OLIGOcene PLOTOPTeridaE SKULLS FROM WESTERN NORTH AMERICA AND THEIR BEARING ON THE PHYLOGENETIC AFFINITIES OF THESE PENGUIN-LIKE SEABIRDS

Gerald Mayr, a,1 James L. Goedert, 2 and Olaf Vogel 3

1 Ornithological Section, Senckenberg Research Institute and Natural History Museum Frankfurt, 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, U.S.A., jgoedert@u.washington.edu;
3 Geological Preparation Laboratory, Senckenberg Research Institute and Natural History Museum Frankfurt, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany, Olaf.Vogel@senckenberg.de

ABSTRACT—Plotopterids are penguin-like, wing-propelled birds with controversial phylogenetic affinities. They are usually regarded as closely related to Sulidae (gannets, cormorants, and allies), with the penguin-like features considered to be of convergent origin. However, it has also been proposed that the similarities shared by plotopterids and penguins are due to common ancestry. An in-depth assessment of plotopterid affinities has been hampered by the fact that very little data about the skull of these birds were available. New fossils of Tonsala from the Oligocene Pysht Formation in Washington State (U.S.A.) include the first well-preserved cranial remains of this taxon. They show that although plotopterid share derived cranial features with members of Sulidae that are absent in species of Sphenisciformes (penguins), they lack diagnostic derived features of the representatives of crown group Sulidae. To assess the affinities of plotopterids, we performed a phylogenetic analysis that included, for the first time, early stem group representatives of Sphenisciformes, resulting in a sister-group relationship between Plotopteridae and Sulidae. Intriguingly, however, our reanalysis of the emended data of a more comprehensive recent analysis that supported a position of Plotopteridae within Sulidae recovered a sister-group relationship between Plotopteridae and Suloidea. Although cranial morphology challenges the hypothesis of close affinities between plotopterids and penguins, more data on early stem lineage representatives of penguins are needed for a robust placement of Plotopteridae relative to Sphenisciformes.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

The extinct Plotopteridae were wing-propelled, flightless seabirds; their fossils have been found in late Eocene to early middle Miocene rocks of Japan and western North America (e.g., Howard, 1969; Olson and Hasegawa, 1979, 1985, 1996; Olson, 1980; Goedert, 1988; Goedert and Cornish, 2002; Sakurai et al., 2008; Dyke et al., 2011). These birds appear to have been fairly diverse in the late Eocene/Oligocene Makah and Pysht formations of the Olympic Peninsula in Washington State, U.S.A. (Goedert and Cornish, 2002); however, only two species have been described from these localities, the Oligocene Tonsala hildegardiae Olson, 1980, and the coeval but larger T. buchanani Dyke et al., 2011.

Plotopterids possessed flipper-like wings that would closely resemble those of extant penguins (Sphenisciformes), a similarity that was attributed to convergence due to the functional constraints imposed on wing-propelled diving (Olson and Hasegawa, 1979, 1996; Olson, 1980). Olson (1980) classified plotopterids into the taxon Sulidae, which includes Sulidae (gannets and boobies), Anhingidae (anings), and Phalacrocoracidae (cormorants). Mayr (2005, 2009), by contrast, hypothesized that Plotopteridae are the sister taxa of Sphenisciformes, and a phylogenetic analysis resulted in a sister-group relationship between the clade (Plotopteridae + Sphenisciformes) and

Suloidea (Mayr, 2005). In order to account for the results of molecular analyses (see below), Mayr (2009) emended this hypothesis to a sister-group relationship between the clades (Plotopteridae + Sphenisciformes) and (Fregatidae + Suloidea).

The hypothesis of close affinities between Plotopteridae and Sphenisciformes was met with skepticism (Sakurai et al., 2008; Kawabe et al., 2014), and was not supported by a comprehensive analysis of 464 morphological characters (Smith, 2010) that resulted in a sister-group relationship between Plotopteridae and Phalacrocoracidae and Anhingidae. Virtual brain endocasts of plotopterids, by contrast, resemble those of penguins in overall shape and some derived features, including a very large flocculus (Kawabe et al., 2014).

At the time the hypothesis of spheniciform affinities of plotopterids was presented (Mayr, 2005), the early history of penguins was little known. Since then, several early Paleogene stem group Sphenisciformes have been described, of which the two species of the taxon Waimanu from the early Paleocene of New Zealand are the oldest and earliest diverging representatives (Slack et al., 2006; Ksepka and Ando, 2011). In the past few years, new molecular analyses have further provided a framework for the interrelationships of modern birds, although the affinities of penguins remain controversial (Fig. 1). Sphenisciformes have often been considered most closely related to Procellariiformes (tubenoses and allies) based on morphological analyses (for example, Livezey and Zusi, 2007; Ksepka and Ando, 2011). A clade including these two taxa has been supported by analyses of nuclear gene
sequences (Hackett et al., 2008; McCormack et al., 2013; Yuri et al., 2013) and complete mitochondrial genomes (Gibb et al., 2013). Another analysis of complete mitochondrial genomes, however, supported a sister-group relationship between Sphenisciformes and Ciconiidae (Pacheco et al., 2011), but in that analysis only a limited sample of taxa traditionally considered members of ‘Pelecaniformes’ was included. Earlier analyses of molecular data resulted in a sister-group relationship between Sphenisciformes and a clade including Fregatidae and Sulidae (nuclear beta-fibrinogen sequences; Fain and Houde, 2004), or in a sister-group relationship between the clades (Phaethontidae + Sphenisciformes) and (Fregatidae + Sulidae) (Brown et al., 2008).

