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博士論文（要約）

Paleofauna transition of seabirds in East Asia, with functional morphological analysis of the tarsometatarsal diaphysis for inferring the diving locomotion of hesperornithiforms

（東アジアにおける海鳥類相の古生物学的変遷および足根中足骨骨幹の機能形態学的解析に基づくヘスペロルニス類の潜水様式の推定）

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Abstract

To reveal the paleofaunal transition is one of the major research issues in paleontology. However, the fossil record of seabirds is still insufficient for discussing the detailed faunal transitions in East Asia, where most seabird fossils have been collected from the Pleistocene deposits in Japan. In order to clarify the faunal transition of seabirds in East Asia, here I report three undescribed seabird fossils from the Pleistocene, Pliocene, and Cretaceous in Japan.

The youngest specimen is a procellariid sternum from the Ichijiku Formation (Pleistocene) in Boso Peninsula, Chiba. Although this specimen lacks all diagnostic characters for detailed classification, I assigned it to Procellariidae based on the size, a rounded corpus sterni, shape of the linea intermuscularis, and aspect ratio of the incisurae costales. Another procellariid fossil, the humerus of *Puffinus*, has been reported from the same formation. However, considering the size of the sternum, it is reasonable to consider that the specimen described here is classified as a different genus. Therefore, various procellariid genera existed in this area in the Pleistocene as in today.

The second youngest specimen is an alcid humerus from the Horokaoshirarika Formation (Pliocene) in Hokkaido. This specimen is an incomplete proximal humerus, with the dorsoventrally flattened diaphysis as in wing-propelled diving birds. Comparisons of this specimen with modern wing-propelled diving birds indicated that it shares similar characteristics with Alcidae, such as the dorsoventrally compressed humeral diaphysis, low and smooth crista

deltopectoralis, and a nearly rectangular supracoracoideus scar. Several alcid fossils have been reported from the Miocene–Pleistocene deposits of the Eastern Pacific. Whereas little is known about the fossils from the Western Pacific, and reliable fossils have been found only from Pleistocene deposits. Thus, this report in this thesis represents the first Pliocene record of Alcidae from the Western Pacific, demonstrating that alcids were already distributed in the Holarctic region during the early Pliocene. Interestingly, the estimated depositional age of the Horokaoshirarika Formation almost coincides with the opening of the Bering Strait and the expansion of the Sea of Japan. In addition, fossils of the extinct plotopterids, a group of wing-propelled diving birds in the Oligocene–Miocene, have never been reported from the Pliocene deposits of Japan. Therefore, the expansion of sea regions and the extinction of Plotopteridae could have allowed the Eastern Pacific alcids to migrate into the Western Pacific to substitute for the extinct plotopterids.

The oldest specimen of the three is a tarsometatarsus of Hesperornithiformes from the Nishichirashinai Formation (Santonian in the Cretaceous) in Hokkaido. Hesperornithiformes is known as a group of Cretaceous foot-propelled diving birds, with most of their remains having been reported from the Campanian of North America. This specimen is a proximal part of the left tarsometatarsus that shares several characteristics with basal hesperornithiforms. It indicates an intermediate stage between *Enaliornis* and *Baptornis*, showing such characteristics as low and rounded eminentia intercotylaris, and the size of the cotyla lateralis and medialis. The CT-scanning data indicates that this specimen has a thick cortical bone, as in typical diving birds.

It implies that this bird has already been adapted for diving since the bone compactness is almost equivalent to that of the derived genus, *Hesperornis*. It is known that most hesperornithiforms are known as flightless; thus, the occurrence of this specimen indicates that this group of birds has already been distributed in East Asia during the Santonian using their developed diving ability.

To infer their diving locomotion, which remained controversial, I tested a functional morphological analysis based on the cross-sectional outlines of the diaphysis. As a result, this tarsometatarsus fossil has been shown to be similar to that of modern cormorants rather than that of highly specialized diving birds, such as loons, grebes, and *Hesperornis*. Therefore, this new specimen might have been an amphibious bird, and the mode of diving locomotion was also different among the genera or species in Hesperornithiformes. This ecological inference may shed light on the radiation history of hesperornithiforms from the viewpoint of aquatic adaptation or loss of flight ability.

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Institutional abbreviations.

AMNH: American Museum Natural History, New York, USA.

CAMSM: Sedgwick Museum of Geology, The University of Cambridge, Cambridge, England.

CFDC: Canadian Fossil Discovery Centre, Morden, Manitoba, Canada.

FHSM: Fort Hays State University, Sternberg Museum of Natural History, Kansas, USA.

FRIJ: Forestry and Forest Products Research Institute Japan, Tsukuba, Japan.

KUVP: The University of Kansas, Vertebrate Paleontology, Museum of Natural History, Lawrence, Kansas, USA.

NSMT AS: Avian Skeleton Collection, Department of Zoology, National Museum of Nature and Science, Tsukuba, Japan.

NSM PO-A: Osteology Collection, Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba, Japan.

NSM PV: Vertebrate Paleontology Collection, Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba, Japan.

NFL: Numata Fossil Museum, Hokkaido, Japan.

NMV: Nakagawa Museum of Natural History, Hokkaido, Japan.

OUS-SH: Okayama University of Science, Okayama, Japan.

PIN: Borissjak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.

PU: Princeton University, Princeton, New Jersey, USA (now at YPM).

SDSM: South Dakota School of Mines and Technology, South Dakota, USA.

SMNH: Royal Saskatchewan Museum, Saskatchewan, Canada.

UMUT: The University Museum, The University of Tokyo, Tokyo, Japan.

UNSM: University of Nebraska State Museum, Lincoln, Nebraska, USA.

YPM: Yale Peabody Museum of Natural History, New Haven, Connecticut, USA.

Bird ecology abbreviation in Chapters 4 and 5.

BOP: Bird of prey

HS-FPD: Highly specialized foot-propelled diver

FPD: Foot-propelled diver

SS: Surface swimmer

WPD: Wing-propelled diver

Chapter 1. General Introduction

Aves (birds) is a highly diversified vertebrate group, about 10,900 extant species have been classified in the world (Gill et al., 2021). Birds are diversified and adapted to various environments and are categorized into arboreal, terrestrial, semi-aquatic, and marine birds, depending on the ecologies. Among the birds, those completely adapted to the marine environment for at least a part of their lives are known as seabirds. However, the definitions of seabirds are somewhat different among researchers. Schreiber and Burger (2002) categorized five orders of birds, Sphenisciformes (penguins), Procellariiformes (albatross, petrels, and shearwaters), Pelecaniformes (pelicans), Suliformes (frigatebirds, cormorants, gannets, and boobies), and Charadriiformes (gulls, skuas, skimmers, terns, phalaropes, and auks) as seabirds. Whereas, Votier and Sherley (2017) categorized nine orders of birds as a seabird, namely, Procellariiformes (albatross and petrels), Sphenisciformes (penguins), Gaviidae (loons), Podicipidiformes (grebes), Anseriformes (waterfowl), Phaethontiformes (tropicbirds), Charadriiformes (gulls, skuas, skimmers, terns, phalaropes, and auks), Pelecaniformes (pelicans), and Suliformes (frigatebirds, cormorants, gannets, and boobies). In this thesis, I basically followed the definition of Votier and Sherley (2017); however, I reorganized it by family names and added extinct typical seabird families. In Anatidae, only diving ducks (Mergini and Aythyini) are treated as seabirds since ducks are diversified in several environments (Table 1-1).

On the basis of paleontological research, it is widely accepted that birds have evolved from theropod dinosaurs, and they had globally distributed during the Cretaceous (e.g., Clarke et al., 2002; Chiappe and Dyke, 2006). However, the Cretaceous avifauna was very different from that of today. Enantiornithes and Ornithuromorpha were the most dominant Cretaceous bird groups, and their fossils have been globally collected (Chiappe and Dyke, 2006). All modern birds are classified as Neornithes. However, until recently, it was not well known when this group emerged. Some loon-like birds, such as *Neogaeornis* and *Polarornis*, have been reported from the Cretaceous, and these birds were assigned as Gaviiformes in Neornithes (e.g., Lambrecht, 1929; Chatterjee, 2002). However, this assignment and phylogenetic position has been questioned due to their poor preservation (Feduccia, 1999; Mayr, 2004). Although Hope (2002) also compiled several taxa of Neornithes from the Late Cretaceous in North America, these fossils are described based on isolated fragmentary fossils. Therefore, her phylogenetic placements of these specimens have been ambiguous (James, 2005). Subsequently, a fossil taxon undoubtedly assigned to Neornithes was reported in 2005. This bird, *Vegavis iaai*, collected from a Maastrichtian deposit in Antarctica, is widely accepted as a Cretaceous neornithid by morphological and phylogenetic analyses (Clarke et al., 2005; Agnolín et al., 2017; Acosta Hospitaleche and Worthy, 2021). Agnolín et al. (2017) established Vegaviidae as an independent family of Anseriforms and integrated *Vegavis*, *Polarornis*, and *Neogaornis* into this family. Field et al. (2020) reported new neornithid materials, which they named *Asteriornis masstrichtensis* from a Maastrichtian deposit in Belgium. The occurrence of these fossils demonstrated that the modern bird group had already emerged during the Cretaceous. In addition, a molecular clock study suggests that Neornithes emerged at the end of the Cretaceous and diversified rapidly during the early Cenozoic after the K-Pg mass extinction (Claramunt and

Cracraft, 2015; Field et al., 2019). This hypothesis does not contradict the fossil record. In fact, several modern taxa have been collected from the Eocene to Oligocene deposits, such as the Green River and Willwood Formations in North America, the Messel oil shale in German, and the Phosphorites de Quercy in France (Feduccia, 1999; Mayr 2016). Records of seabird fossils have been compiled by Warheit (1992, 2002). He indicated that numerous seabird materials had been collected from the Middle Miocene–Pliocene deposits in southern California, whereas the Eocene–Early Miocene seabird fossils are more common in Japan, British Columbia, Washington, and Oregon (Warheit, 1992).

In East Asia, several neornithid fossils have also been reported from the Cenozoic. Phasianidae, Accipitridae, Columbidae, Threskiornithidae, and Struthionidae have been known from China and Mongolia (Rich et al., 1986; Hood et al., 2019; Buffetaut and Angst, 2021). However, seabird records are relatively few. According to the data compiled by Zelenkov (2016a), Phalacrocoracidae, Laridae, Podicipedidae, Pelecanidae, and Anatidae have been reported from Mongolia. These fossils, however, were from Miocene to Pliocene non-marine deposits. Although several anatids have been reported from the Miocene to Pleistocene deposits in China and Mongolia, most of these fossils were assigned as non-marine ducks, such as *Tadorna*, *Aix*, *Anas*, and *Anser* (Rich et al., 1986; Zelenkov, 2012a, b; Stidham et al., 2015). Among the anatid remains from China and Mongolia, the extinct taxa *Aythya shihuibas*, *Aythya molesta*, *Sharganetta mongolica*, *Nogusunna conflictoides*, and *Protomelanitta gracilis* are known as diving duck from non-marine Miocene deposits (Zelenkov and Kurochikn, 2012;

Zelenkov 2012b; Stidham, 2015). Despite many fossils having been collected in China and Mongolia, the absence of seabird fossils may be due to the scarcity of marine deposits.

The fossil records of birds are considerably few in South Korea. Gao et al. (2009) reported three bird specimens from the Cretaceous and assigned these fossils to Cretaceous bird taxa, such as Confuciusornithidae, Enantiornithes, and Ornithurae. However, detailed descriptions and accuracy of phylogenetic positions are still unambiguous (Choi and Lee, 2017). Several bird tracks, which showed a webbed foot, have been reported from the Haman Formation, which is also Cretaceous in age (Kim et al., 2006). The only Cenozoic bird fossil from Korea is a partial tibiotarsus of Galloanserae, collected from the Miocene (Park and Park, 2017). Several bird fossils have been collected from the Paleocene to the Pleistocene deposits in insular Southeast Asia (i.e., Sumatra, Java, Borneo, Flores, and Palawan), and Meijer (2014) compiled these fossil records. According to Meijer (2014), some anatids (*Tadorna tadornoides*, *Branta* cf. *ruficolis*, and Anatidae) and charadriids (*Pluvialis fulva*) have been known from the Pleistocene–Holocene of Java and Flores, however, seabirds remains have never been reported. Most other birds from South Asia are identified as arboreal birds, such as Accipitridae (hawks), Columbidae (pigeons), Bucerotidae (hornbills), and Phasianidae (pheasants). Recently, Tsai and Mayr (2021) reported a tarsometatarsus of a phasianid from the Pleistocene of Taiwan, and this is the first and only bird fossil report from Taiwan.

Although the number of specimens is not many, seabird fossils are notably more abundantly found in Japan than in other East Asian countries (Rich et al., 1986). Several seabird fossils have been reported from the Oligocene and younger deposits in Japan (Table 1-2). These fossil records may be related to the drastic topographical changes in Japan during the Cenozoic. Until the middle Eocene, the Japanese archipelago was a part of the eastern margin of the Eurasia continent. Subsequently, the eastern margin was isolated from the continent as a sea area expanded to form the Sea of Japan (Jolivet and Tamaki, 1992). Many topographical changes occurred before the present Japanese archipelago was formed, and it is certain that the seabird fauna was changed at these times.

According to the fossil record, it is certain that various seabirds had dispersed into East Asia by the Oligocene. Several modern families of seabird fossils, such as Procellariidae, Sulidae, Alcidae, and Phalacrocoracidae, have been collected from the Oligocene in Fukushima Prefecture (Ono and Hasegawa, 1991), and fossils belonging to Sulidae and Procellariidae, have also been reported from the Miocene deposit in Saitama Prefecture (Ono and Sakamoto, 1991). Although the Pliocene fossil record is considerably sparse, it is clear that seabirds diverged notably in East Asia, at least in the Pleistocene, since several specimens have been found. In particular, the reports of seabird fossils from Japan in the past decade are remarkable. For example, Watanabe et al. (2016, 2018a, b, 2020) reported a variety of seabirds fossil from the Pleistocene deposits in the Shiriya area in Aomori Prefecture and the Kazusa and Shimosa Groups in the Kanto area in Tokyo and Chiba Prefecture.

Recent studies revealed that the seabird fauna in Paleogene was different from that of the present since several extinct genera and species have been reported from the Cenozoic deposits in Japan. For example, extinct flightless diving birds, Plotopteridae were the most dominant seabirds during the Oligocene since their remains have been collected from several areas in Japan (Ono and Hasegawa, 1991; Olson and Hasegawa, 1996; Sakurai et al. 2008; Ando and Fukata, 2018; Ohashi and Hasegawa, 2020). The flightless swan, *Annakacygna* is also known from the Miocene marine deposits in Gunma Prefecture (Matsuoka and Hasegawa, 2022). Although several alcid remains have been reported from the Pleistocene in Shiriya, some extinct genera and species are also recognized (i.e., *Uria onoi* and *Mancalla*?; Watanabe et al., 2016, 2018a). In addition, not only alcids but also some extinct flightless ducks, *Shiriyanetta*, and extinct cormorants, *Urile perspicillatus* have been reported from Shiriya as well (Watanabe and Matsuoka, 2015; Watanabe et al., 2018a, b). Although Rich et al. (1986) mentioned that modern avifauna in Japan was formed since the Pleistocene, recent discoveries, which include several reports on extinct seabirds, suggest that seabird fauna has changed between the Pleistocene and the present. To reveal the seabird faunal transition in more detail, the number of the specimen is still insufficient. Unfortunately, birds are not commonly fossilized since their bones are generally fragile or often pneumatic (Tyrberg, 1986). However, even though the fossil is broken or fragmentary, it gives us important information to reveal the ecology. For example, Spheniscidae (penguins) and Alcidae (auks) are wing-propelled diving birds. Spheniscidae wings are modified as in flipper specialized for swimming, whereas Alcidae wings are slightly flattened but not remarkably flattened and broad as in penguins. Sulidae (e.g., boobies and gannets) is also can dive. However, they dive from the air and are known as “plunge-diving” and their wing elements do not flattened as in Spheniscidae or Alcidae (Ashmole, 1971; Smith, 2010). Such ecological differences should appear in the detailed parts of the bone, such as diaphysis and muscular attachment parts. Thus, even if it is difficult to identify the genus or species due to poor preservation, focused on such detailed characteristics, it should be possible to infer what kind of birds lived in that area.

In addition, one of the most noticeable seabird discoveries of the last decade was the report of *Chupkaornis keraorum* from the Cretaceous deposit in Hokkaido (Tanaka et al., 2017). This discovery demonstrated that the fossil record of seabirds in Japan dates back to the Cretaceous. *Chupkaornis keraorum* is assigned as Hesperornithiformes, which is the most diversified Cretaceous flightless foot-propelled diving bird. Most hesperornithiforms remains have been reported from the Campanian deposit of the Western Interior Seaway in North America (Bell and Chiappe, 2022). By contrast, the hesperornithiforms remains from East Asia are notably scarce. Only *Brodavis*, *Judinornis*, and indeterminant Hesperornithidae have been reported from the Maastrichtian deposit in Mongolia (Nessove and Yarkov, 1993; Kurochkin, 2000; Martin et al., 2012). *Chupkaornis* have been collected from the Kashima Formation of the Yezo Group, and the depositional age is estimated as Coniacian–Santonian (Tanaka et al., 2017). Thus, *Chupkaornis* is not only the first Japanese hesperornithifoms but also the oldest record of this group from East Asia. *Enaliornis* is known as the oldest Hesperornithiformes, and their remains have been reported from the Aptian deposit in England (Seely, 1876; Galton and Martin, 2002a, b). Thus, it is certain that Hesperornithiformes have been distributed to East Asia much earlier than previously thought, which is slightly earlier than the drastic diversification that occurred in North America. Although it is known that Hesperornithiformes are highly adapted to aquatic environments through evolution, the phylogenetic position of *Chupkaornis* has been estimated as relatively basal hesperornithiforms (Tanaka et al., 2017). Therefore, they may have already acquired considerable diving ability if they dispersed to East Asia during the early Late Cretaceous. It is extremely important to infer their ecologies and locomotion. However, it is impossible to estimate their diving ability since all the hindlimb materials of *Chupkaornis* are fragmentary.

Considering previous studies, this thesis focused on the following two primary goals. First, to reveal the seabird faunal transition in East Asia, I described three new seabird fossils and discussed them in terms of the paleontological geographic study. This study describes three fossil birds of different ages and phylogenies. Although these bird species are apparently unrelated (Fig. 1-1), their description will allow us to know what kind of birds existed in what region and at what period. In addition, if they are seabirds with various ecologies, it will allow us to have a meaningful paleontological discussion, such as faunal transition or entering timing in conjunction with environmental changes in the region. Second, to infer the locomotion of hesperornithiforms by functional morphological analysis and considered their distribution during the Cretaceous. In Chapter 2, I described a sternum of Procellariidae from the Pleistocene deposit of the Ichijiku Formation in Chiba Prefecture. A recent study by Watanabe et al. (2020) demonstrated that several seabirds existed around the Boso area during the Pleistocene. The description of new additional fossils in this study will help clarify the ornithological fauna in this area. It will provide a new perspective on the faunal transition between the Pleistocene and the present. In Chapter 3, I described a humerus of Alcidae from the Pliocene deposit of the Fukagawa Group in Hokkaido. Alcidae is one of the major diving birds, and they are widely distributed in the Holarctic region in the present. On the basis of fossil records, it is known that they have been diversified in North America during the Miocene (Smith, 2011a, 2016). However, Alcidae remains have never been reported from the Pliocene deposit in East Asia. Therefore, this specimen is important to discuss the dispersal timing and route of this family. In Chapter 4, I described a tarsometatarsus of Hesperornithiformes from the Late Cretaceous (Santonian) deposit of the Nishichirashinai Formation in Hokkaido. Considering the age of this fossil, it is almost equivalent to the Kashima Formation, where the *Chupkaornis* was collected (Tanaka et al., 2017). Thus, this fossil shows evidence that Hesperornithiformes have already been radiated in East Asia during the early Late Cretaceous, at least the Santonian.

To demonstrate the early radiation of Hesperornithiformes in detail, it is necessary to infer their locomotion since their diving ability is notably related to their radiation. The tarsometatarsus is known as the most important element for foot-propelled divers to generate propulsive power during swimming and diving (Hinić-Frlog and Motani, 2010). Therefore, in Chapter 5, I tested a morphological functional analysis using the cross-section of the tarsometatarsal diaphysis described in Chapter 4. This analysis method is a novel approach to inferring the locomotion of the extinct bird. On the basis of these findings, I discussed the seabirds faunal transition from the Cretaceous to the present in Chapter 6.

In this thesis, I employed the taxonomic classification of IOC World Bird List (v. 11.2. Gill et al., 2021) and the osteological terminology of Baumel and Witmer (1993).

Table 1-1. Seabird definition in this thesis. Bold is indicates extinct taxa.

	Schreiber and Burger (2002)		Votier and Sherley (2017)		This study	
	Order	Common name	Order	Common name	Order	Familes
1	Sphenisciformes	penguins	Sphenisciformes	penguins	Sphenisciformes	Spheniscidae
2	Procellariiformes	albatross, petrels, storm-petrels, fulmars,sheawters	Procellariiformes	albatross, petrels	Procellariiformes	Oceanitidae, Diomedeidae, Hydrobatidae, Procellariidae
3	Pelecaniformes	pelicans	Pelecaniformes	pelicans	Pelecaniformes	Pelecanidae
4	Suliformes	frigatebirds, cormorants, gannets, boobies	Suliformes	frigatebirds, cormorants, gannets, boobies	Suliformes	Fregatidae, Sulidae, Anhingidae, Phalacrocoracidae, **Plotopteridae**
5	Charadriiformes	gulls, skuas, jaegers, terns, auks, guillemots, puffins	Charadriiformes	gulls, skuas, skimmers, terns, phalaropes, auks	Charadriiformes	Laridae, Alcidae
6			Gaviiforme	loons	Gaviidae	Gaviidae
7			Podicipidiformes	grebes	Podicipidiformes	Podicipedidae
8			Phaethontiformes	tropicbirds	Phaethontiformes	Phaethontidae
9			Anseriformes	waterfowl	Anseriformes	Anatidae (Aythini, Mergini)
10					**Odontopterygiformes**	**Pelagornithidae**
11					**Hesperornithiformes**	**Enaliornithidae, Baptornithidae, Brodavidae, Hesperornithidae**
12					**Ichthyornithiformes**	**Ichthyornithidae**

Table 1-2. Seabird fossil records in Japan (except remort islands). ● indicates extinct taxa. All tribes of Anatidae are included in this table.

