteridae) and other avian remains from the late Eocene/early Oligocene of Washington State (USA): Geobios, v. 51, p. 51–59.

Mayr, G., Goedert, J.L., and Vogel, O., 2015, Oligocene plotopterid skulls from western North America and their bearing on the phylogenetic affinities of these penguin-like seabirds: Journal of Vertebrate Paleontology, v. 35, e943764, https://doi.org/10.1080/02724634.2014.943764

Mayr, G., Scofield, R.P., De Pietri, V.L., and Tennyson, A.J.D., 2017, A Paleocene penguin from New Zealand substantiates multiple origins of gigantism in fossil Sphenisciformes: Nature Communications, v. 8, n. 1927, https://doi.org/10.1038/s41467-017-01959-6

Mayr, G., Goedert, J.L., De Pietri, V., and Scofield, R.P., 2021, Comparative osteology of the penguin-like mid-Cenozoic Plotopteridae and the earliest true fossil penguins, with comments on the origins of wing-propelled diving: Journal of Zoological Systematics and Evolutionary Research, v. 59, p. 264–276.

Mori, H., and Miyata, K., 2021, Early Plotopteridae specimens (Aves) from the Itanoura and Kakinoura Formations (latest Eocene to early Oligocene), Saikai, Nagasaki Prefecture, western Japan: Paleontological Research, v. 25, p. 145–159.

Nesbitt, E.A., Martin, R.A., Carroll, N.P., and Grieff, J., 2010, Reassessment of the Zemorrian foraminiferal stage and Juanian molluscan stage north of the Olympic Mountains, Washington State and Vancouver Island: Newsletter on Stratigraphy, v. 43, p. 275–291.

Ohashi, T., and Hasegawa, Y., 2020, New species of Plotopteridae (Aves) from the Oligocene Ashiya Group of Northern Kyushu, Japan: Paleontological Research, v. 24, p. 285–297.

Olson, S.L., 1980, A new genus of penguin-like pelecaniform bird from the Oligocene of Washington (Pelecaniformes: Plotopteridae): Natural History Museum of Los Angeles County, Contributions in Science, v. 330, p. 51–57.

Olson, S.L., and Hasegawa, Y., 1985, A femur of *Plotopterum* from the early middle Miocene of Japan (Pelecaniformes: Plotopteridae): Bulletin of the National Science Museum, ser. C, v. 11, p. 137–140.

Olson, S.L., and Hasegawa, Y., 1996, A new genus and two new species of gigantic Plotopteridae from Japan (Aves: Plotopteridae): Journal of Vertebrate Paleontology, v. 16, p. 742–751.

Sakurai, K., Kimura, M., and Katoh, T., 2008, A new penguin-like bird (Pelecaniformes: Plotopteridae) from the Late Oligocene Tokoro Formation, northeastern Hokkaido, Japan: Oryctos, v. 7, p. 83–94.

Shimada, K., Welton, B.J., and Long, D.J., 2014, A new megamouth shark (Lamniformes: Megachasmidae) from the Oligocene–Miocene of the western United States: Journal of Vertebrate Paleontology, v. 34, p. 281–290.

Smith, N.D., 2010, Phylogenetic analysis of Pelecaniformes (Aves) based on osteological data: implications for waterbird phylogeny and fossil calibration studies: PLoS ONE, v. 5, e13354, https://doi.org/10.1371/journal.pone.0013354

Snavely, P.D., Jr., and Wagner, H.C., 1963, Report of Investigations No. 22: Tertiary Geologic History of Western Oregon and Washington: Olympia, Washington, State of Washington, Department of Mines and Geology, 23 p.

Snavely, P.D., Jr., and Wells, R.E., 1996, Cenozoic evolution of the continental margin of Oregon and Washington: U.S. Geological Survey Professional Paper no. 1560, p. 161–182.

Starko, S., Gomez, M.S., Darby, H., Demes, K.W., Kawai, H., Yotsukura, N., Lindstrom, S.C., Keeling, P.J., Graham, S.W., and Martone, P.T., 2019, A comprehensive kelp phylogeny sheds light on the evolution of an ecosystem: Molecular Phylogenetics and Evolution, v. 136, p. 138–150.

Vermeij, G.J., 2018, Comparative biogeography: innovations and the rise to dominance of the North Pacific biota: Proceedings of the Royal Society B, v. 285, n. 20182027, https://doi.org/10.1098/rspb.2018.2027

Vermeij, G.J., Banker, R., Capece, L.R., Hernandez, E.S., Salley, S.O., Vriesman, V.P., and Wortham, B.E., 2019, The coastal North Pacific: origins and history of a dominant marine biota: Journal of Biogeography, v. 46, p. 1–18.

Warheit, K.I., and Lindberg, D.R., 1988, Interactions between seabirds and marine mammals through time: interference competition at breeding sites, *in* Burger, J., ed., Seabirds and Other Marine Vertebrates: Competition, Predation and Other Interactions: New York, Columbia University Press, p. 292–328.

Wells, R.E., and Coe, R.S., 1985, Paleomagnetism and geology of Eocene volcanic rocks of southwest Washington, implications for mechanisms of tectonic rotation: Journal of Geophysical Research, v. 90, p. 1925–1947.