Aside from these uncertainties surrounding the early evolution and phylogenetic position of penguins, a well-founded assessment of the affinities of plotopterids has been impeded by the limited amount of information available on the cranial anatomy of these birds. Although plotopterid skulls from the late Oligocene of Japan were figured by Hasegawa et al. (1979) and Kawabe et al. (2014), these specimens have not yet been described, and the published figures do not allow the recognition of critical osteological details. The only previously described cranial material of North American plotopterids are mandible fragments of Tonsala (Goedert and Cornish, 2002; Dyke et al., 2011). Here we describe well-preserved partial skulls of Tonsala from Oligocene rocks of Washington State and revise the phylogenetic affinities of plotopterids. Furthermore, Waimanu and plotopterids are for the first time considered together in a phylogenetic analysis, and new scorings for plotopterids are added to the revised character matrix of Smith (2010) to evaluate their influence on the resulting tree topology.

**MATERIALS AND METHODS**

The new fossils were prepared with a 4% solution of formic acid buffered with tricalcium phosphate (e.g., Jeppsson and Anehus, 1995). If not indicated otherwise, anatomical terminology follows Baumel and Witmer (1993). Skeletons of the following extant taxa were examined (all in the collection of Senckenberg Research Institute Frankfurt): Galliformes: Megapodius freycinet, Crax alector, Gallus gallus, Meleagris gallopavo, Numida meleagris, Phasianus colchicus. Opisthocomidae: Opisthocomus hoazin. Ardeidae: Agamia agami, Ardea (cinerea, goliath, herodias, purpurea), Ardeola (grayii, idae, ralloides), Botaurus stellaris, Bubulcus ibis, Butorides striatus, Casmerodius albus, Cochlearius cochlearius, Egretta (garzetta, gularis, picata, sacra, thula), Ixobrychus (eurythmus, minutus), Nycticorax nycticorax, Syrigma sibilatrix. Ciconiidae: Anastomus (lamelligerus, oscitans), Ciconia (abdimii, boyciana, ciconia, nigra), Ephippiorhynchus (asiaticus, senegalensis), Leptoptilos crumeniferus, Mycteria (leucocephala, ibis). Threskiornithidae: Eudocimus (albus, ruber), Geronticus (calvus, eremita), Hagedashia hagedash, Lophotibis cristata, Platalea (ajaia, alba, leucorodia, minor), Plegadis (falcinellus, rigdwayi), Threskiornis (aethiopicus, melanophris), Threskiornis (melanocephalus). Gaviidae: Gavia stellata. Diomedieidae: Diomedea (cauta, melanophris, epomophora, exulans), Phoebetria fusca. Oceanitinae: Fregetta tropica, Pelagodroma...
In order to assess the affinities of the affinites, we performed an analysis based on the revised and emended character matrix of Mayr (2005), with 34 new characters (characters 8–10, 16, 19, 25–29, 31, 32, 36, 39, 40, 45, 46, 50, 53, 55–57, 59–65, 71, 73, and 92–94 in Appendix S1) added and eight characters deleted (characters 15, 22, 23, 34, 37, 38, 48, and 55 of Mayr, 2005). Altogether, 94 characters were scored for 20 ingroup taxa; three characters (31, 49, and 66 in Appendix S1) were coded as additive. Outgroup comparisons were made with Galliformes and Otidisciformes. Linnofregata was scored after Olson (1977). Olson and Matsuoika (2005), and Smith (2010), Ecryptes after Ksepka et al. (2008), and Waimanu after Slack et al. (2006). Plotopteridae were scored as a composite taxon based on Tonsala, Copeteryx, and Hokkaidornis. We explicitly stated if a character scoring is based on a plotopterid taxon other than Tonsala hildegardae or the T. buchanani holotype. The usage of composite supraspecific taxon was considered a substantial option (e.g., Brusatte, 2010). However, we consider it to be justified in the case of Plotopteridae, because monophyly of a clade including Tonsala, Copeteryx, and Hokkaidornis is well established (Smith, 2010), and disregarding size and bone proportions, these three taxa exhibit a very similar osteology and are not expected to differ in the features scored in the analysis.

We further added scorings for Tonsala to the analysis of Smith (2010), and corrected some erroneous scorings for other taxa included in that analysis (see Appendix S5). The new phylogenetic analyses were performed with the heuristic search module of NONA 2.0 (Goloboff, 1993) through the WINCLADA 1.00.08 interface (Nixon, 2002), using the commands hold 10000, mult*1000, hold/10, and max*. The consistency index (CI) and retention index (RI) were calculated, as well as bootstrap support values with 1000 replicates, 10 searches holding 10 trees per replicate, and tree bisection and reconnection (TBR) branch swapping without max*.

**Institutional Abbreviations**—SMF, Senckenberg Research Institute and Natural History Museum Frankfurt, Germany; UWBM, Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington, U.S.A.

**SYSTEMATIC PALAEOONTOLOGY**

AVES Linnaeus, 1758

PLOTPTERIDAE Howard, 1969

TONSALA Olson, 1980

**TONSALA HILDEGARDAE** Olson, 1980

**Referred Specimens**—SMF Av 599 (Figs. 2–4; partial skull including caudal part of upper beak and mandibles, both ossa palatina, and ventral portion of right quadrate), collected in 1989 by J.L.G. SMF Av 600 (Figs. 5, 6; poorly preserved partial skull including braincase fragments, caudal portion of upper beak, and caudal portions of both mandibles [the right ramus mandibulae is broken and its caudal end is displaced]), collected in 1985 by J.L.G. SMF Av 601 (Fig. 7; largely complete cervical vertebra and craniodorsal fragment of another cervical vertebra, left ulna lacking the distal end, damaged right femur, both tibiotarsi, and unidentified bones [?rib fragment and ?synsacrum fragments]), collected in 2008 by J.L.G.

**Locality and Horizon**—All specimens are float concretions that eroded from the beach terrace and low banks west of the mouth of Murdock Creek, south shore of Strait of Juan de Fuca, Clallam County, Washington, U.S.A. (GPS data: SMF Av 599: 48.1567° N, 123.8696° W; SMF Av 600: 48.1545° N, 123.8655° W; SMF Av 601: 48.1558° N, 123.8685° W); lower part of Pysht Formation, latest early Oligocene/early late Oligocene (Barnes and Goedert, 2001; Barnes et al., 2001; Prothero et al., 2001), or late Oligocene (Nesbitt et al., 2010).