Locality	Horizon	Environment	Order or Familiy	Genus and species	Refference
Cretaceous					
Hokkaido	Kashima Fm.	Marine	●Hesperornithiformes	●*Chupkaornis keraorum*	Tanaka et al. (2017)
Hyogo (Awaji Island)	Kita-ama Fm.	Marine	●Hesperornithiformes	Fam. gen. et sp. indet	Tanaka et al. (2020)
Paleocene					
Eocene					
Oligocene					
Hokkaido	Tokoro Fm.	Marine	●Plotopteridae	●*Hokkaidornis abashiriensis*	Kimura et al. (1998); Sakurai et al. (2008)
Fukushima	Iwaki Fm.	Inner bay – estuary (Ueda et al., 2003)	Procellariidae	*Puffinus* sp.	Ono and Hasegawa (1991)
			Sulidae	*Morus* sp.	Ono and Hasegawa (1991)
				Sula sp.	Ono and Hasegawa (1991)
			Phalacrocoracidae	*Pharacrocrax* sp.	Ono and Hasegawa (1991)
			Alcidae	Gen. et sp. indet	Ono and Hasegawa (1991)
			●Plotopteridae	Gen. et sp. indet	Ono and Hasegawa (1991)
			●Pseudodontornithidae	Gen. et sp. indet	Ono and Hasegawa (1991)
Yamaguchi	Ashiya Gp.	Marine	●Plotopteridae	●*Stenornis kanmonensis*	Ohashi and Hasegawa (2020)
Fukuoka	Ashiya Gp.	Marine	●Plotopteridae	●*Copepteryx hexeris*	Olson and Hasegawa (1996); Ohashi and Hasegawa (2020)
				●*Copepteryx titan*	Olson and Hasegawa (1996)
				●*Empeirodytes okazakii*	Ohashi and Hasegawa (2020)
			●Odontopterygiformes	Fam. gen. et ap. indet	Okazaki (1989)
Saga	Kishima Gp.	Marine	●Pelagornithidae	Gen. et sp. indet	Okazaki (2006)
			●Plotopteridae	Gen. et sp. indet	Okazaki et al. (2008)
Nagasaki	Shiota Fm.	Marine	●Plotopteridae	●*Copepteryx hexeris*	Olson and Hasegawa (1996)
	Kakinoura Fm.	Marine	●Plotopteridae	Gen. et sp. indet	Mori and Miyata (2020)
	Itanoura Fm.*	Marine	●Plotopteridae	Gen. et sp. indet	Mori and Miyata (2020)
	*(latest Eocene–earliest Oligocene)				

Table 1-2. (continued)

Locality	Horizon	Environment	Order or Familiy	Genus and species	Refference
Miocene					
Miyagi	Aoso Fm.	Marine	Alcidae	*Praemancalla* sp.	Kohno (1997)
Gunma	Tomioka Gp.	Marine	Sulidae	Gen. et sp. indet.	Matsuoka et al. (2002a)
			Phalacrocoracidae	*Phalacrocorax* sp.	Matsuoka et al. (2002a)
			Anatidae	●*Annakacygna hajimei*	Matsuoka and Hasegawa (2022)
				●*Annakacygna yoshiensis*	Matsuoka and Hasegawa (2022)
Saitama	Nagura Fm.	Marine	●Pelagornithidae	●*Osteodontornis* sp.	Ono (1989); Ono and Sakamoto (1991)
			Sulidae	*Sula sp.*	Ono (1983); Ono and Sakamoto (1991)
			Procellariidae	*Puffinus* spp.	Ono and Sakamoto (1991)
	Tomita Fm.	Marine	Anhigidae	*Anhiga* sp.	Ono and Sakamoto (1991)
Nagano	Aoki Fm.	Marine	Diomedidae	Gen. et sp. indet.	Matsuoka et al. (2009)
Gifu	Mizunami Gp.	Marine	●Plotopteridae	●*Plotopterum* sp.	Olson and Hasegawa (1985)
			Gaviidae	Gen. et sp. indet.	Rich et al. (1986)
			Anatidae	Gen. et sp. indet.	Rich et al. (1986)
			Alcidae	Gen. et sp. indet.	Rich et al. (1986)
			Phalacrocoracidae?	Gen. et sp. indet.	Hasegawa et al. (1977)
Mie	Oi Fm.	Marine	●Pelagornithidae	●*Osteodontornis* sp.	Matsuoka et al. (1998)
			Diomedeidae	●*Diomedea tanakai*	Davis (2003)
Pliocene					
Iwate	Yushima Fm.	Marine	●Pelagornithidae	Gen. et sp. indet	Oishi et al. (1985)
Shizuoka	Hijikata Fm.	Marine	Gaviidae	*Gavia* sp.	Matsuoka et al. (2007)
	Daiinichi Fm.	Marine	●Pelagornithidae	Gen. et sp. indet	Ono (1980a); Oishi et al. (1985)
Mie	Kobiwako Gp.	Freshwater	Anhingidae	*Anhiga* sp.	Matsuoka et al. (1991)
Oita	Tsubusagawa Fm.	Lacustrine	Phalacrocoracidae	*Phalacrocorax* sp.	Matsuoka (2001)
			Anatidae	*Cygnus* sp.	Matsuoka (2001)

Table 1-2. (continued)

Locality	Horizon	Environment	Order or Familiy	Genus and species	Refference
Pleistocene					
Aomori (Shiriya area)	-	Marine	Anatidae	*Anas* magn. *plantyrhynchos*	Waranabe et al. (2018a)
				Melanitta fusca	Waranabe et al. (2018a)
				Histrinicus histrinicus	Waranabe et al. (2018a)
				Clangula hyemalis	Waranabe et al. (2018a)
				Shiriyanetta hasegawai	Watanabe and Matsuoka (2015); Waranabe et al. (2018a)
			Podicipedidae	*Podicps cristatus* or *grisegena*	Waranabe et al. (2018a)
			Gaviidae	*Gavia* cf. *stellata*	Waranabe et al. (2018a)
			Hydrobatidae	*Hydrobates leucorhous*?	Waranabe et al. (2018a)
			Diomedeidae	*Phoebastria* cf. *albatrus*	Waranabe et al. (2018a)
			Procellariidae	*Fulmarus* sp.	Waranabe et al. (2018a)
				Ardenna grisea	Waranabe et al. (2018a)
				Ardenna tenuirostris	Waranabe et al. (2018a)
				Puffinus cf. *nativitatis*	Waranabe et al. (2018a)
				Calonectris leucomelas	Waranabe et al. (2018a)
			Phalacrocoracidae	*Phalacrocorax pelagicus*	Waranabe et al. (2018a)
				●*Phalacrocorax perspicillatus*	Waranabe et al. (2018a, b)
			Laridae	*Larus* magn. *argentatus*	Waranabe et al. (2018a)
				Larinae gen. et sp. indet A	Waranabe et al. (2018a)
				Larinae? gen. et sp. indet B	Waranabe et al. (2018a)
			Alcidae	*Uria lomvia*	Waranabe et al. (2018a)
				Uria aalge	Waranabe et al. (2018a)
				●*Uria onoi*	Waranabe et al. (2018a)
				Cepphus columba	Waranabe et al. (2018a)
				Cepphus carbo	Waranabe et al. (2018a)
				Synthliboramphus antiquus	Waranabe et al. (2018a)
				Aethia pusilla	Waranabe et al. (2018a)
				Aethia cristatella	Waranabe et al. (2018a)
				Fraterculini gen. et sp. indet	Waranabe et al. (2018a)
				●*Mancalla*? sp.	Waranabe et al. (2018a)

Table 1-2. (continued)

Locality	Horizon	Environment	Order or Familiy	Genus and species	Refference
Pleistocene					
Chiba	Kami-iwahashi Fm.	Marine	Gaviidae	*Gavia pacifica*	Ono et al. (1984)
	Ichijiku Fm.	Marine	Anatidae	*Clangula hyemalis*	Watanate et al. (2020)
			Gaviidae	*Gavia srellata*?	Watanate et al. (2020)
			Procellariidae	*Puffinus* cf. *puffinus*	Watanate et al. (2020)
			Phalacrocoracidae	gen. et sp. indet	Watanate et al. (2020)
			Alcidae	*Alle* cf. *alle*	Watanate et al. (2020)
				●*Mancalla* sp.	Watanate et al. (2020)
	Mandano Fm.	Marine	Anatidae	*Melanitta fusca*	Watanate et al. (2020)
			Gaviidae	*Gavia srellata*?	Watanate et al. (2020)
	Kiyokawa Fm.	Marine	Anatidae	*Melanitta fusca*	Watanate et al. (2020)
Tokyo	Hirayama Fm.	Marine	Anatidae?	Gen. et sp. indet	Watanate et al. (2020)
			Diomedeidae	*Phoebastria* cf. *albatrus*	Watanate et al. (2020)
Kanagawa	-		Phalacrocoracidae	*Pharacrocrax* sp.	Takahashi and Nokarya (1980)
Ishikawa	Omma Fm.	Marine	Gaviidae	*Gavia* sp.	Matsuura (1996)
Nagano	Nojiri-ko Fm.	Lacustrine	Anatidae	*Anser fabalis*	Nakamura (1975)
			Phalacrocoracidae	*Pharacrocrax* cf. *carbo*	Ono (1980b)
Hiroshima	-	Archaeological site	Anatidae	*Aythya* sp.	Nokariya and Ono (1980)

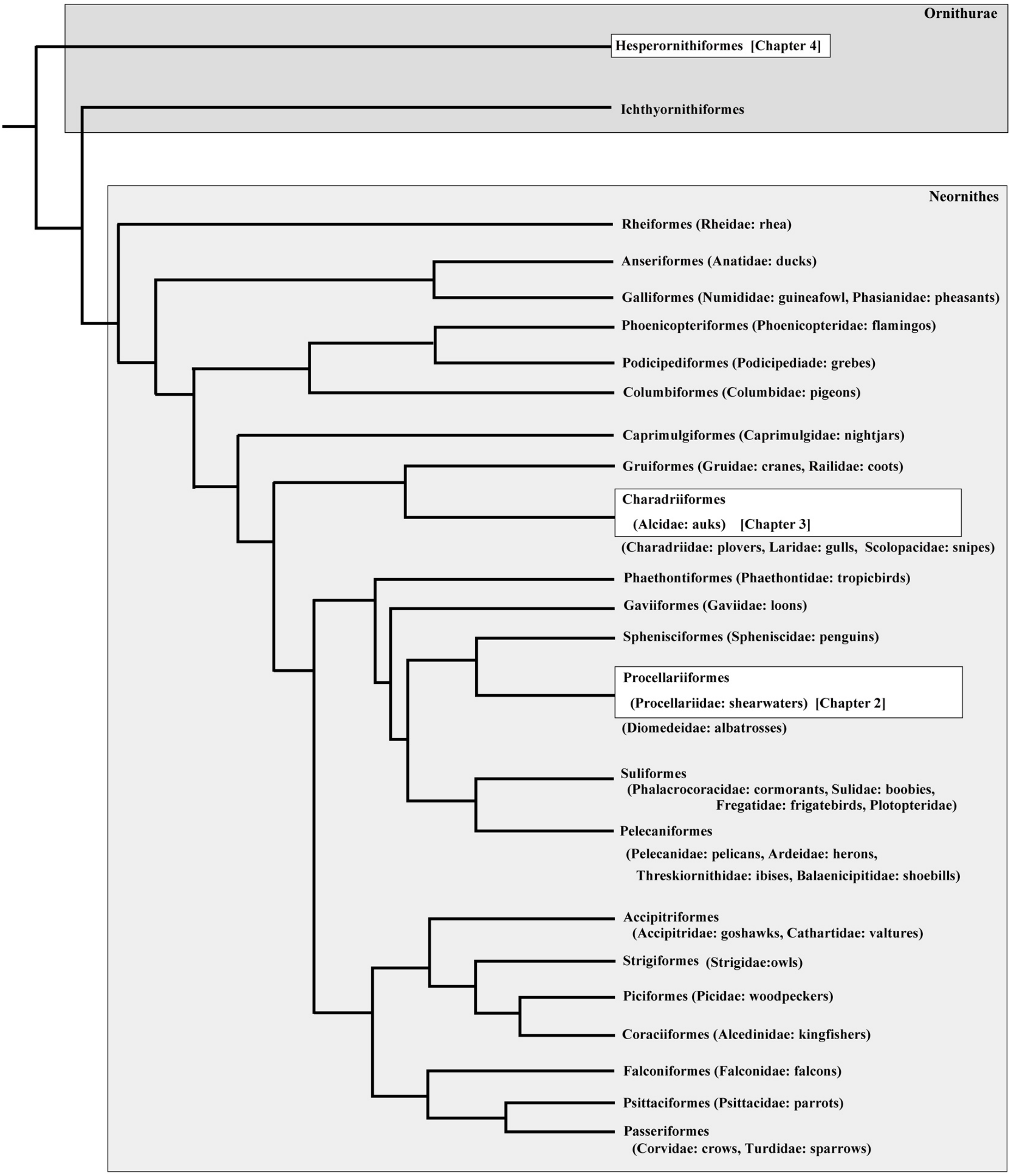


Fig. 1-1. Phylogenetic position of the birds described in this study. Phylogenetic tree is based on Chiappe and Dyke (2006) for Ornithurae and Kimball et al. (2019) for Neornithes.

Chapter 2.

A sternum of Procellariidae from the Ichijiku Formation (Pleistocene) in Chiba, Japan

Introduction

The Ichijiku Formation of the Kazusa Group is known as transgressive shelf successions from the Middle Pleistocene and is widely exposed around Kimitsu City, Chiba Prefecture in Japan (Horikawa and Ito, 2004). This formation is composed of a sandridge complex which was deposited on a shelf environment by a unidirectional ocean current (Nakayama and Masuda, 1987). Numerous invertebrate fossils (i.e. Bivalvia, Gastropoda, Ophiuroidea, Crustacea) from this formation have been documented (e.g. Sakakura, 1935; Baba, 1990; Ishida and Inoue, 1995; Kase et al., 2013; Kato et al., 2017). Several vertebrate fossils have also been collected from the Ichijiku Formation, although most of these have not been formally described with the exception of several shark teeth and three delphinid remains (Goto et al., 1984; Kimura et al., 2004, 2008, 2012). However, Watanabe et al. (2020) recently reported six different taxa of birds from the Ichijiku Formation, namely *Clangula hyemalis* (Anatidae: long-tailed duck), *Gavia stellata*? (Gaviidae: red-throated loon), *Puffinus* cf. *puffinus* complex (Procellariidae: manx shearwater), Phalacrocoracidae (cormorants), and two taxa of Alcidae (auks), *Alle* cf. *alle* (little auk), and *Mancalla* sp. Such discoveries suggest that a variety of vertebrate species existed in this area during the Middle Pleistocene, as it does today in the Boso Peninsula.

Here, I report an avian sternum fossil from the Ichijiku Formation in Kimitsu City (Fig. 2-1 A). I compared this new specimen with modern taxa, and recognized several similarities with Procellariidae. A major part of this chapter has been reported by Aotsuka et al. (2022). In this chapter, on the basis of Aotsuka et al. (2022), I described this specimen with additional remarks to discuss the faunal transition more in detail.

Procellariidae is a highly diversified avian group, which includes 16 genera and 99 species (Gill et al., 2021). Many extinct species of Procellariidae have also been found globally in the Cenozoic, especially from the Neogene deposits of the North Atlantic and North Pacific basins (Warheit, 2002). Furthermore, procellariid fossils have been reported in several localities from the Oligocene to Pleistocene deposits in Japan (Ono and Hasegawa, 1991; Ono and Sakamoto, 1991; Watanabe et al., 2018a). This may suggest that this family had already been widely distributed during these epochs.

Geological setting

The Kazusa Group is widely distributed in the Kanto area. In the present study area, this group is divided into 10 formations (Fig. 2-1 B; Nakajima and Watanabe, 2005). The Ichijiku Formation is an upper part of the Kazusa Group, which is widely exposed around Kimitsu City and Futtsu City in the Boso Peninsula. This formation conformably overlies the Kokumoto Formation and is evenly overlain with small erosion by the Chonan Formation (Nakajima and Watanabe, 2005). The Ichijiku Formation consists of sand wave deposits from the Kuroshio Current in the Middle Pleistocene between 0.8–0.6 Ma (Nakayama and Masuda, 1987; Nakajima and Watanabe, 2005). According to the fission track and magnetostratigraphic study, the deposited age of the Ichijiku Formation has been estimated at about 0.7 Ma (Ito, 1992; Horikawa and Ito, 2004). The outcrops exposed large-scale planar cross-stratification, which was formed by a unidirectional current. The layer is up to 400 m thick and is composed of fine- to coarse-grained sands with lenticular sedimental bodies. The deposits yielded abundant fossil mollusks including both warm- and cold-water faunas (Nakayama and Masuda, 1987; Ishida and Inoue, 1995; Kase et al., 2013). According to the molluscan fauna and sand wave deposits, the Ichijiku Formation was estimated to have been deposited under a shallow marine environment, about 50–130 m deep with a paleoclimate warmer than that of today (Nakayama and Masuda, 1987; Ishida and Inoue, 1995; Kase et al., 2013).

Material and methods

The fossil described here was found *in situ* at an outcrop at Ichijuku, Kimitsu City, Chiba Prefecture, Japan (35° 16’15”N, 139° 59’17”E; Fig. 2-1A), during field research by the Natural History Museum and Institute, Chiba, in 2008. The specimen was numbered with the prefix CBM-PV 8301 and stored at the Natural History Museum and Institute, Chiba. I compared CBM-PV 8301 with the sterna of 17 species of modern Procellariiformes represented by 62 specimens stored at FRIJ and NSM (Table 2-1 and 2-1-1). Osteological measurements were taken in millimeters using a digital caliper (SINWA 19975). Fig. 2-2 indicates the measurement points. The dorsoventral length and craniocaudal length of the incisurae costales were measured from photographs using ImageJ (Schneider et al., 2012). The photographs were taken in the lateral view, with the margo costalis oriented in the horizontal plane (Fig. 2-2; incisurae costales).

Systematic paleontology

Class Aves Linnaeus, 1758

Order Procellariiformes Fübringer, 1888

Family Procellariidae Leach, 1820

Procellariidae gen. et sp. indet.

Fig. 2-3 and Table 2-1, 2-1-1

Locality.—CBM-PV 8301 was collected from Kimitsu City, Chiba, Japan.

Horizon and age.—Ichijiku Formation of the Kazusa Group (Middle Pleistocene).

Description.—CBM-PV 8301 is a partial sternum. Most of the marginal part is crushed, however the left side of the corpus sterni and margo costalis is well preserved. The corpus sterni is swollen and rounded (Fig. 2-3 A, A'). In the ventral view, the linea intermuscularis extends from the labrum extenum to the carina sterni with a gentle curvature (Fig. 2-3 B, B'). In the lateral view, six processus costales are confirmed on the margo costalis, however the first processus is damaged (Fig. 2-3 C, D). All the processus costales extend vertically from the ventral margin of the margo costalis; thus, the incisurae costales display a vertically rectangular outline (Fig. 2-3 D). The measurement data indicates that the second and third incisurae are almost the same size and that the fourth incisura is the largest.

Comparison.—Although CBM-PV 8301 is an incomplete sternum, six of the processus costales are preserved. In general, the number of these processus, representing that of the sternal rib articulating with the sternum, differs between groups of birds. Procellariiformes have six ribs attached to the sternum (Shufeldt, 1907; Kuroda, 1954). In addition to Procellariidae, also Anatidae, Gaviidae, Phalacrocoracidae and Alcidae have been reported from the Ichijiku Formation (Watanabe et al., 2020). However, Phalacrocoracidae possess four processus (Ono, 1980c; Smith ND, 2010), and most Anatidae, Gaviidae, and Alcidae have seven (Kuroda, 1954, 1967; Livezey, 1996; Worthy, 2008; Smith ND., 2010; Smith NA., 2011a). As well as Procellariidae, six processus also recognized in Scolopacidae (woodcoocks) and Laridae (gulls) (Kuroda, 1954). However, their corpus sterni is not as swollen and rounded as in CBM-PV 8301 (Fig. 2-4).

Compared with Procellariiformes, such a rounded corpus sterni is similar to Procellariidae. The corpus sterni of Hydrobatidae (*Hydrobates*) is less rounded, whereas it is prominently rounded and much dorsoventrally deeper as in the funnel in Diomedeidae (*Phoebastria immutabilis* [Laysan albatross]; Fig. 2-4). Moreover, the sternum of Diomedeidae is highly pneumatic and exhibits many pneumatic foramina (Kuroda, 1954; Hamlet and Fisher, 1967). Note that CBM-PV 8301 does not display such foramina. Although the carina sterni of CBM-PV 8301 had been damaged, the ventral margin tapers to the margo caudalis with a sharp and pointed outline as in Procellariidae, rather than being broad and blunt as in Hydrobatidae or Diomedeidae (Fig. 2-4). In the ventral view, the shape of the linea intermuscularis is different between families, with the Procellariidae displaying a curve with a small curvature and steep gradient running toward the middle of the midline as in CBM-PV 8301 (Fig. 2-5). Hydrobatidae exhibits a slanted line with sharp angle that extends more caudally, and Diomedeidae shows a relatively short curve with a large curvature (Fig. 2-5).

As preserved, the craniocaudal length of CBM-PV 8301 is 49.0 mm along the midline of the sternum. It is considerably smaller than Diomedeidae, but much larger than Hydrobatidae (Table 2-1). Compared with the sternum of Procellariidae, CBM-PV 8301 is much larger than those of *Bulweria bulwerii* (Bulwer's petrel) and *Pterodroma hypoleuca* (Bonin petrel). The complete size of this specimen is probably slightly larger than that of *Ardenna grisea* (sooty shearwater), *A. carneipes* (flesh-footed Shearwater) and *A. tenuirostris* (short-tailed shearwater) (Table 2-1). While a humerus of the *Puffinus* cf. *puffinus* complex has been reported from the Ichijiku Formation, their sternum remains undiscovered (Watanabe et al., 2020). Nevertheless, it is known that *Puffinus* is a smaller taxon than *Ardenna* (Tennyson and Mannering, 2018). Assuming the skeletal proportions are similar, CBM-PV 8301 would not be regarded as the *P.* cf. *puffinus* complex, in terms of size.