**Measurements (in mm)**—SMF Av 599: maximum length as preserved, 121.6; width of upper beak at base (on level of insertion of jugal bars), 29.8; medial nasal bar, width at base, 19.0; palatines, width across angularis caudalateralis, 33.8; right ramus mandibulae, maximum dorsoventral depth, 26.3.

SMF Av 600: maximum length of skull as preserved, 156.7; minimum width of interorbital section, 25.9; width across processes postorbitales, 45.2; width of upper beak at base (on level of insertion of jugal bars), 28; medial nasal bar, width at base, 21.1; width of upper beak at nasofrontal hinge, 31.0; left ramus mandibulae, maximum dorsoventral depth, 26.0.

SMF Av 601: Cervical vertebra, maximum length, 27.4; maximum cranial width as preserved, 25.3. Left ulna, length as preserved, 54.5; proximal end, cranio-caudal depth, 16.7; proximal end, dorsoventral width, 12.4. Right femur, maximum length as preserved, 109.4; width of distal end as preserved, 20.4. Right tibiotarsus, maximum length as preserved, 155.0; minimum width of shaft, 11.4; distal width, 21.0. Left tibiotarsus, maximum length as preserved, 161.5.

**Remarks on Taxonomy and Taphonomy**—Our identification of the two skulls as belonging to Plotopteridae is supported by the great similarity of the specimens to figured but undescribed plotopterid skulls from Japan (Kawabe et al., 2014). No large birds other than plotopterids are known from the Pysht Formation, and the only plotopterid species of similar size belong to the taxa Tonsala. The two named plotopterid species from the Pysht Formation differ in size, with Tonsala buchanani being about 1.3 times larger than T. hildegardae. With the exception of the T. buchanani holotype, all of the described plotopterid specimens from the Pysht Formation are from T. hildegardae, and based on size and morphology of the bones, SMF Av 601 can also be referred to this latter species (the length of the femur is 109.4, versus 106.5 in T. hildegardae and 134.2 in T. buchanani; Dyke et al., 2011). Assuming that T. hildegardae had similar proportions to the King Penguin (Aptenodytes patagonicus), the two skulls fit the bones of SMF Av 601 in size and are also assigned to T. hildegardae rather than to the much rarer and larger T. buchanani.

A revision of the plotopterid material from the Makah and Pysht Formations described by Dyke et al. (2011) is beyond the scope of the present study. We note, however, that of the specimens assigned to T. buchanani by Dyke et al. (2011), UWBM 88689 (Whiskey Creek specimen) and UWBM 88675 (holotype) are demonstrably as much as 5 million years different in age (Goedert and Cornish, 2002:fig. 2), with the Whiskey Creek specimen being possibly the oldest known plotopterid from North America (Goedert and Cornish, 2002). The bone labeled as a pterygoid of UWBM 88689 by Dyke et al. (2011:fig. 2A) is actually a vertebra, although a pterygoid is present and was listed by Goedert and Cornish (2002). Morphological differences between the distal ends of the humeri of UWBM 88689 and
FIGURE 2. Partial skull with mandibles of *Tonsala hildegardae* from the Oligocene Pysht Formation of Washington State, U.S.A. (SMF Av 599) in A, B, dorsal, C, D, distal, E, ventral, F, right lateral, and G, left lateral views. Specimen in B coated with ammonium chloride to enhance contrast. In D, the matrix was digitally removed and the mandibles were brought in their correct anatomical positions. **Abbreviations:** ccv, caudodorsal portion of cranial cavity; cor, processus coronoides; cvx, convex bulge on ventral surface of upper beak; gap, midline gap between ossa maxillaria; lmd, left ramus mandibulae; max, os maxillare; nas, nasal bar; nfh, nasofrontal hinge; nas, nasal bar; nos, nostril; nvs, longitudinal neurovascular sulci (along lateral surfaces of upper beak and mandible, respectively); pal, os palatinum; qdr, ventral portion of right quadrate; rmd, right ramus mandibulae; smd, marked fossa along ventral section of medial mandibular surface; sul, sulcus along tomium maxillare; tmd, tomium mandibulare; tmx, tomium maxillare; uib, unidentified rod-like bone. Scale bars equal 50 mm, same scale for A, B, and E–G.
another specimen that was referred to *T. buchanani* by Dyke et al. (2011), UWBM 86871 (Makah Formation, Jansen Creek Member, early? Oligocene), also indicate that these are likely different taxa (Goedert and Cornish, 2002). Dyke et al. (2011) acknowledged these differences, but nevertheless included UWBM 86869 and UWBM 86871 in *T. buchanani*. Morphological disparity of the distal humerus of the *T. hildegardae* holotype ( Olson, 1980) and UWBM 86871 further seems to indicate a different taxon at the genus level. The ulna and scapula are preserved in the partial skeleton UWBM 86871 (Goedert and Cornish, 2002) and provide important additional data, but even though the proximal ulna was figured by Dyke et al. (2011: fig. 2M), it was identified as the proximal end of a radius, and the scapula was not mentioned by Dyke et al. (2011). Therefore, pending a thorough restudy of these fossils along with newly available specimens undergoing preparation, we currently recognize only the holotype specimen (UWBM 86875) as *T. buchanani*; the others that were referred to *T. buchanani* (UWBM 86869, 86870, and 887871) are herein regarded as Plotopteridae incertae sedis.

Like other bones from the same part of the Psyt Formation (Goedert et al., 1995; Kiel et al., 2010; Goedert and Cornish, 2002), the present fossils were heavily damaged prior to fossilization. Boreholes of the marine annelid *Osedax*, like those reported on other plotopterid bones from the Psyt Formation (Kiel et al., 2011), are visible on most bones of SMF Av 601. Notably, some of the bones of this specimen also exhibit distinct parallel scratches on the bone surface (Fig. 7R); these are not preparation artifacts and probably represent traces of marine scavengers. Similar scratches were noted on *Osedax*-damaged fossil whale teeth (Kiel et al., 2013) from this same part of the Psyt Formation. The nodules that held SMF Av 601 also contained a tooth of a cow shark (*Hexanchidae*), and we consider it possible that some of the breakage of the bones—albeit not the scratches on the bone surfaces—is due to the fact that sharks were feeding on the carcasses. In specimen SMF Av 600, fecal pellets of an invertebrate are preserved within the right antorbital fenestra, and these have also been found in association with other plotopterid bones from the Psyt Formation (Goedert and Cornish, 2002).

**Description and Comparisons**—The dimensions of the skulls correspond to those of a large albatross (e.g., *Diomedea epomophora*), thus surpassing the skull size of all extant sulioideans. The beak is not completely preserved in the new specimens, but an undescribed fossil from Japan shows that it was proportionally longer in plotopterids than in most extant sulioideans (Kawabe et al., 2014: fig. 1). The upper beak of *Tonsala* is dorsoventrally very low, as in frigatebirds and pelicans, with a wide nasal bar as in species of Pelecanidae, Fregatidae, and Sulidae, but unlike in sphenisciforms, in which the nasal bar is narrow (Figs. 2, 3). One of the most notable features is the presence of very long, slit-like nostrils, as in the early Eocene taxa *Limnofregata* (Fregatidae) and *Prophaethon* (Phaethontidae; Harrison and Walker, 1976). In extant species of Fregatidae and Sulidae, by contrast, the nostrils are reduced to very small caudal foramina or are completely absent (Sulidae), but a longitudinal furrow still denotes the fused narial openings. Unlike in extant sulioideans and all other ‘pelecaniform’ birds, the caudal sections of the paired osa maxillaria of *Tonsala* are not fused together mediad, so that the ventral surface of the beak is less heavily ossified and a midline gap is visible (Fig. 2D), which is, however, relatively narrower than in sphenisciforms. The ventral surface of the upper beak is further not flat but has sulci along the tomia (as in frigatebirds and sulids, but unlike in phalacrocoracids and anhingas), and the medially adjacent part forms a markedly convex bulge (Fig. 2C, D). On the lateral side of the upper beak, there is a narrow neurovascular sulcus just above the tomium (Fig. 2F).

The well-preserved osa palatina of SMF Av 599 (Figs. 2, 4) do not exhibit the unique and diagnostic derived shape of the palatines of extant sulioideans, which form an essentially rectangular, dorsally flat platform (Fig. 3B). In overall shape, they more closely resemble the palatine bones of sphenisciforms than those of sulioideans (Fig. 3), but there are some differences in detail. Whereas the palatines of sulioideans are of equal width over their entire length, the osa palatina of *Tonsala* widen caudally, with...
FIGURE 4. Partial skull of *Tonsala hildegardae* from the Oligocene Pysht Formation of Washington State, U.S.A. (SMF Av 599). A, detail of partial skull in dorsal view; B, detail of palatal area in ventral view; C, detail of left lateral view; D, upper beak in caudal view; E, bone fragment that is tentatively identified as the caudodorsal portion of cranial cavity; F, detail of right mandible (lateral view) in comparison with the mandible of *G. Phalacrocorax carbo* (ventral lamina of os dentale removed); H, ventral portion of right quadrate in ventral view, in comparison with the quadrates of I, *Sula bassana* ( Sulidae) and J, *Spheniscus humboldti* (Sphenisciformes). Fossil specimens were coated with ammonium chloride. Abbreviations: cdc, condylus caudalis; cdl, condylus lateralis; cdm, condylus medialis; cer, fossa of cerebral hemisphere; cho, choana; den, dorsal lamina of os dentale; fap, hook-like facies articularis pterygopalatini; fos, fossa on ventral surface of processus mandibularis; iom, internal ossification of Meckel's cartilage; jug, os jugale; nvs, neurovascular furrow along lateral surface of mandible; oss, ossicle on rostral end of os jugale; plt, plate-like bone ventromedially adjacent to jugal bar; pmp, processus maxilopalatinus; scl, scleral ossicle; soc, sulcus for occipital sinus; uib, unidentified rod-like bone; vpn, ventral process of os nasale. Scale bars equal 10 mm.
the pars lateralis being wider than in sulidoideans and the angulus caudolateralis more pronounced (Fig. 3). Furthermore, the lamella chaoanalis (lamella dorsalis sensu Zusi and Livezey, 2006) extends over more than half of the length of the palate (exclusive of the pars maxillaris), whereas it is restricted to its rostral portion in sulidoideans. As in sulidoideans, the lamellae choanales are rostrally fused and do not form a processus chaoanalis or a cornu nasale palatini (terminology after Zusi and Livezey, 2006); a processus vomeralis is absent. Both ossa palatina are closely conjoined, but unlike in sulids and anhingas, they do not appear to have been fused in their caudal section, where a suture between the lamellae dorsales is visible. The dorsal surface of the palatines is sculptured; the ventral surface is slightly convex with the lateral portions being dorsoventrally bent. As in sulids but unlike in anhingas and phalacrocoracids, the trough for articulation with the rostrum paraphenoideal is restricted to the caudal portion of the palatines. The processus pterygoideus is short, and the dorsoventrally wide and convex facies articulares pterygoopalatini forms a distinct dorsal hook as in the species of Podicipediformes (Fig. 4A, B). Only the caudalmost portion of the crista ventralis (lamina ventralis choanalis sensu Zusi and Livezey, 2006) is visible in SMF Av 599. As in sulidoideans but unlike in frigatebirds and sphenisciforms, a vomer is absent (SMF Av 599).