Kuroda (1954) described notable osteological characteristics of the Procellariidae, and noticed that a marginal part of the sternum, such as the shape of the rostrum sterni and the apex carinae, and the curvature of the pila carinae are distinctive for the genera or species of Procellariidae. However, these characteristics are all unobservable in CBM-PV 8301. Therefore, I focused on the characteristics of the linea intermuscularis and incisurae costales for identification.

The linea intermuscularis of CBM-PV 8301 is long, extending caudally beyond the level of the sixth processus costalis in the ventral view. In contrast, it does not extend far caudally to the sixth processus costalis in most modern Procellariidae. In our observations, only *Puffinus bryani* (Bryan's shearwater), *Pterodroma hypoleuca*, and a few specimens of *Ardenna* displayed remarkably elongate linea intermuscularis that almost reached the mediolaterally most constricted part of the sternum.

CBM-PV 8301 shows a vertically rectangular outline of the incisurae costales. The dorsoventral length is more than 1.7 times as large as the craniocaudal length in all incisurae costales. Among the procellariids examined, *Ardenna* has a relatively high aspect ratio and indicates a vertically rectangular outline. Especially, *A. carneipes*, *A. grisea*, and *A. tenuirostris* exhibit high aspect ratios in which the dorsoventral length is on average more than over 1.5 times as large as the craniocaudal length in all the incisurae costales on average (Fig. 2-6. Table 2-2).

Although the incisurae costales of *Calonectris leucomelas* also displays vertically rectangular outline, the aspect ratio is slightly lower than those of *Ardenna*. *Puffinus* is a close phylogenetic relationship to *Ardenna* and *Calonectris* (Penhallurick and Wink, 2004), nevertheless, the incisura costalis in *Puffinus* is less elongated dorsoventrally. Especially *Puffinus bannermani* (Bannerman's shearwater) is distinguishable in this genus, which displays nearly square outlines of the incisurae and the aspect ratio indicates nearly 1.00.

Several Procellariidae also display a vertically rectangular outline, however the dorsoventral length is on average less than 1.5 times as large as the craniocaudal length in many Procellariidae (i.e. *Puffinus*, *Fulmarus glacialis* [Northern fulmar] and *Pagodroma nivea*[snow petrel]), with the ratios varying among incisurae costales. In *Pterodroma hypoleuca*, the incisurae costales shows a tendency to gradually become vertically elongated from the 2nd to the 5th. Thus, it is concluded that the characteristics of the incisurae costales in CBM-PV 8301 is relatively similar to *Ardenna*.

Remarks.—Based on the morphological similarities in the sternum with *A. grisea* and *A. carneipes*, Aotsuka and Isaji (2017) announced CBM-PV 8301 as *Ardenna* sp. at a paleontological conference (*Puffinus* sp. in Aotsuka and Isaji, 2017; formerly species of *Ardenna* were regarded as species of *Puffinus*). However, I used a wider variety of procellariid specimens for a detailed comparison, and recognized some interindividual differences in sternal characteristics. In addition, I compared seven genera of Procellariidae, most of which are widely distributed in the Pacific Ocean including around Japan. However, our comparative data lacked nine genera of Procellariidae, especially the Antarctic Oceans taxa such as *Macronectes*, *Daption,* and *Procellaria*, because of the limitation of the osteological collection. Therefore, I conclude that it is appropriate to identify CBM-PV 8301 as a Procellariidae.

Discussion

Sternal character variations

I studied 62 individuals of the extant Procellariiformes for comparison with CBM-PV

8301. As a result, I found several common osteological features between CBM-PV 8301 and Procellariidae, and observed that this specimen is particularly similar to the sternum of *Ardenna* in terms of its overall size and the shape of the incisurae costales. However, I noted that the detailed sternum characteristics, which were preserved in CBM-PV 8301, vary by individual.

For example, Shufeldt (1907) mentioned that the Procellariidae sternum has six processus costalis. However, Kuroda (1967) suggested that the number of ribs increases in a diving habitat. In fact, I recognized an extra processus costales in six specimens. Among the six modern procellariid specimens, one specimen of *A. tenuirostris* (FRIJ 028-27) and one specimen of *P. bammermani* (FRIJ 030-03) showed variation in the number of processus between the both two contralateral sides: seven and six processus were present on the left and right sides, respectively (Table 2-1-1). In contrast, one specimen of *F. glacialis* (FRIJ 013-02) and one specimen of *P. nivea* (NSM PO-A 304) had only five processus on both margines costales. In the ventral view, the linea intermuscularis extended as caudally as the fifth or sixth processus costalis in most specimens. However, I observed that one of the five specimens of *A. grisea* (NSM PO-A 601) and one of the 17 specimens of *A. tenuirostris* (FRIJ 028-04) displayed elongated linea intermuscularis, which extended further caudally than the sixth processus, as in CBM-PV 8301 (Fig. 2-7). By contrast, one of the 13 specimens of *A. pacifica* (wedge-tailed shearwater; FRIJ 11304; Fig. 2-7) displayed notably short linea intermuscularis, which reached only as caudally as the third processus. The outline of the incisurae costales also varied, even within species. Some specimens displayed a clearly rectangular shape as in CBM-PV 8301, and others a nearly oval-like shape (Fig. 2-8). This difference is attributed to the thickness or curvature of the processus costalis.

Even though it is possible to assign CBM-PV 8301 to the Procellariidae, the incompleteness of the specimens, absence of diagnostic features, and interindividual variability in some of the sternal characteristics prevents an assignment to a particular taxon within this family.

Procellariid fossil record

Warheit (1992) suggested that the Procellariidae had diversified during the Miocene and Pliocene, because many fossils had been collected from Miocene deposits. Olson (1985) mentioned that most of the modern species or subgenera of *Puffinus* (including *Ardenna*) already existed by the middle Miocene, and subtle morphological changes had occurred within these lineages in the last 15 million years. In fact, Olson and Rasmussen (2001) reported several Procellariidae such as *Puffinus*, *Calonectris*, *Pterodroma*, *Pachyptila*, *Procellaria* and *Bulweria*? from the Miocene–Pliocene deposit in North Carolina. In addition, several extinct species of *Ardenna* and *Puffinus* such as *A. davealleni*, *P. conradi* (*A. conradi*; *sensu* Tennyson and Mannering, 2018), *P. inceptor*, *P. priscus*, *P. mitchelli*, *P. micraulax*, and *P. nestori* have been described from the Miocene and Pliocene deposits of California, Maryland, Florida, Spain, and New Zealand (Marsh, 1870; Wetmore, 1930; Miller, 1961; Brodkorb 1963; Alcover, 1989; Tennyson and Mannering, 2018). Many procellariid fossils have also been found from the

Pleistocene in several regions. Their remains have been reported not only from the Pacific area such as California, Mexico, New Zealand, and Tasmania (Howard, 1936, 1949; Hubbs and Jehl, 1976; van Tets, 1978; Worthy and Holdaway, 1993; Worthy, 1999; Worthy and Grant-Mackie, 2003; Guthrie, 2005), but also from the Atlantic area such as St. Helena Island, Bermuda, and the Canary Islands (Shufeldt, 1916, 1922; Olson, 1975, 2004, 2008, 2010; Walker et al., 1990). The remains of *A. grisea* are commonly found from the Pleistocene deposits in California, New Zealand, Tasmania and St. Helena Island (Howard, 1936, 1949; Olson, 1975; van Tets, 1978; Worthy and Grant-Mackie, 2003), and extinct species (i.e. *Pterodroma kurodai* Harrison and Walker, 1978) have been reported from Aldabra Atoll (Harrison and Walker, 1978; Hume et al., 2018). These fossils demonstrate that Procellariidae was as globally distributed in the Pleistocene as in today.

The number of bird remains from Japan is not numerous, with most of them having been collected from the Pleistocene (Rich et al., 1986). However, Procellariidae were frequently collected from deposits younger than the Eocene. For example, *Puffinus* sp. has been reported from the Oligocene deposit of the Iwaki Formation in Fukushima (Ono and Hasegawa, 1991), and two different species of *Puffinus* have been discovered in the Miocene deposit of the Nagura Formation in Saitama Prefecture (Ono and Sakamoto, 1991). Recently, several species of Procellariidae, namely *A. grisea*, *A. tenuirostris* (*P. griseus*, *P. tenuirostris* in Watanabe et al., 2018a), *P.* cf. *nativitatis*, *Calonectris leucomelas*?, and *Fulmarus* sp. have been reported from the Pleistocene deposits of Shiriya in Aomori Prefecture (Watanabe et al., 2018a). In addition to

CBM-PV 8301, *Puffinus* cf. *puffinus* complex has also been found in the Ichijiku Formation and the Kiyokawa Formation in Chiba Prefecture (Watanabe et al., 2020). Although the depositional age of the strata of Shiriya (ca. 0.32–0.12 Ma) and the Kiyokawa Formation (ca. 0.22) are slightly younger than that of the Ichijiku Formation (ca. 0.7 Ma), these fossil records indicate that several procellariids were widely distributed across Japan during the Middle to Late Pleistocene. Rich et al. (1986) suggested that a variety of birds had invaded Japan from other localities and formed modern zoogeographic regions during the Pleistocene since the global climate and sea level fluctuations occurred together.

Marine birds are easily affected by environmental changes. For example, a Procellariiformes assemblage has been reported from the assumed Holocene deposits of Kita-Daito Island in Okinawa Prefecture, however, avian fauna changed a following forest development since the bare ground suitable for their colonies was lost (Matsuoka et al., 2002b). Olson (1975) also suggested that climate and oceanographic changes may have caused some of the species of Procellariiformes to extinction on St. Helena Island during the Pleistocene.

The Kimitsu area was located several kilometers north of the paleoisland (now part of the Boso Peninsula) during the Pleistocene, and the oceanographic setting and paleoenvironment were similar to those of today, but slightly warmer (Ishida and Inoue, 1995; Kase et al., 2013). Such habitats must have been suitable for Procellariidae and other seabirds. In fact, procellariid species are still common in the seabird fauna of the Boso Peninsula today (Oka et al., 1985; Oka, 1994). Thus, the report of CBM-PV 8301 suggests that procellariiforms have been living around this area from the Pleistocene to modern days. By contrast, Watanabe et al., (2020) reported some uncommon taxa, such as an Atlantic auk, *Alle* cf. *alle* and an extinct flightless auk, *Mancalla* sp. from the Ichijiku Formation. Interestingly, Kase et al. (2013) described several modern and extinct limpets from the Ichijiku Formation and suggested that the sea-level decline during the glacial age may have caused this selective extinction. Such a glacial regression event might also have caused the selective extinction of marine birds between the Pleistocene and the present in the Boso Peninsula. Therefore, the avifauna in this area was somewhat different from that of the present, including not only birds that can still be seen today, but also extinct taxa that coexisted with the living taxa. Thus, the discovery of CBM-PV 8301 suggests the diversity of Procellariidae in this area with significantly important evidence to reveal the avifauna transition from the Pleistocene to the present.

Table 2-1. Sternum measurements (in mm) of Procellariidae (CBM-PV 8301) and modern Procellariiformes. Rounded off to one decimal place. ( ) indicates the presented dimensions of the specimen preserved. For abbreviations, see the caption of Fig. 2-2.

Taxa	English name	(n)	LC	LM	GB	SBI
Procellariidae (CBM-PV 8301)		**1**	**(42.4)**	**(49.0)**	**(28.8)**	**(23.6)**
Procellariidae						
Ardenna						
A. carneipes	Flesh-footed shearwater	2	59.5 – 59.7	59.8 – 60.6	42.9 – 43.5	34.6
A. grisea	Sooty shearwater	5	57.2 – 69.6	59.5 – 68.1	41.2 – 46.1	33.7 – 36.8
A. tenuirostris	Short-tailed shearwater	17	55.2 – 62.3	55.7 – 63.2	38.3 – 43.6	31.0 – 34.5
A. pacifica	Wedge-tailed shearwater	13	43.0 – 49.0	45.5 – 50.1	33.3 – 39.4	26.3 – 31.1
A. bulleri	Buller's shearwater	1	46.4	47.3	39.2	30.1
Puffinus						
P. bannermani	Bannerman's shearwater	3	55.9 – 56.7	48.7 – 50.3	28.4 – 30.4	23.0 – 23.9
P. nativitatis	Christmas shearwater	1	55.2	48.8	29.3	24.5
P. bryani	Bryan's shearwater	1	39.9	36.6	24.0	20.0
Calonectris						
C. leucomelas	Streaked shearwater	5	48.8 – 50.4	49.9 – 52.9	39.3 – 41.5	30.8 – 33.2
Pterodroma						
P. hypoleuca	Bonin petrel	4	35.3 – 38.3	35.8 – 39.0	25.4 – 28.2	20.3 – 21.6
P. solandri	Providence petrel	1	53.4	56.8	38.2	31.2
Fulmarus						
F. glacialis	Northern fulmar	1	46.1	51.0	40.5	33.6
Pagodroma						
P. nivea	Snow petrel	1	39.5	42.1	30.2	26.2
Bulweria						
B. bulwerii	Bulwer's petrel	2	29.7 – 30.4	30.2 – 30.3	22.7 – 23.5	18.3 – 18.8
Diomedeidae						
Phoebastria						
P. immutabilis	Laysan albatross	3	79.1 – 90.1	85.1 – 92.0	73.2 – 83.2	63.2 – 68.4
Hydrobatidae						
Hydrobates						
H. tristrami	Tristram's storm petrel	1	26.0	28.4	19.3	17.1
H. furcatus	Fork-tailed storm petrel	1	25.1	27.7	19.0	15.9

Table. 2-1-1. Sternum measurments (mm) of Procellariidae (CBM-PV 8301) and modern Proceralliiformes (each specimen). Round off to one decimal place. ( ) indicates slightly damaged material. Abbreviations see Fig. 2-2.

			Number of the process costalis		Mesurements (mm)			
Taxa	**English name**	**Specimen No.**	**Left**	**Right**	**LC**	**LM**	**GB**	**SBI**
Procellariidae (This study)		CBM-PV 8301	6	-	(42.4)	(49.0)	(28.8)	(23.6)
Procellaridae								
Ardenna								
A . carneipes	Flesh-footed shearwater	NSM PO-A 313	6	6	59.7	60.6	42.9	34.6
		NSM PO-A 314	6	6	59.5	59.8	43.5	34.6
A . grisea	Sooty shearwater	FRIJ 11303	6	6	61.1	61.1	41.2	33.7
		FRIJ 027-01	6	6	66.2	64.4	43.5	34.8
		FRIJ 027-02	6	6	65.0	65.5	45.5	34.4
		FRIJ 027-04	6	6	69.6	68.1	46.1	36.8
		NSM PO-A 601	6	6	57.2	59.5	44.8	36.3
A . tenuirostris	Short-tailed shearwater	FRIJ 10073	6	6	56.0	56.4	41.5	34.5
		FRIJ 10074	7	7	59.6	58.4	42.8	33.9
		FRIJ 10077	6	6	55.7	56.4	40.8	34.2
		FRIJ 10078	6	6	55.7	55.7	39.6	33.9
		FRIJ 10080	6	6	56.9	57.7	43.2	33.9
		FRIJ 10355	6	6	57.6	58.4	43.6	34.4
		FRIJ 10624	6	6	58.1	57.1	42.8	33.3
		FRIJ 10626	6	6	56.2	58.1	39.7	31.1
		FRIJ 028-04	6	6	58.5	61.3	42.4	33.5
		FRIJ 028-05	6	6	56.3	56.6	38.6	32.1
		FRIJ 028-10	6	6	61.0	60.8	40.9	33.4
		FRIJ 028-11	6	6	55.6	56.4	39.7	31.0
		FRIJ 028-19	6	6	62.3	63.2	40.7	33.0
		FRIJ 028-20	6	6	55.2	56.6	38.3	31.3
		FRIJ 028-24	6	6	56.4	56.7	38.7	31.8
		FRIJ 028-27	7	6	59.2	59.6	39.9	32.6
		FRIJ 028-28	6	6	58.0	58.3	41.1	33.6

Table. 2-1-1. (continued)

Taxa	English name	Specimen No.	Number of the process costalis		Mesurements (mm)			
			Left	Right	LC	LM	GB	SBI
Procellaridae								
Ardenna								
A . pacifica	Wedge-tailed shearwater	FRIJ 10206	7	7	45.9	47.9	33.3	27.6
		FRIJ 10321	6	6	46.8	48.5	38.2	29.6
		FRIJ 10716	6	6	43.0	45.9	37.4	30.9
		FRIJ 11070	6	6	45.7	47.4	37.2	29.4
		FRIJ 11071	7	7	46.7	47.4	36.0	28.2
		FRIJ 11073	6	6	46.0	47.2	33.8	28.2
		FRIJ 11304	6	6	46.7	47.3	38.3	30.5
		FRIJ 024-46	6	6	44.4	47.6	37.0	30.7
		FRIJ 024-48	6	6	46.1	49.6	39.4	30.7
		FRIJ 024-56	6	6	49.0	50.1	36.9	31.1
		FRIJ 024-58	6	6	46.0	48.8	36.6	29.4
		FRIJ 024-59	6	6	45.9	47.9	34.6	29.2
		FRIJ 024-62	6	6	43.1	45.5	34.6	26.3
A . bulleri	Buller's shearwater	NSM PO-A 312	6	6	46.4	47.3	39.2	30.1
Puffinus								
P. bannermani	Bannerman's shearwater	FRIJ 10155	6	6	55.9	50.3	30.4	23.9
		FRIJ 030-01	6	6	56.7	50.2	29.6	23.0
		FRIJ 030-03	7	6	56.3	48.7	28.4	23.7
P . nativitatis	Christmas shearwater	NSM PO-A 341*	6	6	55.2	48.8	29.3	24.5
P. bryani	Bryan's shearwater	FRIJ 11539	6	6	39.9	36.6	24.0	20.0
Calonectris								
C . leucomelas	Streaked shearwater	FRIJ 10313	7	7	50.4	52.0	41.5	32.0
		FRIJ 023-02	6	6	49.6	51.6	41.4	31.6
		FRIJ 023-15	6	6	49.1	52.9	40.7	30.8
		FRIJ 023-17	6	6	49.6	49.9	39.3	31.2
		FRIJ 023-18	6	6	48.8	50.4	40.6	33.2

Table. 2-1-1. (continued)

			Number of the process costalis		Mesurements (mm)			
Taxa	**English name**	**Specimen No.**	**Left**	**Right**	**LC**	**LM**	**GB**	**SBI**
Procellaridae								
Pterodroma								
P. hypoleuca	Bonin petrel	FRIJ 11301	6	6	35.4	36.6	25.4	20.3
		FRIJ 11385	6	6	38.3	39.0	25.5	21.5
		FRIJ 019-11	6	6	37.3	38.5	27.1	21.6
		FRIJ 019-15	6	6	35.3	35.8	28.2	21.2
P. solandri	Providence petrel	NSM PO-A 302	6	6	53.4	56.8	38.2	31.2
Fulmarus								
F. glacialis	Northern fulmar	FRIJ 013-02	5	5	46.1	51.0	40.5	33.6
Pagodroma								
P. nivea	*Snow petrel*	NSM PO-A 304	5	5	39.5	42.1	30.2	26.2
Bulweria								
B. bulwerii	Bulwer's petrel	FRIJ 022-09	6	6	30.4	30.3	22.7	18.3
		FRIJ 022-26	6	6	29.7	30.2	23.5	18.8
Diomedeidae								
Phoebastria								
P. immutabilis	Laysan albatross	FRIJ 011-01	6	6	79.1	85.1	73.2	62.2
		FRIJ 011-06	6	6	87.2	92.0	83.2	64.6
		FRIJ 011-10	6	6	90.1	91.3	79.7	68.4
Hydrobatidae								
Hydrobates								
H. tristrami	Tristram's storm petrel	FRIJ 036-07	6	6	26.0	28.4	19.3	17.1
H. furcata	Fork-tailed storm petrel	FRIJ 032-01	6	6	25.1	27.7	19.0	15.9

Table 2-2. The aspect ratio of the incisurae costales (dorsoventral length/craniocaudal length) on the left margo costalis of Procellariidae (CBM-PV 8301) and modern Procellariidae on average. The measurement data of the incisurae costales were taken by ImageJ and the value rounded off to two decimal places. * indicates the right margo costalis. For abbreviations, see the caption of Fig. 2-3.