In SMF Av 599, sheet-like processus maxillopalatini (processus palati maxillaris sensu Zusi and Livezey, 2006) are preserved (Fig. 4D). The nasofrontal hinge (Figs. 2B, 6A) is a rostrocaudally extensive bending zone as in phalacrocoracids rather than a sharply delimited hinge as in sulids and anhingas. An os lacrymale is not preserved, and in SMF Av 600, the corresponding area of the skull does not show articulation facets for this bone (overall, however, this region of the skull is rather poorly preserved). In SMF Av 599, there is a small dorsal tuberosity on the rostral end of the right os jugale and an oscille on the left one (Fig. 4C); whether this represents a homologue to the os supragnagale of sulidoideans is uncertain. A plate-like, elongated bone ventromedially adjacent to the jugal bar (Fig. 4D) is identified as a caudal process of the tomium of the upper beak, which is absent in extant sulidoideans. In caudal view into the beak, two ventral processes of the nasal bar are visible (Fig. 4D).

In SMF Av 599, only a fragment of the braincase is preserved, which is here tentatively identified as the caudodorsal portion of the cranial cavity. The fragment exposes the interior surface and two fossae can be discerned, which are separated by a marked sulcus (Fig. 4E). These structures are interpreted as the fossae for the two cerebellar hemispheres and the sulcus for the occipital sinus, which is very prominent in plothopterids (Kawabe et al., 2014). The braincase of SMF Av 600 is more complete, but the caudal portion is crushed and the poor preservation of the fossil does not allow the recognition of many osteological details (Figs. 5, 6). In its proportions, the braincase of Tonsala closely matches those of sulids, and as in the latter but unlike in sphenisciforms, the interorbital section is wide and there are no supraorbital fossae for glandulae nasales (Fig. 6). The processus postorbitales appear to have been short in SMF Av 600, but these processes may be broken because they are better developed in a plothopterid skull figured by Kawabe et al. (2014:fig. 1). In SMF Av 600, the cranial margins of the fossae temporales are preserved, and these are sigmoidally curved as in sulids (Fig. 6A); as shown by the undescribed skull figured by Kawabe et al. (2014:fig. 1), the temporal fossae of plothopterids were well developed. The crushed caudal portion of the cranium of SMF Av 600 is difficult to interpret owing to its poor preservation, and it is to be hoped that future radiographic investigations will shed more light on the identity of the bones. Clearly visible is the caudodorsally projected left processus paroccipitalis, as well as the dorsal rim of the left otic cavity. A circular foramen in the left caudolateral portion of the cranium (Fig. 5D) may represent the dorsal opening of the recessus tympanicus dorsalis.

SMF Av 599 includes the ventral portion of the right quadrate. As in sulids but unlike in sphenisciforms, there is a deep fossa on the ventral surface of the processus mandibularis (Fig. 4H–J). The condylus caudalis is mediolaterally broad as in sulids, but the condylyus lateralis and the condylyus medialis are less splayed. The medial surface of the condylyus medialis is concave; unlike in sulids and members of crown group Sphenisciformes, however, there is no distinctly concave articulation facet lateral of this condyle.

The preserved portions of the mandibles agree with the mandible of sulids in proportions. The mandibular ramus deepens in the midsection, and the dorsal portion of its lateral surface exhibits a distinct longitudinal neurovascular sulcus, perpendicular to which dendrite-like smaller furrows diverge, as in phalacrocoracids and sulids (SMF Av 599; Fig. 4F). The medial mandibular surface bears a marked fossa along its ventral section (SMF Av 599; Fig. 2D), with such a fossa being also present in species of Fregatidae, Sulidae, Phalacrocoracidae, Gaviidae, and the late Eocene sphenisciform Perhydrol (Ksepka and Clarke, 2010). The dorsal surface of the tomium is ridge-like and not planar as in sulids (Fig. 2D). There are no fenestrae mandibulare. The os dentale is deeply forked caudally, with a well-developed dorsal lamina (sensu Zusi and Warheit, 1992:fig. 1). There also appears to have been an internal ossification of Meckel’s cartilage as in extant frigatebirds and sulidoideans, in which this ossification is associated with an intraramal joint (Fig. 4F; Zusi and Warheit, 1992). The processus coronoides is well defined and marked (Fig. 2F). The articular end of the mandible is best visible in SMF Av 600 and closely resembles that of extant sulids. As in the latter, it is caudally truncate, with a concave caudal surface, and unlike in sphenisciforms, there is no caudally prominent processus retroarticularis and the processus mediialis is developed as a dorsoventrally deep crest (this process is narrow and pointed in sphenisciforms; Fig. 64D–F). Also as in sulids, the cotyla lateral is markedly concave and forms a distinct notch (Figs. 5F, 6H). On the ventral surface, there is a sharp ridge, which is medially bordered by a fossa (Fig. 6D).

In SMF Av 599, two rod-like bones are preserved (Figs. 2E, 4B), and even though these are situated in the appropriate anatomical position, they are too large and straight to be osa ceratabranchiali of the hyoid apparatus. Likewise, the morphology of these bones does not suggest them to be jugal bars, and they are too long for sphenoid rami.

The nodule containing these bones of SMF Av 601 also included a caudal cervical vertebra, which is probably vertebra 10, 11, or 12 (if compared with sulidoideans) or 7, 8, or 9 (if compared with sphenisciforms), as well as a fragment of the craniodorsal portion of another cervical vertebra (Fig. 7A–F). The more complete vertebra (Fig. 7A–D) lacks the zygaphyses craniales, ansae costotransversariae, and processus caroticus, and some edges of the bone are broken or damaged. Because the bone was completely encased in matrix, all of the damage to this and the other bones in the nodule occurred prior to embedding in the sediment and may indicate action of a predator or scavenger (see above). The vertebrae are only slightly larger than the caudal thoracic vertebrae of Sula bassana and Aptenodytes patagonicus (Fig. 7G, H). They exhibit a rather generalized morphology and differ from the caudal cervical vertebrae of both sphenisciforms and sulidoideans. In the fragmentary vertebra, the articulation facet of the left zygaphysis cranialis is preserved and matches that of sphenisciforms (in sulidoideans this facet is less horizontally oriented). As in sphenisciforms but unlike in sulidoideans, the cranial rim of the arcus vertebrae is deeply concave. The processus spinosus forms a very low ridge. On the lateral surface of the corpus, there is a shallow, elongate fossa. The zygaphysis caudales are short, the lacuna interzygapophysialis is broadly rounded; the torus dorsalis is low, and there is no crista transverso-oblquia. A processus ventralis is absent. The ventral
FIGURE 5. A–C, Partial skull of *Tonsala hildegardae* from the Oligocene Pysht Formation of Washington State, U.S.A. (SMF Av 600), upper skull in A, dorsal, B, left lateral, and C, right dorsolateral views. D, detail of caudal portion of cranium in dorsal view; F, G, proximal ends of mandible. Abbreviations: *cre*, crest formed by processus medialis; *ftp*, cranial border of fossa temporalis; *jug*, os jugale; *lmd*, left mandible; *ntc*, notch formed by cotyla lateralis; *par*, processus paroccipitalis; *ppo*, processus postorbitalis; *rmd*, right mandible; *rtd*, recessus tympanicus dorsalis. Scale bars equal 50 mm in A–D and 20 mm in F and G.
FIGURE 6. A, Partial skull of Tonsala hildegardae from the Oligocene Pysht Formation of Washington State, U.S.A. (SMF Av 600) in comparison with the skull of Sula capensis (Sulidae; B) and Spheniscus demersus (Sphenisciformes; C); D–F, proximal end of left mandible in ventral view of D, T. hildegardae (SMF Av 600), E, S. capensis, and F, S. demersus; G, H, proximal ends of right mandibles in lateral view of G, S. capensis and H, T. hildegardae (SMF Av 600). Abbreviations: cre, crest formed by processus medialis; fgn, fossa glandulae nasalis; ftp, fossa temporalis; ftp(cr), cranial border of fossa temporalis; ifo, interorbital section of os frontale; nfh, nasofrontal hinge; nos, nostril; ntc, notch formed by cotyla lateralis; par, processus paroccipitalis; rdg, ridge on ventral surface of proximal end of mandible. Scale bars equal 50 mm in A–C and 20 mm in D–H.
surface of the corpus vertebrae is wide as in sulidoines and not narrow as in sphenisciforms. The facies articulares cranialis et caudalis are heterocoelous, and the facies articulares cranialis is not as deeply concave as in sphenisciforms.

The ulna of Tonsala hildegardeae was described by Olson (1980), and in its proportions and overall shape, the bone is remarkably similar to the ulna of Waimanu. The new specimen (SMF Av 601; Fig. 7I–K) lacks the distal end and the processus condylaris dorsalis. It matches the description of the T. hildegardeae holotype except that the row of eleven pits for the attachment of feather quills is less strongly marked. The cotyla dorsalis has a slightly convex plane, as noted by Olson (1980), and is more elevated than the cotyla ventrais. The low and caudally situated olecranon forms a rounded knob; on its ventral surface, there is a marked fossa. The cranial surface of the shaft is rounded, whereas the caudal surface forms a ridge.

The femur (SMF Av 601; Fig. 7L, M) agrees well in size and morphology with a femur of T. hildegardeae described by Goedert and Cornish (2002). The specimen is badly damaged, with the caput femoris and the medial portion of the proximal half of the shaft being broken. As already detailed by Goedert and Cornish (2002), the bone is much more elongated and slender than the femora of the plotopterid taxa Copepteryx and Hokkaidornis. The distal section of the shaft has a flat medial surface, which is oriented perpendicular to the cranial and caudal planes of the bone, so that the cross-section of the distal femur shaft is nearly rectangular. The sulcus patellaris is wide and shallow. Unlike in sulidoines but as in sphenisciforms, the fossa poplitea is deeply excavated (Fig. 7N, O). The crista supracondylaris medialis is distinct and sharply defined.

Only fragmentary proximal ends of the tibiotarsi of Tonsala were previously known (Goedert and Cornish, 2002; Dyke et al., 2011). In SMF Av 601, both tibiotarsi are preserved, with the right one being nearly complete, except for some breakage on the proximal end (Fig. 7P–V). The left tibiotarsus, however, is severely damaged, with extensive areas of the shaft being broken; the caudal surface of the shaft exhibits numerous parallel scratches (Fig. 7R; see above). The marked length difference between the left and right tibiotarsi is due to the fact that the left bone is broken, with the fragments of the distal fourth being misaligned (as a result of preservation, not preparation). The tibiotarsus of Tonsala is proportionally more slender than that of Copepteryx, and is also much more elongated than the tibiotarsi of sulids. Most of the crista cnemialis cranialis is broken, but its preserved distal section is unusually well developed and reaches far down the tibiotarsus shaft, almost to the distal end of the crista fibularis. As in anhingas and phalacrocoracids, there is an elongate fossa on the lateral surface of the crista cnemialis lateralis. The proximal section of the shaft is very wide, with a flat to slightly concave cranial surface and a convex caudal surface; the medial part of the bone, that is, the distal section of the crista cnemialis cranialis, is markedly cranially slanted. The fossa flexoria, on the cranial surface of the proximal end, is very shallow. The distal end of the shaft exhibits a marked medial constriction, just above the condylus medialis (Fig. 7V). The distal end of the bone is medially inflected. There is a marked, cranially protruding embossment lateral of the pons supratendineus, which also occurs in some sphenisciforms but is absent in sulidoines (Fig. 7V–X). The sulcus extensorius is wide, and as in sulidoines the pons supratendineus is oriented obliquely to the longitudinal axis of the tibiotarsus; in sphenisciforms, this osseous bridge is wider and extends perpendicular to the axis of the bone. The proximodistally deep trochlea cartilaginis tibialis forms a prominent medial ridge. With regard to the craniocaudally flattened and wide proximal end, the tibiotarsus of Tonsala resembles that of sulidoines, whereas it corresponds with the tibiotarsus of sphenisciform birds in the long crista cnemialis cranialis and the embossment lateral to the pons supratendineus.