Taxa	English name	(n)	ic-1	ic-2	ic-3	ic-4	ic-5
Procellariidae (CBM-PV 8301)		**1**	**N/A**	**1.98**	**2.10**	**1.77**	**1.74**
Procellariidae							
Ardenna							
A . carneipes	Flesh-footed shearwater	2	1.90	1.70	1.62	1.54	1.61
A . grisea	Sooty shearwater	5	1.59	1.65	1.57	1.59	1.51
A . tenuirostris	Short-tailed shearwater	17	1.59	1.58	1.62	1.60	1.78
A. pacifica	Wedge-tailed shearwater	13	1.49	1.56	1.57	1.42	1.49
A . bulleri	Buller's shearwater	1	1.15	1.41	1.53	1.61	1.54
Puffinus							
P . bannermani	Bannerman's shearwater	3	0.96	0.88	1.06	0.96	1.00
P . nativitatis *	Christmas shearwater	1	1.02	1.05	1.30	1.05	0.99
P. bryani	Bryan's shearwater	1	1.26	1.14	1.27	1.17	1.47
Calonectris							
C . leucomelas	Streaked shearwater	5	1.34	1.39	1.52	1.43	1.42
Pterodroma							
P . hypoleuca	Bonin petrel	4	1.47	1.29	1.45	1.53	1.61
P . solandri	Providence petrel	1	1.56	1.26	1.33	1.29	1.52
Fulmarus							
F . glacialis	Northern fulmar	1	1.34	1.34	1.07	1.12	-
Pagodroma							
P. nivea	Snow petrel	1	1.21	0.99	0.97	1.12	-
Bulweria							
B . bulwerii	Bulwer's petrel	2	1.67	1.27	1.17	1.02	1.30

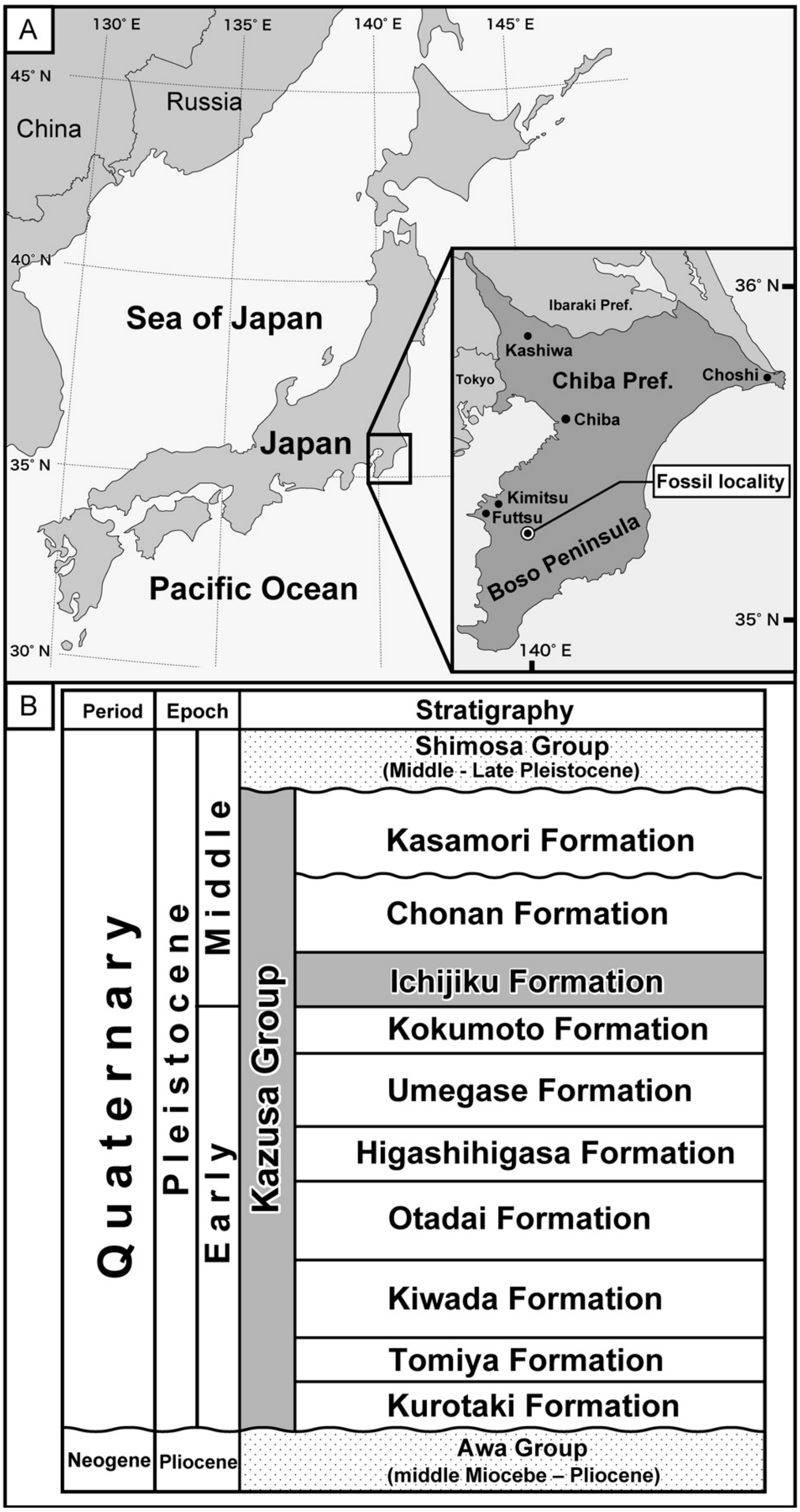


Fig. 2-1. **(A)** Locality map. **(B)** stratigraphic of the Kazusa Group. Stratigraphy based on Nakajima and Watanabe (2005), and Haneda and Okada (2019).

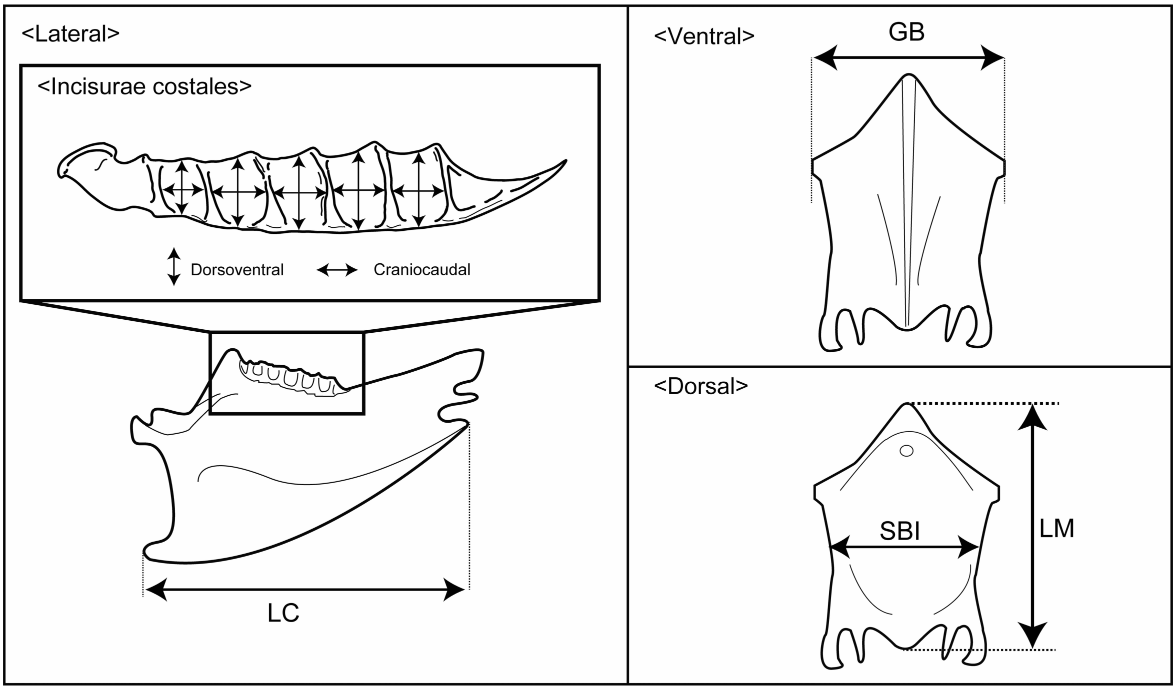


Fig. 2-2. Measurement points and terminology of measurements. Abbreviations: GB, greatest breadth; LC, length of the crina sterni; LM, length of the midline (from the rostrum sterni to the trabecula mediana); SBI, smallest breadth between the incisurae costales.

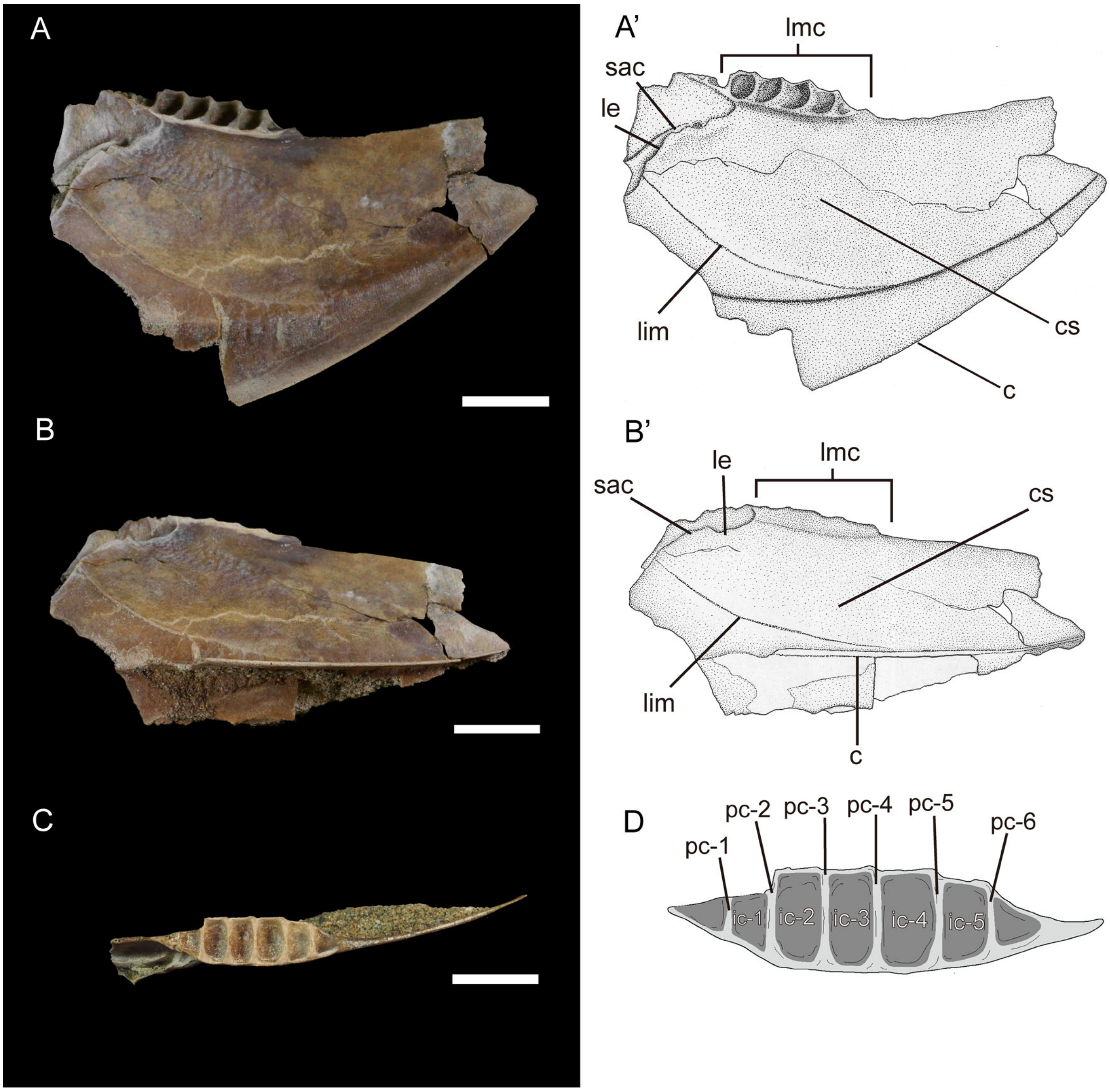


Fig. 2-3. Photographs and drawings of the Procellariidae sternum (CBM-PV 8301) from the Ichijiku Formation. (**A–A'**) left lateral view, (**B–B'**) ventral view, (C) left lateral view of the margo costalis. (**D**) drawing of incisura costalis. Abbreviations: c, carina sterni; cs, corpus sterni; ic, incisura costalis; le, labrum externum; lim, linea intermuscularis; lmc, left margo costalis; pc, processus costalis; sac, sulcus articularis coracoideus; tm, trabecula mediana. The scale bar represents 1 cm.

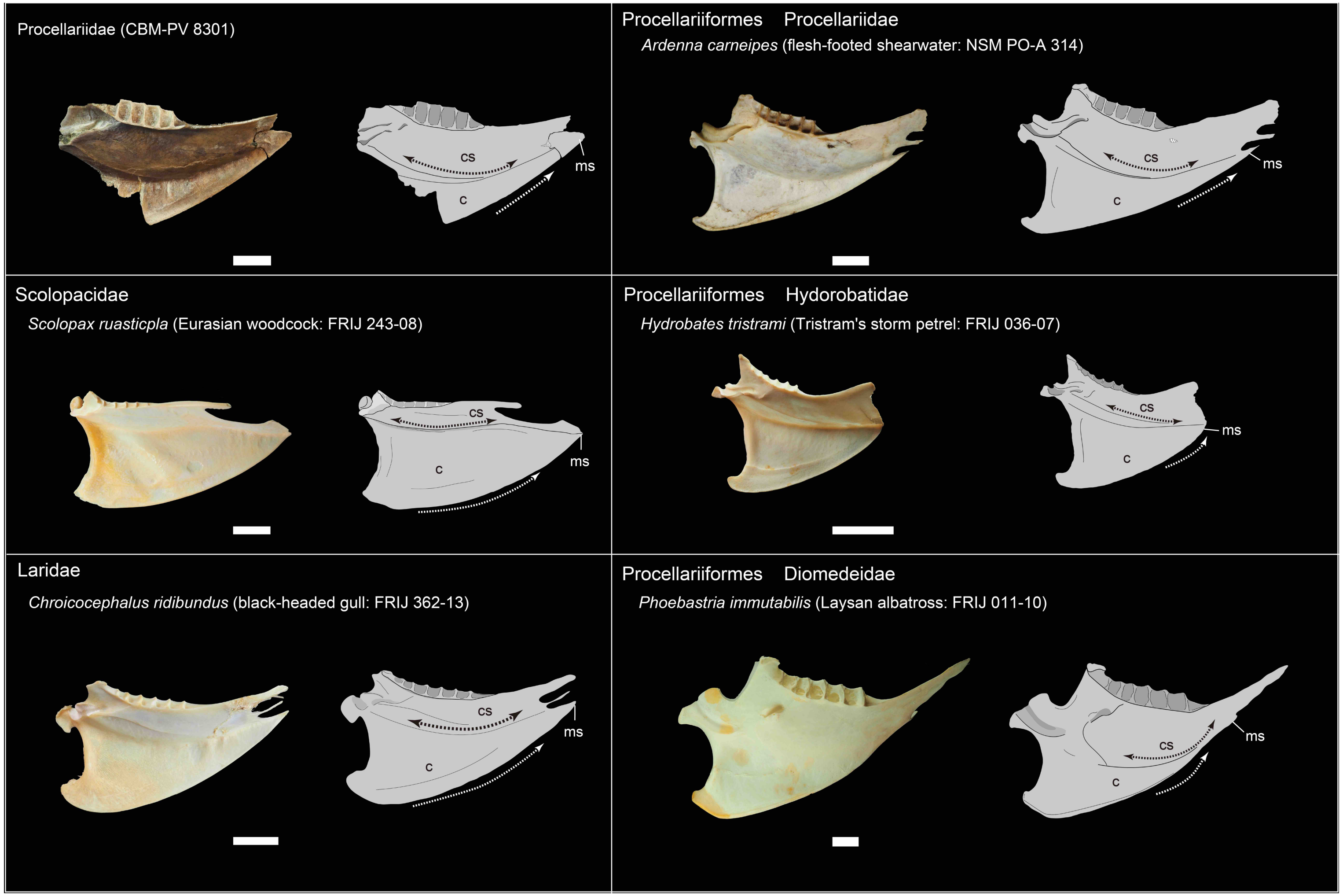
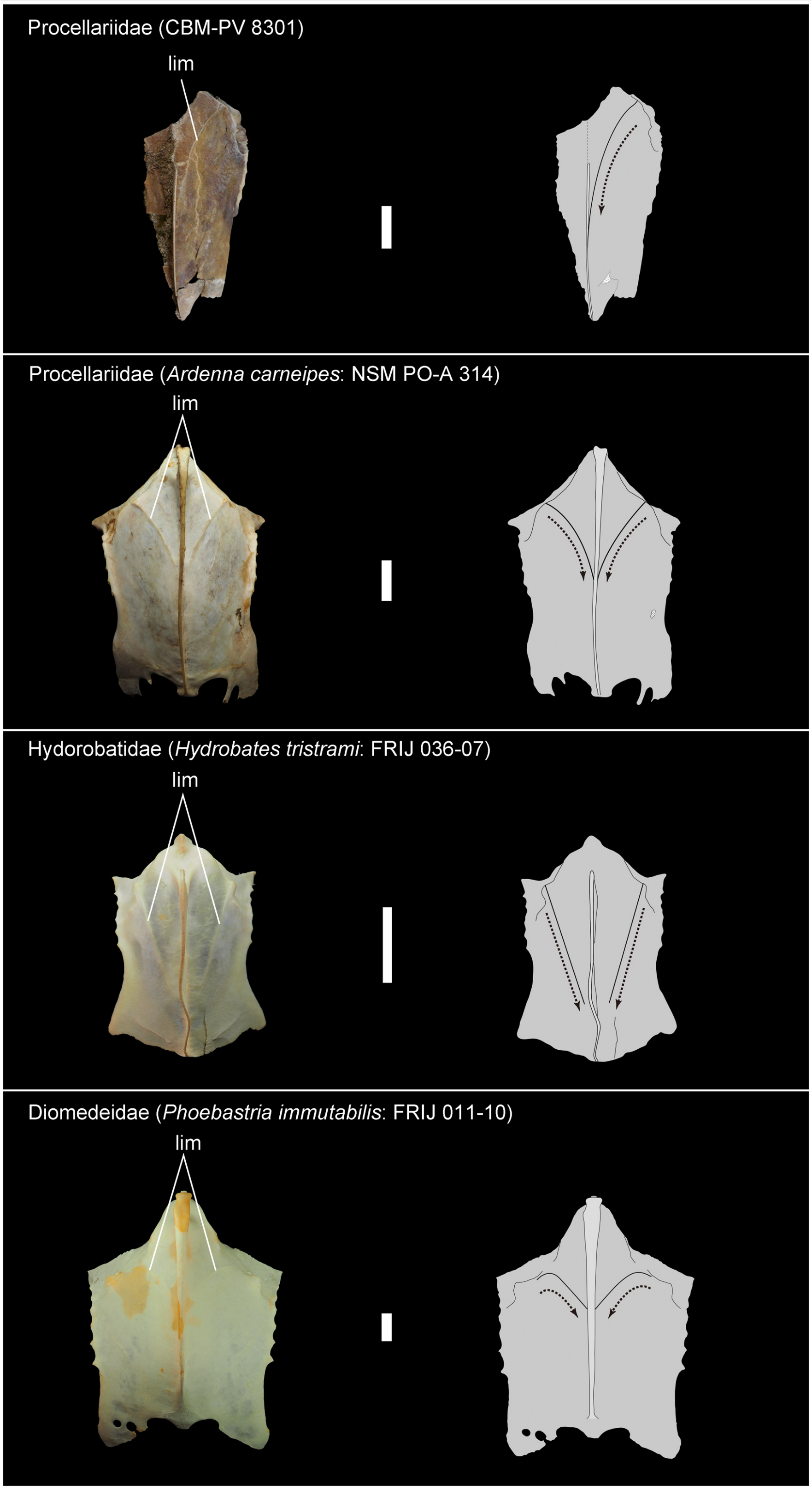


Fig. 2-4. Comparison of the shape of the corpus sterni and carina sterni of CBM-PV 8301 and modern birds. The dashed black arrow indicates the roundness of the corpus sterni. The dashed white arrow indicates the marginal curvature of the carina sterni. The scale bar represents 1 cm. For abbreviations, see the caption of Fig. 2-3.


Procellariidae (CBM-PV 8301)

Procellariidae (*Ardenna carneipes*: NSM PO-A 314)

Hydorobatidae (*Hydrobates tristrami*: FRIJ 036-07)

Diomedeidae (*Phoebastria immutabilis*: FRIJ 011-10)

Fig. 2-5. Comparison of the shape of the linea intermuscularis of Procellariiformes. The dashed black arrow indicates the shape and direction of the linea intermuscularis. The scale bar represents 1 cm. For abbreviations, see the caption of Fig. 2-3.

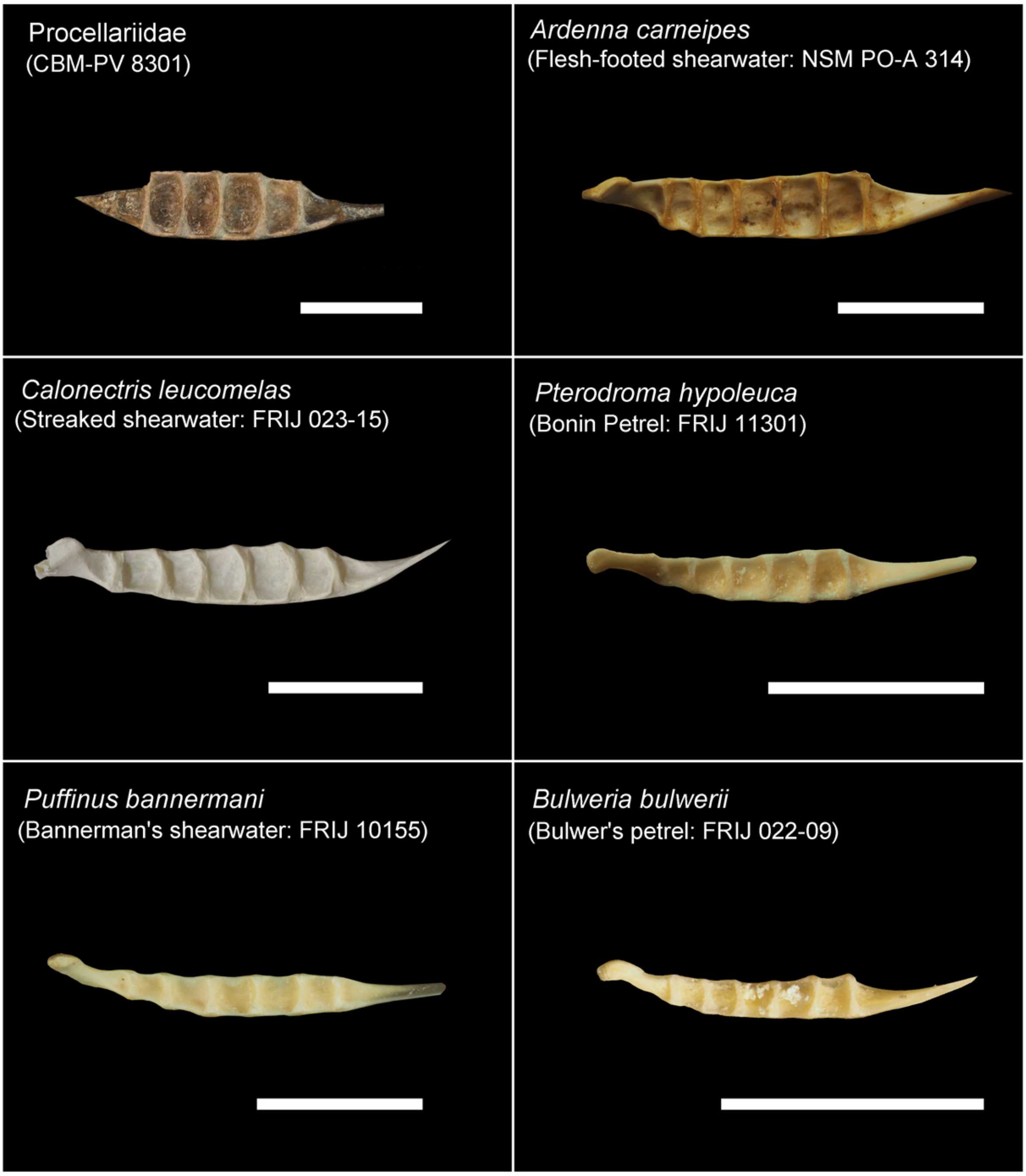


Fig. 2-6. Comparison of the shape of the incisurae costales of Procellariidae. The scale bar represents 1 cm. For abbreviations, see the caption of Fig. 2-3.