**RESULTS OF PHYLOGENETIC ANALYSES**

The analysis of the character matrix in Appendix S2 resulted in four most parsimonious trees that showed Plotopteridae to be the sister group of Suluidoidea (Fig. 8A). Eight characters were unambiguously optimized as apomorphies of the clade including Plotopteridae and Suluidoidea: (1) loss of vomer (char. 15 in Appendix S1); (2) processus paroccipitales prominent and strongly protruding in a caudal direction (char. 18); (3) presence of very marked fossae temporales that extend to midline of cranium (char. 21); (4) extremitas oimalis of furcula with marked, laterally protruding facies articulare acrococacoidae (char. 37); (5) acromion of scapula very long and markedly cranially projecting (char. 43); (6) humerus with very low crista deltoteorporalis (char. 51); (7) pelvis elongate and narrow, ratio width across antrochancers: length of ilium less than 0.35 (char. 60); and (8) distal end of tibiotarsus bent medially, and condylus medialis protruding farther distally than condylus lateralis (char. 68).

A suloid clade, to the exclusion of Plotopteridae, is supported by the following four unambiguously optimized characters: (1) caudal portions ofossa palatina completely fused along their midline, with suture obliterated (char. 13; secondarily reversed in some phalacrocoracids); (2) osa palatina forming an essentially flat plate with virtually no dorsoventral extension (char. 14); (3) processus flexorius of humerus very short, abruptly ending distally, with flat distal surface, which forms a marked edge-like step (char. 53); and (4) pelvis with crista iliaca dorsales extensively fused with crista spinosa of synsacrum (char. 62).

Analysis of the revised and emended data matrix of Smith (2010) did not support the tree topology obtained by that author, that is, a position of plotopterids within Suluidoidea as sister taxon of the clade (Phalacrocoracidae + Anhingidae). Instead, the analysis resulted in 12 most parsimonious trees, with Plotopteridae being the sister taxon of Sphenisciformes (Fig. 8B). We added 38 new scorings to the matrix of Smith (2010) and corrected 35 erroneous scorings of altogether 23 characters (see Appendix S3). A (Plotopteridae + Sphenisciformes) clade is, however, already obtained in half of the 24 trees resulting from an analysis in which only four character scorings are modified, with characters 4, 8, and 22 of Smith (2010) scored as absent for Tonsala, and character 198 scored as present for Eudyptula. Three of these characters (4, 8, 22) are derived features of suloids and are absent in Tonsala, and character 198 is a derived feature shared by plotopterids and sphenisciforms, which, together with a few others (see Appendix S3), was erroneously scored variable for sphenisciforms by Smith (2010).

**DISCUSSION**

Our analysis of the revised and emended data set of Mayr (2005), who proposed sphenisciform affinities of plotopterids, resulted in a clade composed of Plotopteridae and Suluidoidea. Intriguingly, however, analysis of a revised and emended data matrix of Smith (2010) supported sphenisciform affinities of Plotopteridae. Concerning the extant taxa, the results of our analysis agree with molecular data in that Fregatidae and Suluidoidea are recovered as sister taxa, and Pelecanidae form a clade with Scopidae and Balaenicipitidae. However, our data supported a sister-group relationship between Phaethontidae and a clade including Fregatidae, Plotopteridae, and Suluidoidea, whereas tropicbirds are widely separated from other ‘pelecaniform’ birds in analyses of nuclear sequences (e.g., Ericson et al., 2006; Hackett et al., 2008; Yuri et al., 2013). Furthermore, Gaviiformes resulted in a clade with Procellariiformes and Sphenisciformes in our analysis, whereas loons are the sister taxon of a clade including Procellariiformes, ‘Ciconiiformes,’ and ‘Pelecaniformes’ in molecular studies based on comprehensive nuclear data sets (Hackett et al., 2008; Yuri et al., 2013).
FIGURE 7. Postcranial bones of *Tonsala hildegardae* from the Oligocene Pysht Formation of Washington State, U.S.A. (SMF Av 601). A–E, nearly complete caudal cervical vertebra in A, dorsal, B, ventral, C, right lateral, D, left lateral, and E, cranial views; F, fragmentary cervical vertebra in dorsal view; G, 11th vertebra of *Sula bassana* (Sulidae); H, eighth vertebra of *Spheniscus humboldti* (Sphenisciformes); I–K, left ulna in I, dorsal, J, ventral, and K, proximal views; L, M, right femur (with attached remains of ?synsacrum) in L, cranial and M, caudal views; N, O, right femur (caudal view) of *Anhinga anhinga* (Anhingidae) and O, *Spheniscus humboldti* (Sphenisciformes); P, Q, left tibiotarsus in P, cranial and Q, caudal views; R, detail of bone surface showing parallel scratches of a scavenger and *Oseax* boreholes; S–V, right tibiotarsus in S, distal, T, caudal, U, medial, and V, cranial views; W, X, right tibiotarsus of *W. A. anhinga* and X, *S. humboldti*. Abbreviations: *brh*, *Oseax* boreholes; *ccc*, crista cnemialis cranialis; *cdl*, condylus lateralis; *cdm*, condylus medialis; *cfl*, crista fibularis; *cst*, constriction of shaft; *ctd*, cotyla dorsalis; *ctv*, cotyla ventralis; *emb*, embossment lateral of pons supratendineus; *fac*, facies articularis cranialis; *liz*, lacuna interzygapophysialis; *pit*, pits for attachment of feather quills; *pop*, fossa poplitea; *prc*, processus caroticus; *pst*, pons supratendineus; *spi*, processus spinosus; *tct*, trochlea cartilaginis tibialis; *tor*, torus dorsalis; *zca*, zygapophysis caudalis; *zcr*, zygapophysis cranialis. Scale bars equal 10 mm; same scales for A–F, I–K, L and M, P and Q, and T–V.
Smith’s (2010) data set is more comprehensive than ours, but only includes crown group representatives of Sphenisciformes. In the resulting trees of the revised character matrix of Smith (2010), the clade including Plotopteridae and Sphenisciformes is the sister taxon of a clade including Gaviiformes and Podicipediformes. A clade including these three extant taxa is not supported by any current analyses of molecular data. As noted by all previous authors, the osteology of plotopterids indicates close affinities to Suloidea (Olson and Hasegawa, 1979, 1996; Olson, 1980; Mayr, 2005; Sakurai et al., 2008). In addition to some postcranial characters (Olson, 1980; Mayr, 2005, and above), plotopterids and suloideans share derived skull features, including a nasofrontal hinge, caudally projecting processus paroccipitales (Kawabe et al., 2014:fig. 1), loss of the vomer, and the presence of an internal ossification of Meckel’s cartilage, which is also found in frigatebirds and tropicbirds (Zusi and Warheit, 1992). On the other hand, plotopterids lack diagnostic apomorphies of crown group suloideans. In particular, the palaetine bones are not fused in their caudal sections and do not form a dorsally flat and subrectangular platform, the presence of which is a unique apomorphy of suloideans (Fig. 3; Mayr, 2003). Furthermore, the nostrils are not reduced to tiny openings, the caudal sections of the maxillary bones are not ventrally fused (Fig. 3), and unlike in suloideans (including the extinct giant anhingas; Noriega, 1992; Alvarenga, 1995), the cristae iliacae dorsales of plotopterids are not fused with the crista spinosa of the synsacrum (Goedert and Cornish, 2002:fig. 7). Based on the above character evidence, we thus consider a position of Plotopteridae outside crown group Suloidea to be well supported, and the derived similarities shared with Phalacrocoracidae and Anhingidae, such as a very large patella, opisthocoelous vertebrae, and laterally expanded alae praeacetabulares iliorum, are here regarded to be of convergent origin. The new data challenge the hypothesis of a sister-group relationship between Plotopteridae and Sphenisciformes (Mayr, 2005), because penguins lack all of the above-listed derived features shared by plotopterids and suloideans. We note, however, that there exists a possibility that character states were reversed into the primitive condition in penguins due to paedomorphosis (see Mayr, 2005), and in some osteological aspects, such as the shape of the palatines, plotopterids more closely resemble penguins than the taxa of the Suloidea.