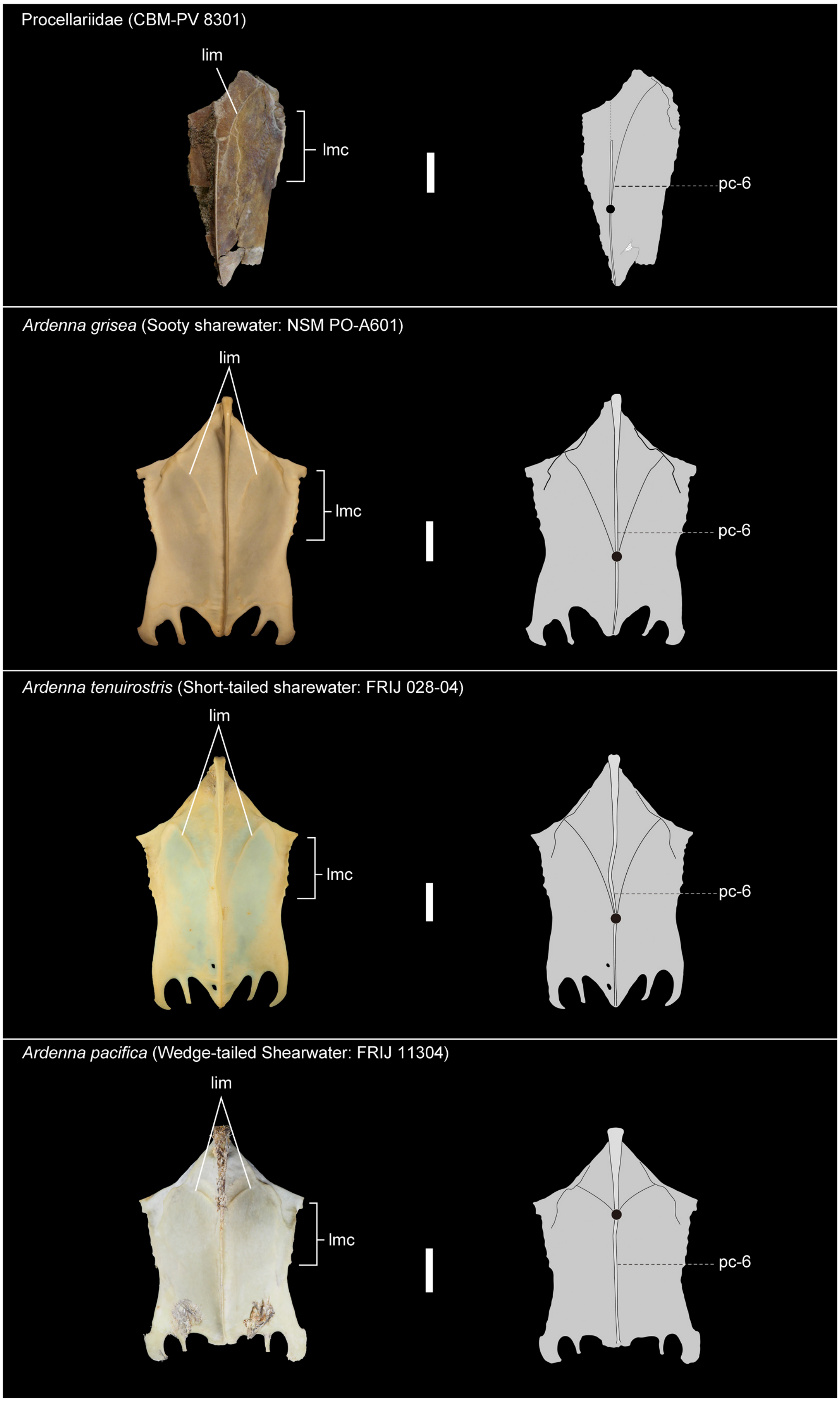


Fig. 2-7. Comparison of the length of the linea intermuscularis. ● indicates the end of the linea intermuscularis. The dashed line indicates the horizontal level of the sixth processus costalis. The scale bar represents 1 cm. For abbreviations, see the caption of Fig. 2-3.

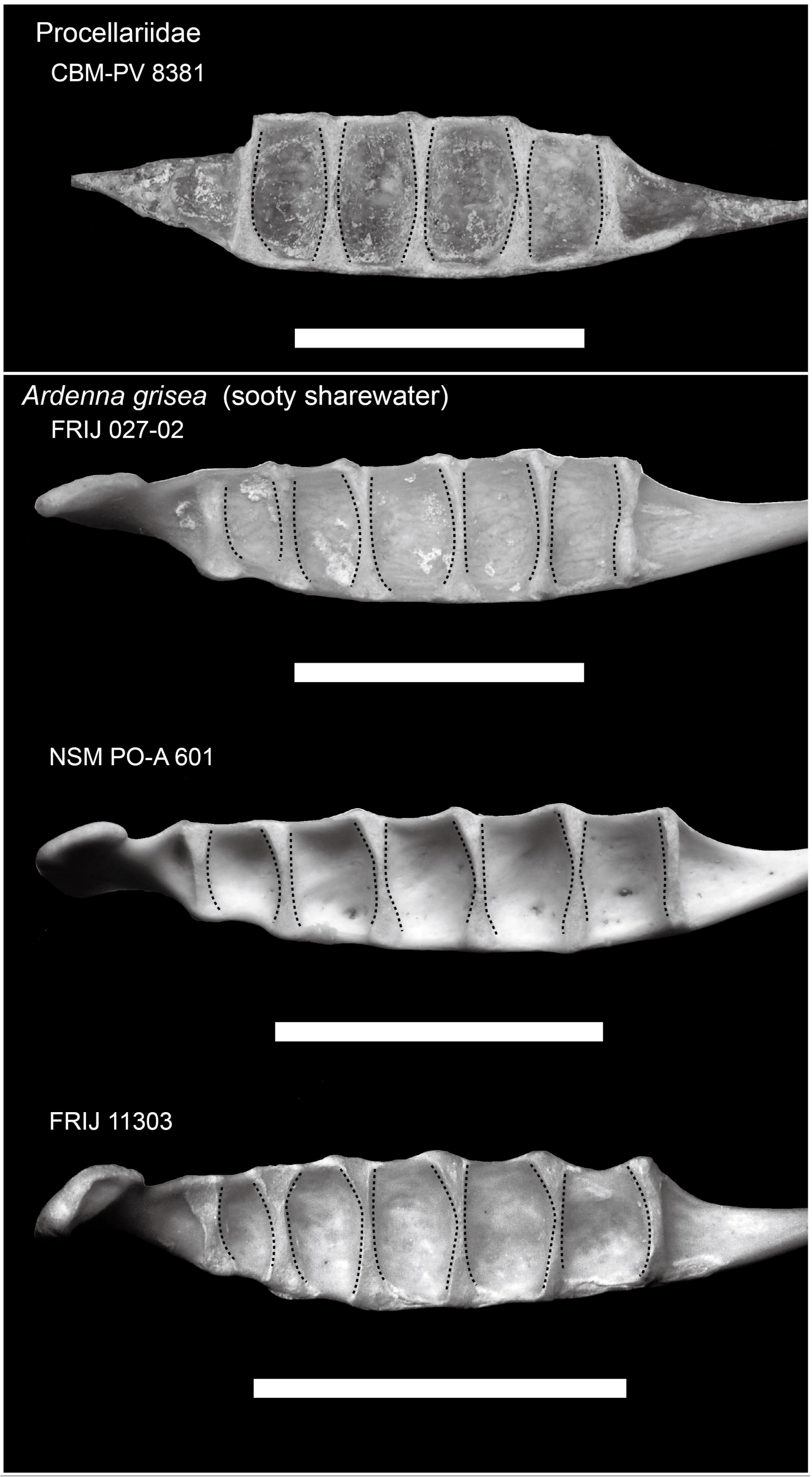


Fig. 2-8. The shape of the incisurae costales in Procellariidae (CBM-PV 8301) and *Ardenna grisea*. The scale bar represents 1 cm. Dashed line indicates the outline of the incisurae costales.

Chapter 3.

A humerus of Pliocene Alcidae from the Fukagawa Group in Hokkaido, Japan

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Introduction

Alcidae (auks) is a family of wing-propelled diving Charadriiformes that includes 10 genera and 24 extant species distributed in the Holarctic region (Gill et al., 2021). According to molecular phylogenetic studies, the Alcidae split from their sister lineage, the Stercorariidae around 35 Ma, during the Late Eocene (Smith and Clarke 2015). This estimation corresponds with the fossil records as a partial humerus of Alcidae was reported from the late Eocene deposit (36.0–34.2 Ma) in Georgia, USA, as the oldest fossil Alcidae (Chandler and Parmley, 2003). Thus, Alcidae is regarded as having diverged from Stercorariidae (skuas) at least 34.2 Ma (Smith 2016). Despite their early emergence, reliable fossil records of Alcidae have been documented from deposits younger than the Oligocene (>23.0 Ma). Since the Miocene (<23.0 Ma), they have been widely distributed across the Holarctic with taxonomic diversification, including several extinct genera and species. The extinct flightless auk Mancallinae (Pan-Alcidae in Smith 2011a: the term for the total clade, namely, Alcidae as the crown + Mancallinae as the stem) was highly diversified during the Miocene to Pliocene (>2.58 Ma), and many fossils have been reported (e.g., Lucas, 1901; Howard, 1982; Chandler, 1990; Smith, 2011a). Many Alcidae fossils (e.g., *Aethia*, *Uria*, *Cepphus*, *Cerorhinca*, *Synthliboramphus*, and *Mancalla*) have been reported from the Miocene–Pleistocene deposits (>0.0117 Ma) of the eastern Pacific, especially from Mexico and California, USA (e.g., Lucas, 1901; Howard, 1968, 1971, 1982; Chandler, 1990; Guthrie, 1992, 2005; Smith, 2011a, 2013, 2014; Powell et al., 2019). Alcidae fossils have also been reported from the Atlantic Ocean basin. However, differing from the Pacific taxa, *Alca*, *Pinguinus*, and *Miocepphus* are known as the dominant genera there (e.g., Olson and Rasmussen, 2001; Dyke and Walker ,2005; Smith et al., 2007; Wijnker and Olson, 2009; Smith and Clarke, 2011; Smith and Mayr, 2013; Kilmer and Steadman, 2016).

Conversely, little is known about Alcidae distribution in the western Pacific (i.e., Asia). To date, fossil remains from the western Pacific have been reported from only five localities in Japan (Fig. 3-1A). The oldest fossil record from Japan consists of three humeri and a femur of Alcidae from the Oligocene deposit in Fukushima Prefecture reported by Ono and Hasegawa (1991). However, Smith (2013, 2016) doubted these Oligocene Alcidae records due to their poor preservation. As for the Miocene fossil records, Rich et al. (1986) briefly mentioned an Alcidae humerus and a proximal carpometacarpus which were found from the Mizunami Basin of Gifu Prefecture with their photo. Kohno (1997) reported *Praemancalla* (*sensu* Howard, 1966) from the Miocene deposit of Miyagi Prefecture at a conference. However, a detailed description of these Miocene fossils has not yet been published. Therefore, reliable fossil records of Alcidae from the western Pacific are known from only two localities: at Shiriya, in Aomori Prefecture, where several alcids including *Uria*, *Synthliboramphus*, *Cepphus*, *Aethia*, Fraterculini, and *Mancalla*? sp. were reported from the Pleistocene deposit (ca. 0.32 Ma and ca. 0.12 Ma) (Watanabe et al., 2016, 2018a), and in Chiba Prefecture where *Alle* cf. *alle* and *Mancalla* sp. were reported from the Pleistocene of the Ichijiku Formation (ca. 0.7 Ma) (Watanabe et al., 2020).

Several researchers have discussed the biogeography of Alcidae (e. g., Bédard 1985; Olson, 1985; Konyukhov, 2002; Smith and Clarke, 2015). Most of these studies focused on the taxonomic interchange between the eastern Pacific and Atlantic oceans, and they did not discuss extensively when or how the Alcidae entered the western Pacific. As previously mentioned, Alcidae fossils from the Miocene and pre-Miocene of the western Pacific are few, and the assignment of these fossils to Alcidae remains ambiguous. However, the fossil records imply that Alcidae were as widely distributed in the eastern and western Pacific with taxonomic diversification as today, at least in the Pleistocene (Watanabe et al., 2016, 2018a, 2020).

Here I describe an incomplete proximal left avian humerus from the Horokaoshirarika Formation (Pliocene) of the Fukagawa Group, in Hokkaido, Japan (Fig. 3-1A). This fossil was assigned as an Alcidae gen. et sp. indet. by Aotsuka and Endo (2022), on the basis of the osteological characteristics. This identification is reasonable, however, this specimen is fragmentary humerus and observable features are limited. Therefore, I described this humerus here, on the basis of the Aotsuka and Endo (2022) with some additional comparison results, such as compression ratio and the detailed description of the shape of the supracoracoideus scar, as a more definite basis for this identification. This fossil humerus provides the first record of Alcidae from the Pliocene of the western Pacific. Although this specimen represents only a partial humerus, it helps to elucidate the history of alcid distribution in the Pacific.

Geological setting

The Fukagawa group comprises the Miocene–Pliocene marine sediment, and contains the Horokaoshirarika Formation, Ichinosawa Formation, and Bibaushi Formation (Fig. 3-1B; Kobayashi et al., 1969; Watanabe and Yoshida, 1995). The Horokaoshirarika Formation is widely distributed in Numata Town and divided into the upper and lower parts by a thin tuff layer, named Ops (Kobayashi et al., 1969; Watanabe and Yoshida, 1995). The lower part is composed of siltstone and fine-grained sandstone, and the upper part consists of medium- to coarse-grained sandstone (Watanabe and Yoshida 1995). A diatom study has suggested that the Horokaoshirarika Formation corresponds to 7A (7.7–6.5 Ma) to 7Bb (5.6 to [3.9–3.5] Ma) of the Neogene North Pacific Diatom zone (NPD) (Yanagisawa and Akiba, 1998; Nakashima and Watanabe, 2000; Yanagisawa and Watanabe, 2011; Watanabe and Tanaka, 2017; Tanaka and Watanabe, 2018, 2019). The tuff layer (Ops) age has been estimated as 4.5 ± 0.7 Ma using fission track dating (Wada et al., 1986). Thus, the age of the Horokaoshirarika Formation is regarded as latest Miocene–early Pliocene (approximately 7.7–5.2 Ma) at the lower part and as early Pliocene (approximately 4.5–3.5 Ma) at the upper part.

Many marine mammals, such as Sirenia (sea cows), Pinnipedia (otariids), Cetacea (whales), and Delphinoidea (porpoises), have been reported from the upper and/or lower part of this formation (Kimura et al., 1987; Furusawa and Group, 1990; Yamashita and Kimura, 1990; Furusawa et al., 1993; Kohno et al., 1995; Ichishima and Kimura, 2000; Shinohara, 2006, 2012; Tanaka, 2016; Tanaka and Ichishima, 2016; Tanaka et al., 2018; Tanaka and Watanabe, 2018, 2019). However, other vertebrate fossil records are scarce. Yamashita (1989) briefly mentioned the occurrence of an avian fossil from Numata Town; however, the fossil has not yet been formally described.

The fossil described here is an alcid humerus which was collected from the 4th Ebishima district in Numata Town in June 1988 by members of the Numata Fossil Laboratory (now the Numata Fossil Museum). According to the collection data, this humerus stems from the Pliocene deposit of the Fukagawa Group. Although the geographical coordinate of the collection locality was not recorded, the fossiliferous outcrops of the Horokaoshirarika Formation are exposed along the Horonitachibetsu River in this district (Fig. 3-1C; Kobayashi et al., 1969). Several marine mammals have been collected from the upper part of this formation at the riverbed (e.g., Furusawa et al., 1993; Kohno et al., 1995; Shinohara, 2006; Tanaka and Ichishima, 2016). Thus, this fossil humerus presumably stems from the upper Horokaoshirarika Formation.

Material and methods

I compared the new specimen (NFL 45) with the humeri of seven genera and 14 species of extant and extinct Alcidae (including 20 fossil specimens, which were collected from the Pleistocene deposit on Aomori Prefecture, Japan), a total of 46 specimens stored at FRIJ, NSM, and NSMT. I also compared NFL 45 with non-alcid Charadriiformes and other diving birds, such as Procellariidae (shearwaters), Sulidae (boobies), Spheniscidae (penguins), and Anatidae (diving ducks: foot-propelled) a total of 24 specimens (13 genera, 15 species) stored at FRIJ and UMUT (Table 3-1 and 3-1-1). Osteological measurements were taken to the nearest 0.01 mm using a digital caliper (SINWA 19975), and values greater than 150 mm were measured by hand caliper (Mitutoyo 300 mm: accuracy 0.05 mm). I were unable to observe *Alca*, *Alle*, and *Pelecanoides* directly, due to the limitations of the osteological collection, thus, I based the humerus characteristics on the supplementary material of Smith (2011a) for *Alca* and *Alle*, and on data in the literature (Kuroda, 1967; Harrison, 1977a; Warham, 1977, 1996) for *Pelecanoides*.

Systematic paleontology

Order Charadriiformes Huxley, 1867

Family Alcidae Leach, 1820

Alcidae gen. et sp. indet.

Referred specimen. — NFL 45, an incomplete proximal left humerus (Fig. 3-2).

Horizon and age. — Presumably upper Horokaoshirarika Formation of the Fukagawa

Group (Pliocene).

Description. — NFL 45 comprises an incomplete proximal left humerus. The caput humeri and the humeral diaphysis are crushed. The preserved proximal–distal length is 38.03 mm. The cross-section of the diaphysis exhibits an elliptical outline with dorsoventral compression (Fig. 3-2 F). The crista deltopectoralis is low and smooth. The dorsal surface of the crista deltopectoralis is flat. The distal margin of the tuberculum dorsale is preserved and protruding from the diaphysis. The supracoracoideus scar (i.e., crista m. supracoracoidei) exhibits a long and narrow rectangular outline.

Comparison. —Mayr (2009) stated that the osteological features of Charadriiformes are difficult to characterize because members of this group have diversified into many different habitats. However, the humeral diaphysis of Alcidae is dorsoventrally compressed, much as in other wing-propelled diving birds, and differs from all other Charadriiformes (Table 3-1; Strauch, 1985). Although it is incomplete, the humeral diaphysis of NFL 45 is slender and notably compressed dorsoventrally as in Alcidae (Fig. 3-3). Compared the compression ratio, NFL 45 indicates 0.60 and most of Alcidae suggests around 0.60, except *Cepphus* and *Aethia*. Although Spheniscidae is known as the excellent wing-propelled diver, their humeral diaphysis is extremely flattened with broad. The compression ratio indicates 0.33–0.43. Sulidae are known as plunge divers that use their wings and feet underwater (Ashmole, 1971), and reach great depths by using their wingbeats (Ropert-Coudert et al., 2009; Capuska et al., 2011). However, they differ from Alcidae or Spheniscidae in that the humeral diaphysis of Sulidae is not compressed; rather, it has a nearly rounded cross-section and the compress ratio indicates 0.92 (see character 210 of Smith ND, 2010). In addition, the crista deltopectoralis of Sulidae is less prominent than in NFL 45 (Fig. 3-4).

Some Procellariidae, such as *Puffinus* and *Ardenna* (shearwaters), are known as pursuit divers that use their wings and feet for underwater propulsion (Ashmole, 1971; Burger, 2001). As Kloess and Parham (2017) mentioned that some procellariids and alcids have similar mechanical characters and diving foraging strategies; also, the humeral diaphysis is dorsoventrally compressed in both families (Kuroda, 1954; Warham, 1977; Habib, 2010). The measurement data in this study demonstrated this convergence, the compression ratio in *Ardenna* and *Puffinus* indicates similar values to Alcidae (Table 3-1). However, the features of the crista deltopectoralis differ between Alcidae and Procellariidae. In most Alcidae, generally, the projection of the crista deltopectoralis is low, and the tip of the crista is smooth or slightly swollen (Fig. 3-3). On the other hand, the crista is remarkably projected with a nearly triangular outline, and the tip is pointed or angled in Procellariidae (Fig. 3-4). Also, the dorsal surface of the crista deltopectoralis is typically flat in extant Alcidae (see character 106 of Smith 2011a), while this surface is concave in Procellariidae (Fig. 3-4: dorsal view). NFL 45 shares the osteological features of the crista deltopectoralis of Alcidae rather than Procellariidae (see description and Fig. 3-3). I noted that the humerus of *Pelecanoides* (diving petrels) is similar to Alcidae (Harrison, 1977a). However, compared with *Ardenna grisea* (sooty shearwater), the humeral diaphysis of *Pelecanoides* is slightly less compressed (Kuroda, 1967; Warham, 1996). The humeral diaphysis of NFL 45 is notably compressed as in *Ardenna grisea* and most Alcidae (Table 3-1). In addition, *Pelecanoides* is a relatively small taxon of Procellariidae, and their humerus length is roughly 43–45 mm (Kuroda, 1967; Warham, 1977). Although NFL 45 represents only a partial proximal specimen, its length is about 38 mm. Therefore, even if the humeral characteristics of NFL 45 are similar to *Pelecanoides*, the complete humerus length of NFL 45 could estimate much beyond the range of that of this genus.

Although the compression of the diaphysis is extremely weak, the characteristics of the crista deltopectoralis of Anatidae (i.e., *Aythya* and *Netta*) are similar to Alcidae (Fig. 3-4); the crista deltopectoralis is low and smooth with a smooth dorsal surface. However, NFL 45 is distinguishable from Anatidae by its tuberculum dorsale. In general, the tuberculum dorsale is situated on the dorsal margin of the caput humeri on the caudal surface, and it does not protrude or protrudes weakly from the diaphysis in Anatidae. However, in Alcidae, the tuberculum dorsale is long and situated more distally, protruding distinctly from the diaphysis at the distal margin. NFL 45 is missing its proximal end; nevertheless, the distal margin of the tuberculum dorsale is preserved, and it protrudes at the distal margin, as in Alcidae (Fig. 3-5).

The scar for the insertion of m. supracoracoideus (supracoracoideus scar) of NFL 45 is recognizable on the tuberculum dorsale; it exhibits a long and narrow rectangular outline that extends proximally as in Alcidae (see character 113 of Smith, 2011a). This scar shape also distinguishable characteristics Alcidae from other wing-propelled diving birds. Spheniscidae also displays a long and narrow supracoracoideus scar. However the scar is seen on the dorsal surface rather than the caudal surface, and it elongated diagonally. In Procellariidae, the tuberculum dorsale is protrude, however, the supracoracoideus scar shows a circular outline. Although the outline of the scar in Sulidae also displays a circular outline, it is smaller and more obscure than other wing-propelled diving birds. In addition, the supracoracoideus scar in Anatidae (i.e., *Aythya* and *Netta*) displays a small and triangular outline (Fig. 3-5; Zelenkov, 2016b).

Thus, I identified NFL 45 as belonging to the Alcidae based on the combination of the following five features: (1) the humeral diaphysis is dorsoventrally compressed; (2) the tip of the crista deltopectoralis is low and smooth; (3) the dorsal surface of the crista deltopectoralis is flat; (4) distal margin of the tuberculum dorsale is protruded from the diaphysis; and (5) the shape of the supracoracoideus scar is long and narrow. The characteristics of the humerus mentioned above are features common to most extant Alcidae taxa. However, I note that some exceptions have been identified in extinct Alcidae. For example, it has been documented that extinct flightless alcids (e.g., *Mancalla* and *Pinguinus*) have an extremely compressed humeral diaphysis, as in Spheniscidae (see Fig. 3 of Smith, 2013). In addition, the dorsal surface of the crista deltopectoralis in *Alca stewarti* (an extinct species from the Miocene–Pliocene) is slightly concave, differing from other alcids, and is one of the diagnostic characters of this species (see character 57 of Smith and Clarke, 2011).

Smith (2011a) distinguished Mancallinae from other alcids by some of the apomorphic characters, including the following two osteological features of the humerus: the crista deltopectoralis extends to the midpoint of the diaphysis, and the "mancalline scar" (*sensu* Smith, 2011a) is present on the proximocaudal surface (see character 104 and 120 of Smith, 2011a). The crista deltopectoralis of NFL 45 does not extend to the midpoint of the diaphysis, and the "mancalline scar" could not be recognized on the caudal surface of this specimen. Since NFL 45 does not have either of the above two features, it is appropriate to classify it as crown clade Alcidae rather than Mancallinae (i.e., stem Alcidae).

A comparison with the Alcidae taxa shows that the diameter of the remaining diaphysis of NFL 45 is similar to that of *Uria*, and slightly larger than that of *Fratercula cirrhata* (tufted puffin). Despite its incompleteness, the cross-section of the diaphysis of NFL 45 appears almost flattened, as in most Alcidae, rather than sub-rounded, as in *Cepphus* (see Fig. 3 of Smith, 2013). In my measurement data, *Cepphus* and *Aethia* indicate a relatively high compression ratio among Alcidae (Table 3-1). In the dorsal view, the projection of the crista deltopectoralis of NFL 45 is low and the tip of its crista is smooth, as in *Uria* and *Alca* (Fig. 3-6; see character 105 of Smith, 2011a); the projection of the crista deltopectoralis is slightly swollen in *Aethia*, *Alle*, *Fratercula*, and *Cerorhinca*, and is swollen with an abrupt slope in *Cepphus* (Fig. 3-6; Watanabe et al., 2020). However, unlike *Uria* and *Alca*, NFL 45 has a relatively short margin of the crista deltopectoralis and does not have the rugose ridge that is seen in *Uria* (Fig. 3-6; Watanabe et al., 2016). The shape of the supracoracoideus scar is different for each taxon; for example, in *Fratercula*, *Cerorhinca* and *Cepphus*, the proximal end of the scar is much broader than the distal end, thus it displays inverted-pear like outline. Whereas in *Uria*, *Alca* and *Aethia*, the width of the scar is almost the same throughout its length (see character 113 of Smith, 2011a). In NFL 45, the remaining scar extends with almost the same width from the distal to the proximal, suggesting that the complete scar might be similar to *Uria*, *Alca*, and *Aethia* (Fig. 3-6). However, a reliable comparison of this feature is not possible for NFL 45, since the proximal end is missing.

Based on the size, dorsoventraly compressed humeral diaphysis, the shape of the crista deltopectoralis, and the supracoracoideus scar, NFL 45 appears to resemble *Uria*. Nevertheless, the detailed features of the crista deltopectoralis of NFL 45 are not identical with this genus (e.g., the crista is relatively short, and there is no rugose ridge as in *Uria*). In summary, it was difficult to identify the genus or species due to the poor fossil preservation, thus, I determined that NFL 45 is most appropriately classified as Alcidae gen. et sp. indet.

Discussion

Whether Alcidae originated in the Pacific or the Atlantic Ocean has been controversial due to the inadequacy of the fossil record (Smith and Clarke, 2015). However, Alcidae were distributed in the Holarctic region during the Miocene. Their remains have been reported from the Miocene deposits in the Pacific and Atlantic Ocean basins in North America and the Atlantic Ocean basin in Europe (e.g., Howard, 1968, 1978; Wijnker and Olson, 2009; Smith and Mayr, 2013). Warheit (1992, 2002) and Smith and Clarke (2015) reported that taxonomic diversification of the Alcidae dramatically increased during the Miocene and then decreased during the Pliocene to the Pleistocene due to such environmental changes as a major paleoclimatic transition and oceanographic fluctuations. In fact, various Alcidae have been discovered from the Miocene–Pliocene deposit of the eastern Pacific and the Atlantic Ocean basin, especially from North America (e.g., Howard, 1982; Chandler, 1990; Olson and Rasmussen, 2001; Smith and Clarke, 2011).

On the basis of fossil records, *Uria* and *Cepphus* had already emerged in the eastern Pacific during the Miocene (Howard, 1981, 1982). However, their fossil remains have not been reported from the pre-Pleistocene deposit of the Atlantic basin (Table 3-2; Ray et al., 1968; Olson, 1985; Tyrberg, 1999, 2008; Warheit, 2002). They were widely distributed in the Pacific and Atlantic oceans during the Pleistocene, and both genera have also been found in Japan (Table 3-2; Watanabe et al., 2016, 2018, 2020). Meanwhile, *Alca* and *Pinguinus* dominated in the Atlantic (Tyrberg, 1999, 2008; see Appendix 2.1 of Warheit, 2002). The Pleistocene alcids of the western Pacific shared more Alcidae genera with the eastern Pacific than with the Atlantic; the only genus that distributed in both the western Pacific and Atlantic is *Alle* (Table 3-2; Watanabe et al., 2020). Such a taxonomic similarity implies that a taxonomic interchange might have occurred between the eastern and western Pacific before the Pleistocene.

The coastal topography and ocean current changes, which were related to the opening and closing events of seaways (e.g., between the North and South America, and the Bering Strait), might have affected not only the species diversity of Miocene and Pliocene Alcidae but also their geographic radiation (Bédard, 1985; Konyukhov, 2002; Smith and Clarke, 2015). The timing of the opening of the Bering Strait has been studied by several methods (i.e., biochronology and climate models), however it remains uncertain (e.g., Repenning and Brouwers, 1992; Brierley and Fedorov, 2016; Haywood et al., 2016). According to fossil-based study (diatoms and molluscs), the Pacific Ocean was connected to the Arctic Ocean by the Bering Strait in the late Miocene or early Pliocene, and the initial opening occurred between 7.4–7.3 Ma and 4.8 Ma (Marincovich and Gladenkov, 1999). Interestingly, the Fukagawa Group comprises a Miocene–Pliocene marine sediment. Diatom studies indicate that the upper Horokaoshirarika Formation, from which NFL 45 was presumed to have been collected, has been assigned to NPD 7Bb (5.6 to [3.9–3.5] Ma) (Nakashima and Watanabe, 2000; Yanagisawa and Watanabe 2011). Thus, the depositional age of this formation almost corresponds with the opening of the Bering Strait, as was estimated by fossil records (Marincovich and Gladenkov, 1999). In addition, the Sea of Japan had also opened around the early Miocene, creating a narrow seaway between the Japanese archipelago and mainland Asia, then it expanded to its present size (Jolivet and Tamaki, 1992; Pavlyutkin et al., 2016). Alcidae fossils reported from the Oligocene and Miocene deposits in Japan are either controversial or require more detailed descriptions (Rich et al., 1986; Ono and Hasegawa, 1991; Kohno, 1997). However, it is plausible that the Bering Strait and the Sea of Japan opening events might have enabled Alcidae migration from the eastern to the western Pacific during the late Miocene to the early Pliocene. This hypothesis is also reasonable to explain the discovery of Atlantic auk, *Alle* cf. *alle*, from the Pleistocene deposit in Japan (Watanabe et al., 2020), in fact, this genus has never been reported from the eastern Pacific (Table 3-2). Conversely, it is necessary to consider other hypotheses that why the eastern Pacific Alcidae did not disperse during the Miocene. Although Alcidae fossils from the western Pacific are scarce, NFL 45 is an important specimen to test the distribution route and migration timing of Alcidae between the eastern and western Pacific.

Table 3-1. Humerus mid-diaphysis measurements in mm of NFL 45 and the compared taxa. Values in parentheses indicate the specimen is crushed. [ ]= number of fossil specimens included. *=fossil specimens: the genus and species are indeterminate (see Watanabe et al., 2018a).

			Width mid-diaphysis		Compression Ratio
Taxa	**English name**	**n**	**Dorsoventral**	**Craniocaudal**	**Dorsoventral/ Craniocaudal**
Alcidae gen. et sp. indet.					
NFL 45 (This study)		1 [1]	(4.50)	(7.48)	0.60
Alcidae (Charadriiformes)					
Uria lomvia	Thick-billed murre	6 [4]	3.69 – 4.30	6.41 – 8.10	0.48 – 0.65
Uria aalge	Common murre	3 [0]	3.79 – 4.76	6.83 – 8.22	0.55 – 0.58
Uria onoi (extinct)		5 [5]	4.35 – 5.16	7.47 – 9.36	0.52 – 0.64
Cepphus carbo	Spectacled guillemot	1 [0]	4.06	5.21	0.78
Cepphus columba	Pigeon guillemot	1 [0]	3.57	4.81	0.74
Cerorhinca monocerata	Rhinoceros auklet	3 [0]	3.27 – 3.62	5.61 – 5.97	0.58 – 0.61
Synthliboramphus antiquus	Ancient murrelet	10 [5]	2.20 – 2.62	3.81 – 4.64	0.54 – 0.59
Synthliboramphus wumizusume	Japanese murrelet	2 [0]	2.14 – 2.23	3.49 – 4.21	0.53 – 0.61
Aethia psittacula	Parakeet auklet	1 [0]	2.90	3.82	0.76
Aethia pusilla	Least auklet	2 [1]	1.84 – 1.86	2.61 – 2.64	0.70
Aethia cristatella	Crested auklet	4 [2]	2.44 – 2.54	4.10 – 4.34	0.59 – 0.60
Fratercula cirrhata	Tufted puffin	3 [0]	3.51 – 4.15	5.98 – 6.82	0.59 – 0.68
Fratercula corniculata	Horned puffin	2 [0]	3.11 – 3.37	5.13 – 5.36	0.61 – 0.63
Fraterculini gen. et. sp. indet.*		2 [2]	3.87 – 4.17	6.45 – 6.68	0.60 – 0.62
Mancallinae (Pan-Alcidae)					
Mancalla ? sp. (extinct)		1 [1]	4.42	11.40	0.39
Stercorariidae (Charadriiformes)					
Stercorarius longicaudus	Long-tailed jaeger	2 [0]	4.03 – 4.22	4.76 – 4.77	0.84 – 0.89
Laridae (Charadriiformes)					
Onychoprion fuscatus	Sooty tern	4 [0]	3.28 – 3.78	3.14 – 4.01	0.92 – 1.08
Larus argentatus	European herring gull	1 [0]	8.10	6.64	1.22
Chroicocephalus ridibundus	Black-headed gull	1 [0]	4.56	3.70	1.23
Rissa tridactyla	Black-legged kittiwake	1 [0]	4.87	4.80	1.01
Anous stolidus	Brown noddy	2 [0]	3.41 – 3.56	3.61 – 3.66	0.94 – 0.97
Spheniscidae (Sphenisciformes)					
Pygoscelis papua	Gentoo penguin	1 [0]	6.33	19.33	0.33
Spheniscus humboldti	Humboldt penguin	1 [0]	6.48	15.24	0.43
Sulidae (Suliformes)					
Sula leucogaster	Brown booby	1 [0]	6.59	7.18	0.92
Procellariidae (Procellariiformes)					
Ardenna grisea	Sooty shearwater	2 [0]	3.73 – 3.99	6.86 – 7.01	0.53 – 0.58
Ardenna tenuirostris	Short-tailed shearwater	2 [0]	3.77 – 3.84	6.05 – 6.22	0.62
Ardenna pacifica	Wedge-tailed shearwater	2 [0]	4.06 – 4.13	5.08 – 5.15	0.80
Puffinus bannermani	Bannerman's shearwater	2 [0]	2.81 – 2.86	4.73 – 4.86	0.58 – 0.60
Anatidae (Anseriformes)					
Aythya marila	Greater scaup	1 [0]	4.92	5.21	0.94
Netta peposaca	Rosy-billed pochard	1 [0]	5.84	6.27	0.93

Table 3-1-1. Measurements of NFL 45 and left humerus of compared taxa in millimeter (each specimen). Measurements were taken in millimeters using a distal caliper (SINWA 19975), and the values greater than150 mm were measured by hand caliper (Mitutoyo 300mm).Values in parentheses indicate crushed specimens. ●= indicates fossil specimen. △= indicates young individual (based on the specimen label). *= indicates right humerus.

		Width mid-diaphysis		**Compression Ratio**
Taxa	**Length**	**Dorsoventral**	**Craniocaudal**	**Dorsoventral/ Craniocaudal**
Alcidae gen. et sp. indet.				
● NFL 45 (This study)	(38.03)	(4.50)	(7.48)	0.60
Alcidae (Charadriiformes)				
Uria lomvia **(thick-billed murre)**				
NSMT AS 01055	84.11	3.69	6.91	0.53
NSMT AS 01475	91.25	4.17	7.41	0.56
● NSM PV 23735*	(83.94)	4.14	6.41	0.65
● NSM PV 23736*	(63.76)	3.94	8.10	0.49
● NSM PV 24238	(70.22)	3.80	7.90	0.48
● NSM PV 24246	(77.08)	4.30	6.69	0.64
Uria aalge **(common murre)**				
NSMT AS 00148	88.55	4.01	7.35	0.55
NSMT AS 01533	80.01	3.79	6.83	0.55
NSM PO-A 565	94.75	4.76	8.22	0.58
Uria onoi **(extinct)**				
● NSM PV-23722*	100.92	5.16	9.36	0.55
● NSM PV-23723*	(81.17)	4.76	7.47	0.64
● NSM PV-23724	(94.57)	5.00	8.09	0.62
● NSM PV-23731*	101.00	5.16	8.63	0.60
● NSM PV-23732*	(70.56)	4.35	8.40	0.52
Cepphus carbo **(spectacled guillemot)**				
FRIJ 298-01	74.36	4.06	5.21	0.78
Cepphus columba **(pigeon guillemot)**				
NSMT AS-00877	66.00	3.57	4.81	0.74
Cerorhinca monocerata **(rhinoceros auklet)**				
FRIJ 306-02	67.94	3.62	5.97	0.61
FRIJ 306-03	71.34	3.27	5.61	0.58
FRIJ 306-04*	71.83	3.33	5.63	0.59

Table 3-1-1. (continued)

Taxa	Length	Width mid-diaphysis		Compression Ratio
		Dorsoventral	Craniocaudal	Dorsoventral/ Craniocaudal
Alcidae (Charadriiformes)				
Synthliboramphus antiquus **(ancient murrelet)**				
FRIJ 300-01	51.39	2.35	4.38	0.54
FRIJ 300-02	52.84	2.52	4.64	0.54
FRIJ 300-03	48.91	2.42	4.39	0.55
NSM PO-A 60	48.41	2.20	3.81	0.58
NSM PO-A 428	51.00	2.48	4.57	0.54
● NSM PV 24324*	48.90	2.44	4.29	0.57
● NSM PV 24325*	49.85	2.45	4.24	0.58
● NSM PV 24326	49.50	2.62	4.44	0.59
● NSM PV 24327	49.80	2.35	4.15	0.57
● NSM PV 24328	(48.47)	2.48	4.18	0.59
Synthliboramphus wumizusume **(Japanese murrelet)**				
NSM PO-A 10	47.30	2.14	3.49	0.61
NSM PO-A 359*	50.74	2.23	4.21	0.53
Aethia psittacula **(parakeet auklet)**				
NSM PO-A 355	53.07	2.90	3.82	0.76
Aethia pusilla **(least auklet)**				
NSM PO-A 356	35.59	1.84	2.61	0.70
● NSM PV 24494*	(21.88)	1.86	2.64	0.70
Aethia cristatella **(crested auklet)**				
NSMT AS 00835	53.01	2.50	4.17	0.60
NSMT AS 00845	52.70	2.54	4.34	0.59
● NSM PV 24380	51.59	2.48	4.10	0.60
● NSM PV 24381*	52.09	2.44	4.15	0.59
Fratercula cirrhata **(tufted puffin)**				
△ NSM PO-A 362	80.02	3.51	5.98	0.59
NSM PO-A 363*	76.14	4.15	6.10	0.68
NSM PO-A 575	80.31	4.15	6.82	0.61
Fratercula corniculata **(horned puffin)**				
NSM PO-A 566*	67.76	3.11	5.13	0.61
NSM PO-A 577	68.22	3.37	5.36	0.63
Fraterculini gen. et sp. indet				
● NSM PV 24351	68.91	3.87	6.45	0.60
● NSM PV 24352*	68.19	4.17	6.68	0.62

Table 3-1-1. (continued)

		Width mid-diaphysis		Compression Ratio
Taxa	**Length**	**Dorsoventral**	**Craniocaudal**	**Dorsoventral/ Craniocaudal**
Mancallinae (Pan-Alcidae)				
Mancalla **? sp. (extinct)**				
● NSM PV 24504	(51.12)	4.42	11.40	0.39
Stercorariidae (Charadriiformes)				
Stercorarius longicaudus **(long-tailed jaeger)**				
△ NSM PO-A 239	81.09	4.03	4.77	0.84
△ NSM PO-A 243	84.19	4.22	4.76	0.89
Laridae (Charadriiformes)				
Onychoprion fuscatus **(sooty tern)**				
FRIJ 289-06	61.60	3.39	3.14	1.08
FRIJ 289-07	64.54	3.30	3.60	0.92
FRIJ 289-10	61.31	3.28	3.24	1.01
NSM PO-A 424	63.48	3.78	4.01	0.94
Larus argentatus **(European herring gull)**				
UMUT 19520	142.04	8.10	6.64	1.22
Chroicocephalus ridibundus **(black-headed gull)**				
FRIJ 262-10	75.00	4.56	3.70	1.23
Rissa tridactyla **(black-legged kittiwake)**				
FRIJ 273-01	92.16	4.87	4.80	1.01
Anous stolidus **(brown noddy)**				
FRIJ 292-06	66.17	3.41	3.61	0.94
FRIJ 292-22	65.12	3.56	3.66	0.97
Spheniscidae (Sphenisciformes)				
Pygoscelis papua **(Gentoo penguin)**				
UMUT 16355	86.25	6.33	19.33	0.33
Spheniscus humboldti **(Humboldt penguin)**				
UMUT 18050	72.36	6.48	15.24	0.43
Sulidae (Suliformes)				
Sula leucogaster **(brown booby)**				
FRIJ 042-07	157.20	6.59	7.18	0.92

Table 3-1-1. (continued)

Taxa	Length	Width mid-diaphysis		Compression Ratio
		Dorsoventral	Craniocaudal	Dorsoventral/ Craniocaudal
Procellariidae (Procellariiformes)				
Ardenna grisea **(sooty shearwater)**				
FRIJ 027-01	104.58	3.99	6.86	0.58
FRIJ 027-04	107.99	3.73	7.01	0.53
Ardenna tenuirostris **(short-tailed shearwater)**				
FRIJ 028-07	98.79	3.84	6.22	0.62
FRIJ 028-30	93.27	3.77	6.05	0.62
Ardenna pacifica **(wedge-tailed shearwater)**				
FRIJ 024-58	104.70	4.13	5.15	0.80
FRIJ 024-77	103.18	4.06	5.08	0.80
Puffinus bannermani **(Bannerman's shearwater)**				
FRIJ 030-01	69.09	2.81	4.86	0.58
FRIJ 030-03	72.54	2.86	4.73	0.60
Anatidae (Anseriformes)				
Aythya marila **(greater scaup)**				
FRIJ 10438	81.30	4.92	5.21	0.94
Netta peposaca **(rosy-billed pochard)**				
UMUT 21011	90.84	5.84	6.27	0.93

Table 3-2. Comparison of Miocene–Pleistocene Alcidae fossil (genus) records in the western Pacific (i.e., Asia) and the eastern Pacific/Atlantic (including Greenland and Ellesmere Island). EI=Ellesmere Island, EU=Europe, GL=Greenland, JPN=Japan, MEX=Mexico, USA=United States of America; AK=Alaska, CA=California, ME=Maine, VA=Virginia, *=including the fossil collected from the Pliocene–Pleistocene layer, **= including the fossil collected from the Miocene–Pliocene layer [Based on Marsh 1872a; Howard 1936, 1971, 1981, 1982; Ray et al., 1968; Kohl 1974; Hubbs and Jehl 1976; Chandler 1990; Harington 1990; Guthrie 1992, 2005; Bennike et al., 1994; Boessenecker 2011; Smith 2011a, b, 2014; Olson 2013; Watanabe et al., 2016, 2018a, 2020. The Pleistocene European fossil records followed Mourer-Chauviré (1975), Larsen et al. (1987), and compiled data of Tyberg (1999, 2008)].