An ultimate appraisal of the affinities between Plotopteridae and Sphenisciformes depends on a more detailed study of the osteology of Waimanu and other early representatives of Sphenisciformes as well as on a robust higher-level phylogenetic placement of extant penguins based on molecular data. Overall, the osteology of Waimanu is more similar to that of plotopterids than to that of Gaviiformes or Procellariiformes, but there are some distinct differences in detail. The extremitas omalis of the furcula of Waimanu, for example, exhibits the derived shape of sphenisciforms and lacks a well-developed facies articularis acrocoracoidea, which is found in plotopterids and suloideans. Unlike plotopterids and crown group sphenisciforms, the corpus of the scapula of Waimanu is not greatly widened (Slack et al., 2006:fig. 1A [j, k]), and the distal end of the tarsometatarsus of Waimanu is distinguished from that of plotopterids in that the trochlea metatarsi II is not markedly longer than the trochlea.

**FIGURE 8.** A, strict consensus tree of four most parsimonious trees resulting from an analysis of the character matrix in Appendix S2 (length = 265; CI = 0.41; RI = 0.62). In this tree Plotopteridae are the sister taxon of Suloidea; B, strict consensus tree of 12 most parsimonious trees resulting from a reanalysis of the emended and revised (see Appendix S3) character matrix of Smith (2010) (length = 1257; CI = 0.42; RI = 0.84). In this phylogeny, Plotopteridae is placed as sister taxon to Sphenisciformes. Bootstrap support values are indicated next to the internodes.
metatarsi IV, with the latter furthermore not being asymmetric in dorsoplantar view. The shape of the *Waimanu* coroid is different from that of the elongate coracid of plotopterids. The upper beak of the late Eocene stem group sphenisciform *Icadyptes* resembles that of plotopterids in the very long and slit-like nostrils and the presence of distinct vascular impressions on the lateral surfaces (Ksepka et al., 2008), but because the bill morphology of *Waimanu* and that of other Paleogene sphenisci-

forms is poorly known, the significance of these features is diffi-
cult to assess.

If sphenisciform affinities of plotopterids can be upheld, these birds most likely are the sister taxon of a clade including *Waimanu* and other sphenisciiforms, which share well-developed dorsi-

sal fossae for glandulae nasales, a derived shape of the extremitas omalis of the furcula, and, probably correlated therewith, a nar-

row, hook-like extremitas omalis of the coracid. Because the scapula of *Waimanu* is, however, not greatly widened as in other sphenisciiforms and plotopterids, widening of the scapula must then have occurred convergently in members of Plotopteridae and Sphenisciiformes other than *Waimanu*.

If, on the other hand, the diving adaptations of plotopterids and penguins are of convergent origin, they would not only testi-

fy to a remarkable adaptive radiation within Aequornithes, the ‘waterbird clade,’ to which penguins and Suloidea belong (Mayr,

et al., 2002). In such a scenario, plotopterids would have evolved in closely related taxa, that is, wing-propelled diving in Plotopter-

idae and Sphenisciiformes and long-distance soaring in Fregatidae and the procellariiform Diomedeidae.

In any case, recognition of a sister-group relationship between Plotopteridae and Suloidea allows a reconstruction of the ances-
tral state of some morphological features of sulidoans. In particu-

lar, long open nostrils are likely to be plesiomorphic for a clade including Fregatidae, Plotopteridae, and Suloidea and were closed at least twice independently in Fregatidae and in Suloidea (if Phaethontidae are indeed the sister taxon of Fregatidae and Suloidea, a third reduction of the nostrils occurred in tropic-

birds). *Limnorn新西gela* lived in a lacustrine palaeoenvironment (Olson, 1977), and closure of the nostrils in the stem lineage of Fregatidae may be related to the transition into a marine environ-

ment. Plotopterids, however, were highly specialized seabirds, and why open nostrils are present in these birds but were reduced in members of crown group Sulidoidea remains an open question.

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