		Pleistocene		**Pliocene**		**Miocene**	
Western Pacific		**Eastern Pacific**	**Atlantic**	**Eastern Pacific**	**Atlantic**	**Eastern Pacific**	**Atlantic**
Pleistocene							
Aethia	JPN	–	–	USA(CA)	–	USA(CA)	–
Alle	JPN	–	EI, GL, EU	–	–	–	–
Cepphus	JPN	USA(CA)	EU	USA(CA)**	–	USA(CA)	–
Mancalla	JPN	USA(CA)*	–	USA(CA)**	–	MEX	–
Synthliboramphus	JPN	USA(CA), MEX	–	USA(CA)	–	–	–
Uria	JPN	USA(CA)	USA(ME, VA), EU	USA(AK)	–	USA(CA)	–

Notes: 1) The table is excluding uncertain taxa (e.g., *Uria*? sp.). 2) Alle from the Pliocene of North Carolina (Olson and Rasmussen, 2001) is reassigned *Miocepphus mergulellus* (Wijinker and Olson, 2009), thus Pliocene Alle record is not cited. 3) *Cepphus storeri* from the Pleistocene of England (Harrison, 1977b) is regarded as a nomen dubium (Smith, 2011b). Therefore, Pleistocene *Cepphus* in Europe is indicating *Cepphus grylle* (Larsen et al., 1987; Tyberg, 1999, 2008). 4) *Mancalla cedrosensis* has reported from the Pliocene deposit in Mexico (Howard, 1971), however, Barnes (1984) regarded that the type locality of this species is the late Miocene. Therefore, the table addressed *Mancalla cedrosensis* as the Miocene record (Barnes, 1984; Powell et al., 2019; see also table 1 of Smith, 2011a).

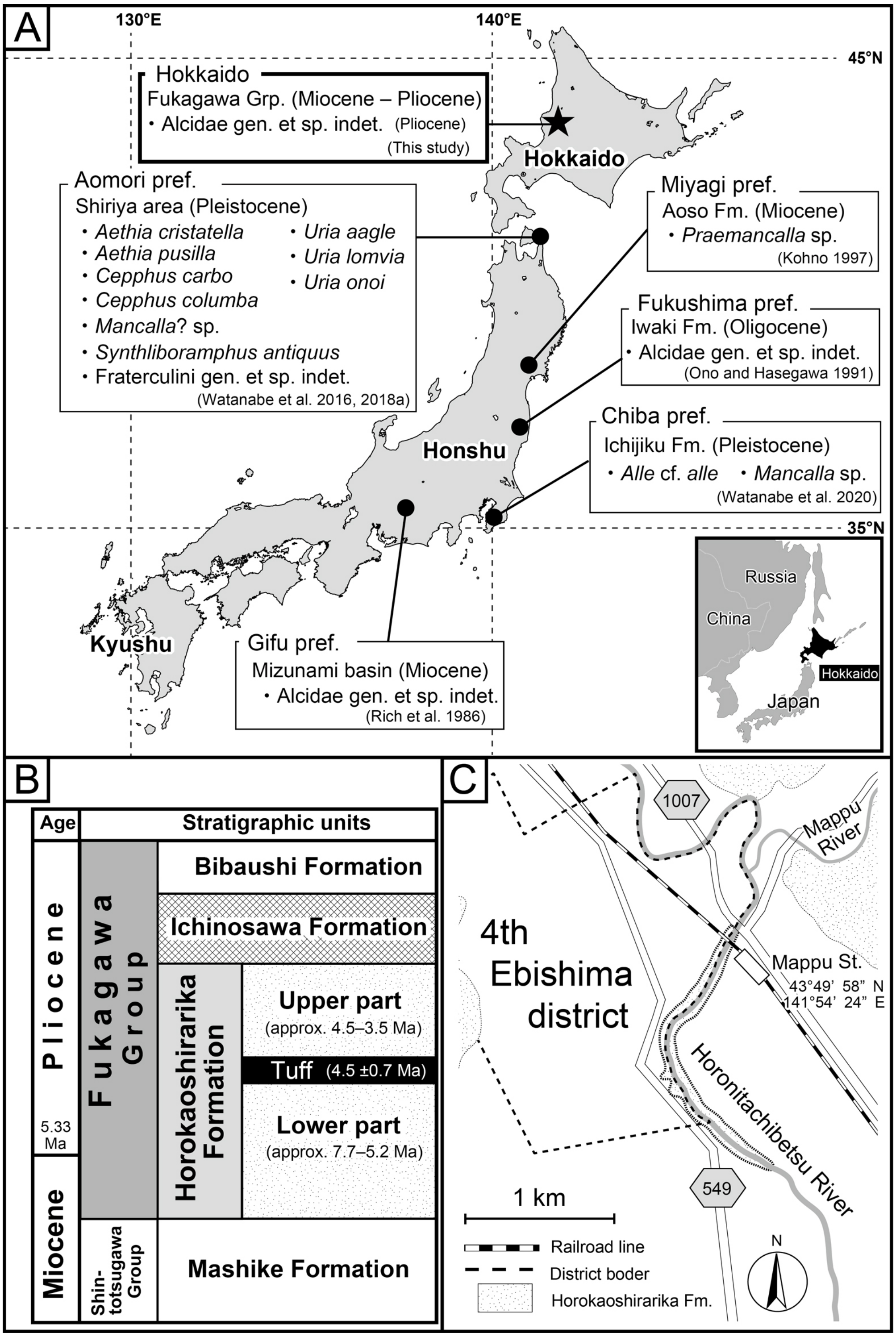


Fig. 3-1. **(A)** Alcidae fossil localities in Japan. **(B)** Stratigraphic sections of the Fukagawa Group (based on Kobayashi et al., 1969; Watanabe and Yoshida ,1995; Nakashima and Watanabe, 2000; Watanabe and Tanaka, 2017). **(C)** Geological map of the 4th Ebishima district, Numata Town (based on Kobayashi et al., 1969; Watanabe and Yoshida, 1995).

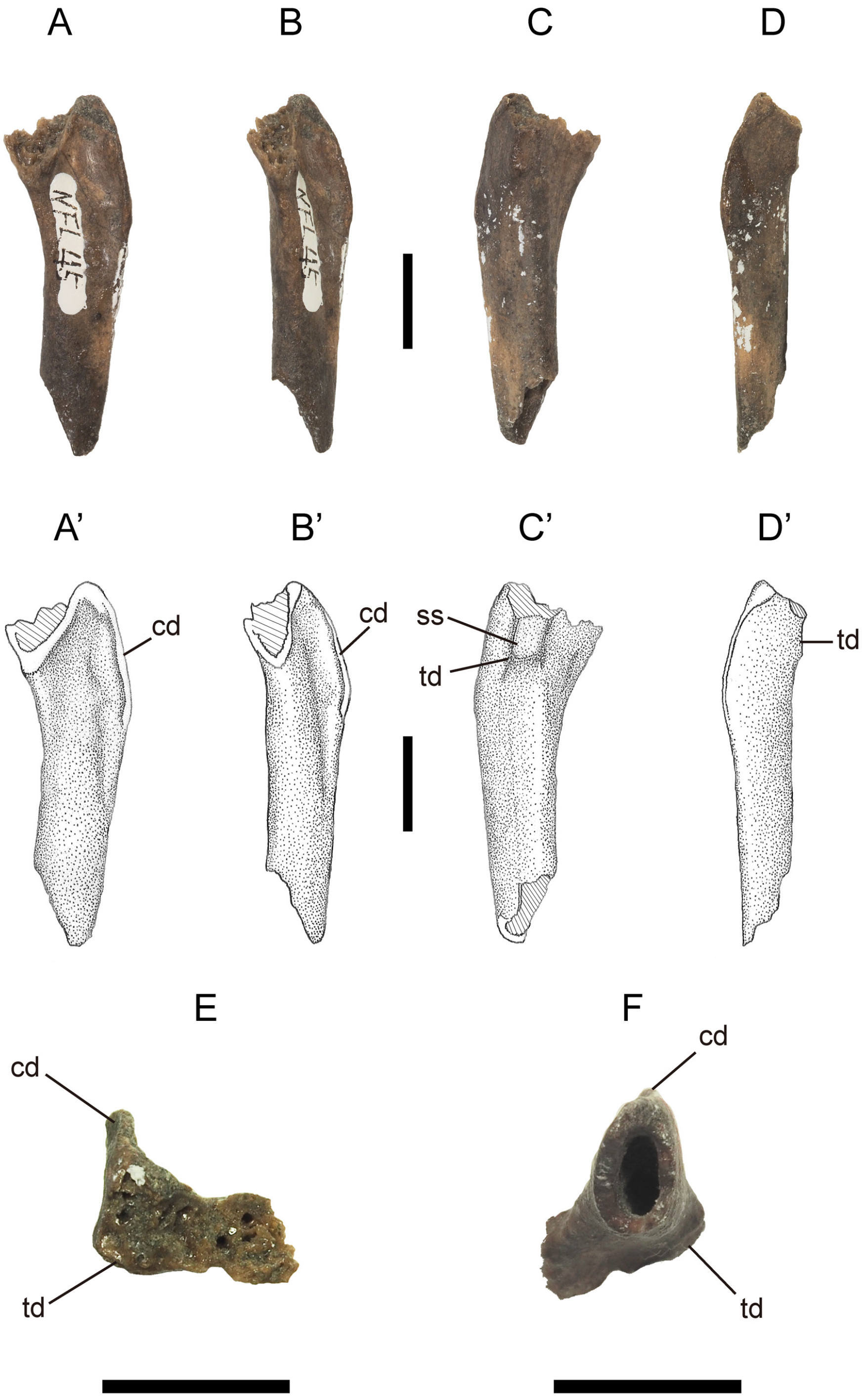


Fig. 3-2. The left humerus of NFL 45 (Alcidae gen. et sp. indet.). **(A–F)** photos of NFL 45 and **(A'–D')** pointillism sketches of NFL 45: **(A, A')** cranial view, **(B, B')** ventral view, **(C, C')** caudal view, **(D, D')** dorsal view, **(E)** proximal view, **(F)** distal view. Scale bar represents 1 cm. Abbreviations: cd = crista deltopectoralis, ch = caput humeri, ru = rugose ridge, ss = supracoracoideus scar, td = tuberculum dorsale.

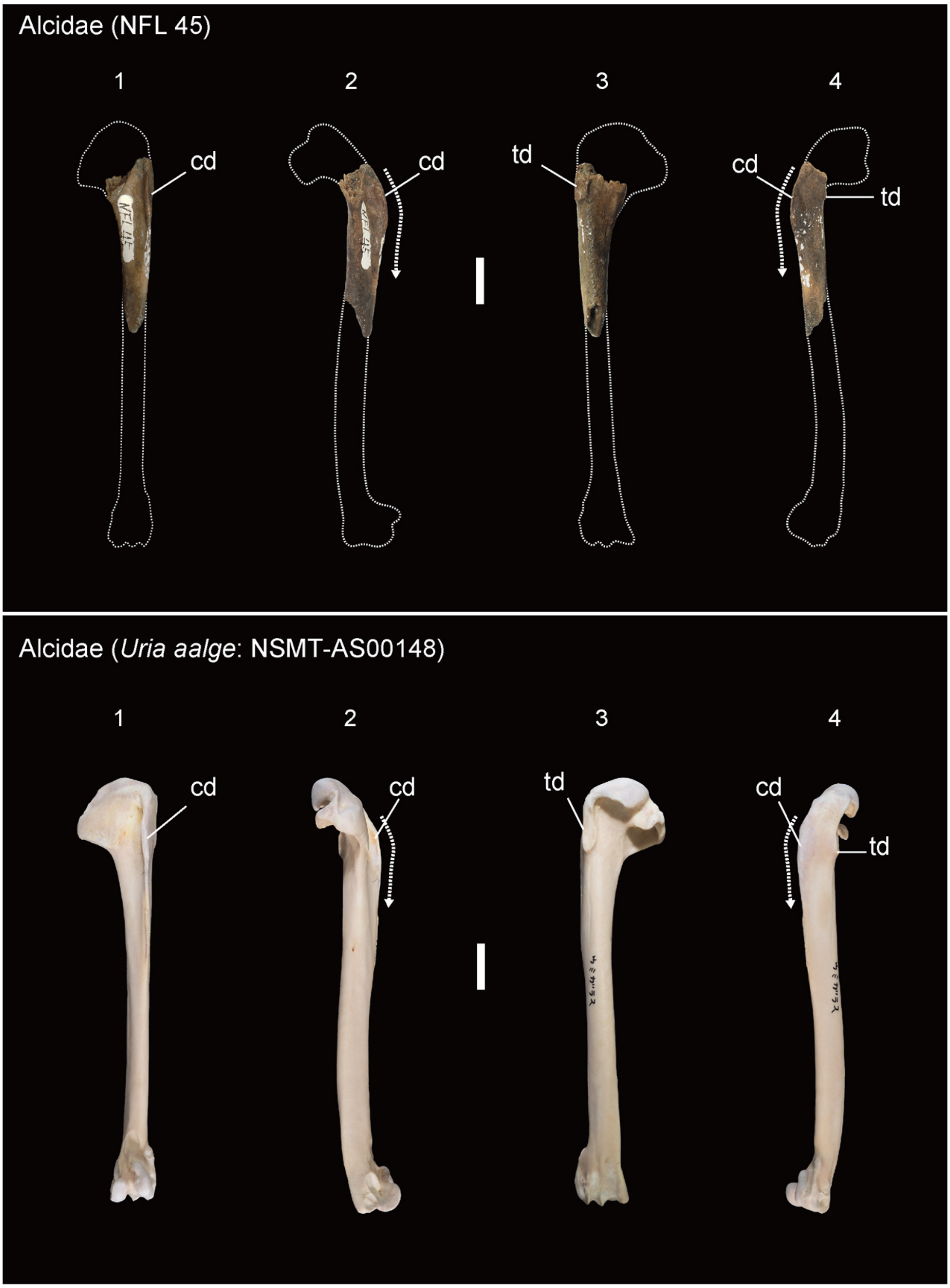
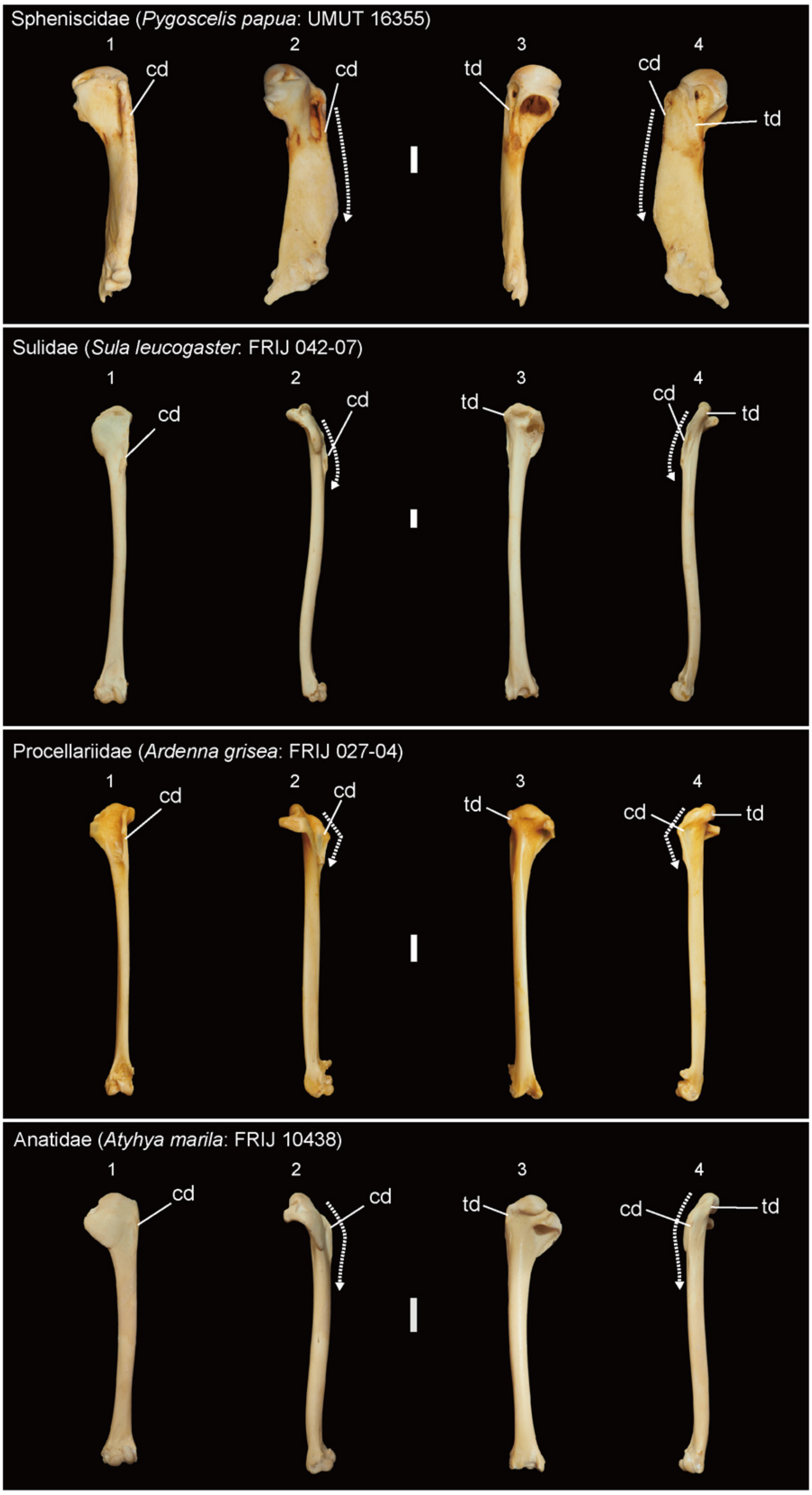


Fig. 3-3. Comparison of NFL 45 (Alcidae gen. et sp. indet.) with modern Alcidae. 1 cranio-dorsal view, 2 ventral view, 3 caudal view, 4 dorsal view. The dashed white arrow indicates the marginal curvature of the crista deltopectoralis. Scale bar represents 1 cm. For abbreviations, see Fig. 3-2.



Spheniscidae (*Pygoscelis papua*: UMUT 16355)

Sulidae (*Sula leucogaster*: FRIJ 042-07)

Procellariidae (*Ardenna grisea*: FRIJ 027-04)

Anatidae (*Atyhya marila*: FRIJ 10438)

Fig. 3-4. Comparison of the humerus between the modern birds. 1 cranio-dorsal view, 2 ventral view, 3 caudal view, 4 dorsal view. The dashed white arrow indicates the marginal curvature of the crista deltopectoralis. Scale bar represents 1 cm. For abbreviations, see Fig. 3-2.

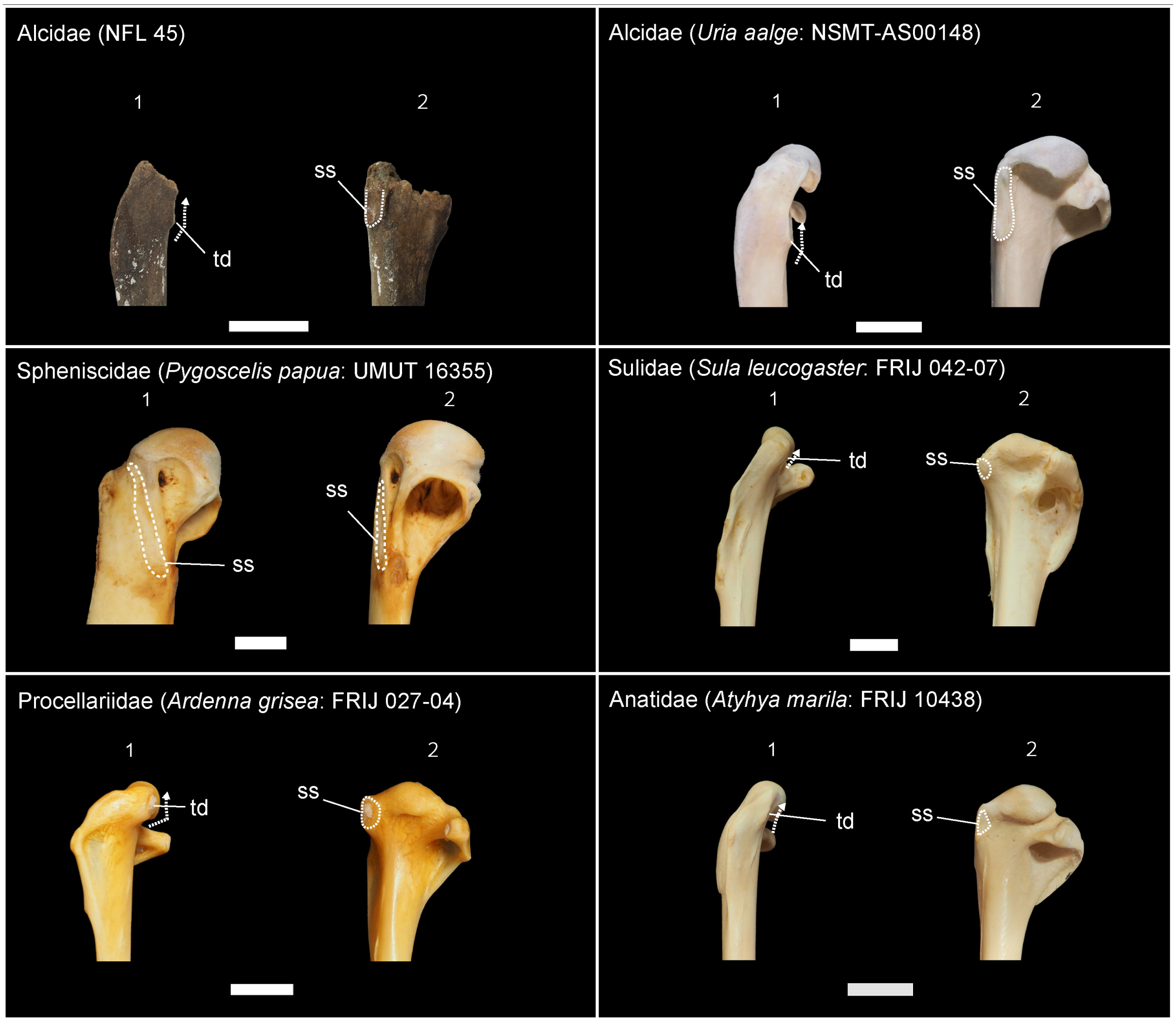


Fig. 3-5. Comparison of the tuberculum dorsale and the supracoracoideus scar of NFL 45 (Alcidae gen. et sp. indet.) with modern birds.1 dorsal view, 2 caudal view. The dashed white arrow indicates protrusion of the distal margin of the tuberculum dorsale. The dashed white line indicates the outline of the supracoracoideus scar. For abbreviations, see Fig. 3-2.

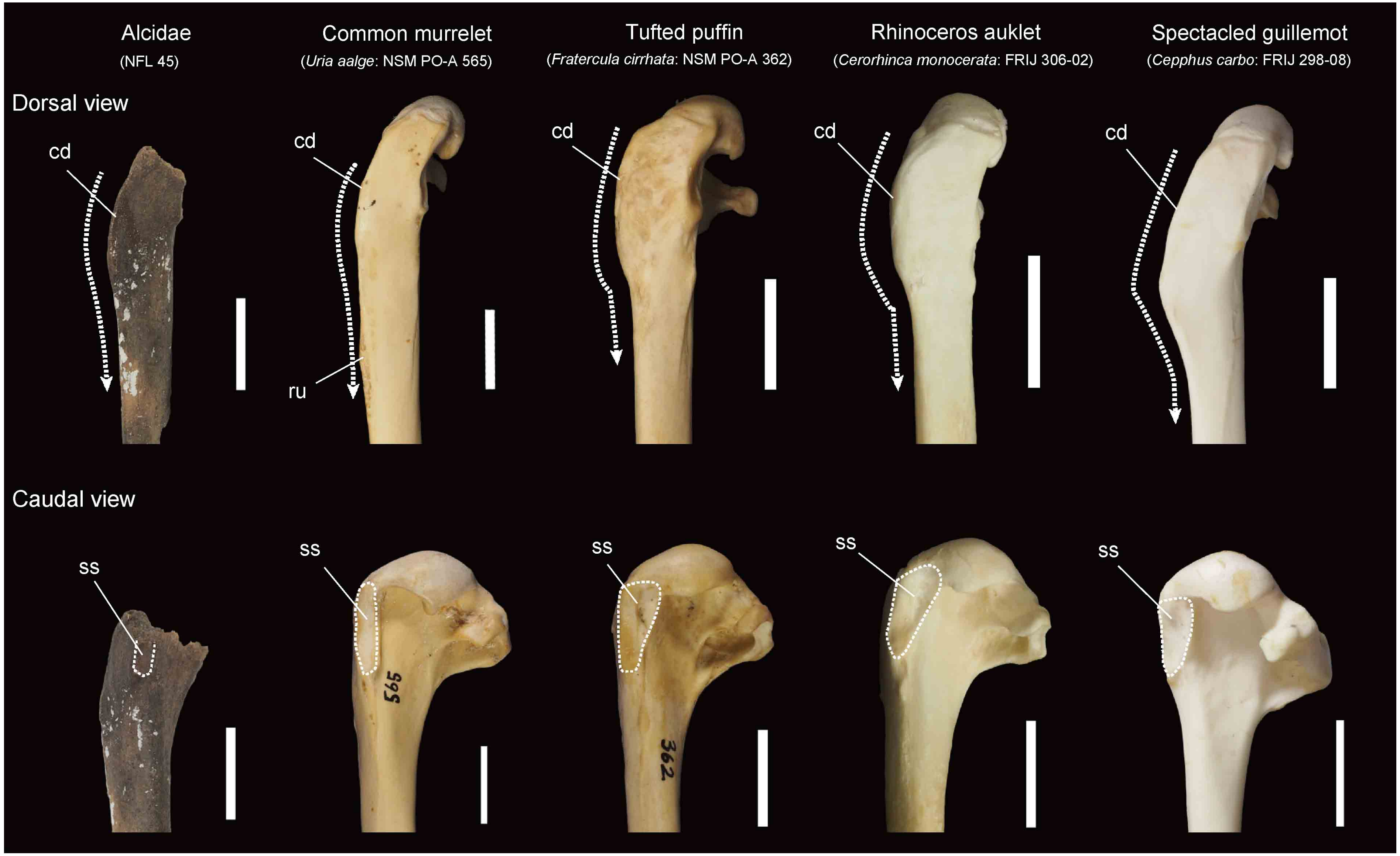


Fig. 3-6. Comparison of NFL 45 (Alcidae gen. et sp. indet.) with modern Alcidae. The dashed white arrow indicates the marginal curvature of the crista deltopectoralis. The dashed white line indicates the outline of the supracoracoideus scar. Scale bar represents 1 cm. For abbreviations, see Fig. 3-2.

Chapter 4.

A tarsometatarsus of Hesperornithiformes (Aves: Ornithurae) from the Nishichirashinai Formation (Cretaceous) in Hokkaido, Japan

第４章

本章については、５年以内に雑誌等で刊行予定のため非公開

Chapter 5.

The diving locomotion of hesperornithiforms: functional morphological analysis of the tarsometatarsal diaphysis

第５章

本章については、５年以内に雑誌等で刊行予定のため非公開

Chapter 6. General discussion

第６章

本章の一部については、５年以内に雑誌等で刊行予定のため一部非公開

Seabirds faunal transition in East Asia

In this study, I described three fossil birds from the Cretaceous, Pliocene, and Pleistocene. Fig. 6-1 summarizes the fossil record and the results of this study.

The Cretaceous bird fossils are scarce in Japan. Among the Cretaceous bird records, Hesperornithiformes is known as the only seabird family from Japan. In Chapter 4, I described the third Japanese hesperornithiforms material (NMV-204) from the Nishichirashinai Formation (Santonian) in Hokkaido. Considering that two other hesperornithiforms materials have been reported from the Mikasa Formation (Coniacian–Santonian) in the Yezo Group and the Kita-ama Formation (Maastrichtian) in the Izumi Group (Tanaka et al., 2017, 2020), it implies that this group of birds has existed in East Asia for a long time, at least from the Coniacian to Maastrichtian. The undescribed ulna has been reported at the paleontological conference from the Hakobuchi Formation (Campanian) in Hokkaido. Although the taxonomic identification of this specimen is still unknown, Hasegawa and Obata (1975) mentioned the similarity to *Ichthyornis*, which was found in the Western Interior Seaway in the USA. Hesperornithiformes is a significant seabird taxon in the Western Interior Seaway. Considering the fossil biota in the Yezo Group and the Izumi Group, the Late Cretaceous marine fauna might be similar between East Asia and North America since several common taxa such as Mosasauridae, Plesiosauria, and Chelonioidea have been reported (Nicholls and Russell, 1990; Sato et al., 2012). Although the Cretaceous seabird records from East Asia are notably scarce, it would not be surprising that the seabird fauna was similar to those in North America inhabited, even though they belonged to different genera. Since various fossils have been discovered from the Western Interior Seaway, if more fossils are discovered from East Asia in future research, it will be possible to discuss the similarities and differences of biota in the East and West Pacific during the Cretaceous, including ecosystems.

All Hesperornithiformes have been extinct at the end of the Cretaceous. The modern birds group, Neornithes, has diversified after the K-Pg event. Although seabirds have diversified and globally distributed during the early Neogene, their fossil remains have never been reported from the Paleocene and Eocene deposits in Japan. Therefore, it is uncertain how the fauna of seabirds recovered after the K-Pg event in East Asia. However, it is no doubt that the extinct taxon, Plotopteridae, was a dominant Oligocene seabird in East Asia after the K-Pg event. This family is known as the penguin-like wing-propelled diving bird. Their remains have been collected from several localities in Japan, from Hokkaido, Fukushima, Yamaguchi Prefectures, and Kyushu Island (Olson and Hasegawa, 1996; Sakurai et al., 2008; Ando and Fukata, 2018; Ohashi and Hasegawa, 2020). Thus, fauna of seabirds was significantly different from today. With the exception of Plotopteridae, reports of Oligocene seabird fossils are almost limited to the Iwaki Formation in Fukushima Prefecture. Ono and Hasegawa (1991) reported seven families of bird fossils from the Iwaki Formation. The following seabirds have been reported in the excavation report: Procellariidae, Sulidae, Phalacrocoracidae, Alcidae, Pelagornithidae (Pseudodontornithdae in Ono and Hasegawa, 1991), and Plotopteridae. Although I described Procellariidae sternum from the Pleistocene in Chapter 2, this family has already been reported from the Oligocene deposit in Fukushima Prefecture. However, based on photos in Ono and Hasegawa (1991), most of these specimens are partial or incomplete isolated elements, and detailed descriptions of each fossil have yet to be reported. Smith (2013, 2016) also mentioned that the taxonomic status of Alcidae from the Iwaki Formation needs reevaluation due to poor preservation. To reveal the Oligocene seabird fauna, reinvestigating of the bird fossils from the Iwaki Formation will be required in future studies.

The fossil records suggest that the modern seabird taxa were commonly seen in Japan after the Oligocene, which might relate to forming of the Sea of Japan during the late early Miocene. In fact, several modern taxa have been collected from the Miocene deposits. For example, Sulidae and Procellariidae have been found from the Nagura Formation in Saitama Prefecture (Ono, 1983; Ono and Sakamoto, 1991). Phalacrocoracidae? has also been reported from the Mizunami Basin (Hasegawa et al., 1977). Gaviidae and Anatidae have also been found from the Mizunami Basin; however, they are only listed in Rich et al. (1987), and detailed descriptions still need to be reported, as well as Alcidae. Considering the Miocene topography, the Japanese archipelago was divided into several small islands (Ogasawara, 1994). Such environments might be suitable for seabirds, especially for forging, breeding, or nesting offshore. For example, Procellariidae usually makes the nest underground and breeds on the island or offshore (Rodríguez et al., 2019). In addition, island topography is thought to facilitate interspecies variation, including island rule, as in the Galapagos Islands today. In fact, some extinct genera or species of birds have been reported from the Miocene deposit in Japan. For example, *Annakacygna* is the flightless marine Anatidae, and the fossil has been collected from the Tomioka Formation in Gunma Prefecture (Matsuoka and Hasegawa, 2022). *Diomedia tanakai* have been found from the Oi Formation in Mie Prefecture (Davis, 2003). By contrast, the fossil record of Plotopteridae has been discontinued since the Miocene, and it is considered to have become extinct worldwide.

Other extinct family, Pelagornithidae, reported from the Oligocene–Pliocene deposits of Fukushima, Iwate, Shizuoka, and Mie Prefectures (Oishi et al., 1985; Matsuoka et al., 1998). Anhigidae, which does not live around Japan today, have also been reported from Miocene–Pliocene. Therefore, there was a mixture of avifauna different from the present, until the Pliocene. In terms of climate and sea-level change, Rich et al. (1986) mentioned that the modern zoological regions in Japan formed in the Pleistocene. This hypothesis may support since many modern taxa have been reported from the Pleistocene deposit. However, the Pliocene seabird fossil records are notably rare in Japan. Excluding Pelegornithidae, only Gaviidae and *Anhiga* sp. have been found from the Hijikata Formation in Shizuoka Prefecture and the Kobiwako Group in Gifu Prefecture, respectively (Matsuoka et al., 1991; Matsuoka et al., 2007). Although *Phalacrocorax* sp. has been reported from the Tubusagawa Formation in Oita, this formation is composed of flesh water deposits (Matsuoka 2001b). I described new Alcidae material from the Pliocene deposit in Chapter 3. However, it is still insufficient to reveal the faunal transition between the Miocene to the Pliocene and the Pliocene to the Pleistocene (Fig. 6-1). Therefore, it must fill this gap to reveal a more specific faunal transition. However, considering the age and location of the fossil finds, it is likely that not all seabirds dispersed at the same age. I estimated that the Alcidae had entered East Asia around the Pliocene in Chapter 3, and it seems that the invasion timing of Alcidae was relatively recent among seabirds. Despite the fossil record from the Pliocene being scarce, considering the expansion timing of Alcidae into East Asia and the absence of Pelagornithidae and Anhigidae in the Pleistocene, it is plausible that faunal transition of some seabirds had occurred during the Pliocene and the Pleistocene. It is plausible that not only Alcidae but also some other birds must have been affected by the opening event of the Bering Strait, which may cause some faunal transition for seabirds. Thus, the expansion of the Sea of Japan during the Miocene and the opening of the Bering Strait during the late Miocene or early Pliocene may have significantly affected the evolution of the seabird fauna of East Asia.

Sea bird comparison between the Kanto and Shiriya areas

Pleistocene–Holocene seabird remains, especially many Procellariiformes, have been reported from isolated islands, such as Hahajima, Kita Daito Island, and Minami Daito Island (Rich et al., 1986; Matsuoka et al., 2002b, c). However, Pleistocene seabird records are not many from Honshu. In Honshu, the Shiriya area in Aomori Prefecture is the most remarkable site for seabird diversity in the Pleistocene. Hasegawa et al. (1988) have reported the Pleistocene seabirds assemblage from this area, and recently Watanabe et al. (2018a) have described fossils in this area in detail. In addition, Watanabe et al. (2020) also reported several Pleistocene seabirds from the Kazusa and Shimosa Groups in the Kanto area, Tokyo and Chiba Prefecture.

Therefore, the Shiriya and the Kanto areas are significant seabird fossil localities in the Pleistocene deposit in Japan (Watanabe et al., 2018a; 2020).

Although the Shiriya and the Kanto areas are geographically distant, the depositional age of those fossil horizons is almost continuous. The Shiriya assemblage locality was divided into four localities by Hasegawa et al. (1988), and the bird fossils have been reported from Loc. 1–3 (Watanabe et al., 2018a). According to Watanabe et al. (2018a), the depositional age was estimated as ca. 0.12 in Loc. 1 and Loc. 3, and ca. 0. 32 Ma in Loc. 2. In the Kanto area, bird fossils are known from the four formations in the Kazusa and Shimosa groups in Tokyo and Chiba Prefecture; the Hirayama Formation (ca. 1.7 Ma), Ichijiku (ca. 0.7 Ma), Mandano (ca. 0.6 Ma), and the Kiyokawa Formations (ca. 0.22 Ma). Ono et al. (1984) also reported *Gavia pacifica* (Pacific loon) from the Kami-iwahashi Formation in Chiba Prefecture, and the depositional age is correlated to the Kiyokawa Formation (Sakata et al., 2018). Thus depositional age of the Shiriya area is slightly younger than the Kazusa Groups (Hirayama, Ichijiku, and Mandano Formations), and the Kiyokawa and the Kami-iwahashi Formations indicate an age that fills the geological gap between Loc. 1 and 3, and Loc. 2 in the Shiriya area.

Compared to the seabird taxa between the Shiriya and Kanto areas, no significant differences in seabird fauna at the family level (Fig. 6-2; Table 6-1). Although Hydrobatidae, Laridae, and Podicipedidae have been reported only from the Shiriya area, the number of specimens is only three to five for each family. This difference may attribute to a sampling bias. Focused on the number of specimens, Anatidae, Procellariidae, and Alcidae are the most dominant seabirds in Shiriya. In Anatidae, *Clangula hyemalis* and *Melanitta fusca* are commonly found in both areas, the latter taxon being discovered consecutively since 0.6 Ma. A variety species of *Puffinus* and *Ardenna* were found in Shiriya, and *Puffinus* cf. *puffinus* have been reported in the Kanto area, which suggests that the diversification and radiation of Procellariidae were similar to today. The Procellariidae sternum (CBM-PV 8301), which I described in Chapter 2, shows similar characteristics to *Ardenna*. It indicates that various procellariids lived in the Kanto area in the Pleistocene. Other Procellarriformes also support this hypothesis since *Phoebasteria* has been found in both areas.

Alcidae is the most remarkable seabird in those areas. Various genera and species has been reported from Shiriya, whereas only two genera have been known from the Ichijiku Formation in the Kanto area. Considering the modern alcids distribution, the fossil records in Shiriya are similar to today. However, the fossil of Atlantic auk, *Alle* is only known from the Boso area. Based on the result in Chapter 3, it is plausible that the opening event of the Bering Straits might allow the migration of *Alle* into the western Pacific. Although *Alle* is not been discovered in the Shiriya area yet, considering that *Mancalla* (including *Mancalla*? sp. in Watanabe et al., 2018a) is commonly found in both areas, it is no wonder if that *Alle* will be found in the Shiriya area. In fact, not only *Mancalla*, but also some extinct taxa, such as *Shiriyanetta*, *Uria onoi*, and *Phalacrocorax perspicillatus* have also been reported from Shiriya (Watanabe and Matsuoka, 2015; Watanabe et al., 2016, 2018a, b). Thus, it is plausible that minor faunal changes may have occurred in seabirds between the Pleistocene and the present. The reason for this faunal transition might be different in each taxon. However, there is no doubt that climate and sea-level changes must affect seabirds. Watanabe et al. (2018) mentioned that decreasing the oceanic productivity by the Last Glacial Maximum might affect *P. perspicillatus* disappearance. Matsuoka et al. (2002b) suggested that some seabirds have lost their colonies for breeding with forest developments, and seabird faunal transition had occurred on Kita-Daito Island in the recent era (assumed in the early Holocene).

As I mentioned in Chapter 2, the Boso peninsula was isolated from Honshu Island in the Pleistocene. Therefore, environmental change must have occurred in the Boso area with the topographical change from the island to the peninsula. Such environmental change must have affected seabird ecologies and may have caused local extinction for *Mancalla* and *Alle*.

According to the fossil record, it is no doubt that a variety of seabirds existed during the Pleistocene in the Kanto area, especially in the Boso area. Therefore, a great variety of seabird fossils will likely be collected from the Boso area in future research. The Kazusa Group and the Shimousa Group are sediments of continuous ages. Thus, it is expected that a detailed examination of the fossils found in these groups will reveal the seabird faunal transition from an island to a peninsula in the Boso area with high resolution.

Faunal transition of wing-propelled diving birds in the Cenozoic

Among the Pleistocene seabirds, Alcidae is one of the major seabird families. Despite several genera and species of Alcidae having been reported from the Pleistocene deposit in

Shiriya and the Boso Peninsula, alcid fossils have never been reported from pre-Pleistocene deposits in East Asia. As I mentioned in Chapter 3, compared to other seabirds, the radiation of Alcidae in the western Pacific is thought to have occurred relatively recently, after the Bering Strait opened. Although Alcidae has flight ability, their wing structure is not highly adapted for flight since their wings are slightly reduced and adapted for diving (Pennycuick, 1987). Therefore the continental connection between North America and Eurasia might become a barrier to their migration. Thus, such topographical change more significantly affected the migration of Alcidae.

However, considering the fossil records, various alcids have been reported from the Miocene deposit on the west coast of North America. Nevertheless, it is questionable why they do not migrate along the coastline from North America to Eurasia before the opening event of the Bering Strait in the Pliocene. In view of the migration ability of modern alcids, it is unnatural that eastern Pacific alcids did not migrate to Asia via Alaska.

As a possible hypothesis, competition for food resources may have occurred among wing-propelled diving birds. Plotopteridae is a large flightless wing-propelled diving bird. The fossil remains have been reported from the Oligocene deposits from Hokkaido to Kyushu island (Ono and Hasegawa, 1991; Olson and Hasegawa, 1996; Sakurai et al., 2008; Ando and Fukata, 2018; Ohashi and Hasegawa, 2020), and the Miocene deposits in Gifu Prefecture (Olson and Hasegawa, 1985). Therefore, Plotopteridae is one of the dominant seabirds in Japan during the Oligocene to Miocene. Plotopteridae remains have also been found in the Oligocene and

Miocene deposits on the west coast of North America (Howard, 1969; Goedert and Cornish, 2002). However, Goedert and Cornish (2002) suggested that the local extinction of Plotopteridae had occurred since offshore volcanic islands disappeared by the regional tectonism at the Oregon and Washington coastline by the Late Oligocene, and they lost their breeding and nesting site. In addition, Olson and Hasegawa (1979) mentioned that the evolution and radiation of marine mammals had caused Plotopteridae extinction by the middle Miocene. This hypothesis has also been supported by the comprehensive diversity comparison study (Ando and Fordyce, 2014). By contrast, the diversity correlation between the flightless auks (i.e., Mancallinae and *Pinguinus*) and marine mammals lacked a negative correlation (Ando and Fordyce, 2014). Interestingly, Alcidae diversification occurred in the Miocene. Various genera and species have been found in a Miocene deposit on the east and west coasts of North America. Therefore, it is possible that Alcidae gradually replaced that niche after Plotopteridae declined in North America. Subsequently, Alcidae dispersal into East Asia after Plotopteridae had been extinct in North America and Japan with the expansion of the sea route. Therefore, not only the topographical change but also the extinction of Plotopteridae may have caused faunal turnover for wing-propelled diving birds in East Asia.

Distribution and migration of Hesperornithiformes

本項目については、５年以内に雑誌等で刊行予定のため非公開

Flightlessness hypothesis in Hesperornithiformes

本項目については、５年以内に雑誌等で刊行予定のため非公開

Table 6-1. The number of specimens of seabirds between the Kanto and Shiriya areas. Compiled Ono et al. (1984), Watanabe and Matsuoka (2015), and Watanabe et al. (2018a, b, 2020).

Kanto area (Tokyo and Chiba)	n	**Shiriya area (Aomori)**	n
Anatidae	**4**	Anatidae	**151**
Melanitta fusca	2	*Clangula hyemalis*	10
Clangula hyemalis	1	*Melanitta fusca*	3
Anatidae?	1	*Histrionicus histrionicus*	7
		Anas magn. *platyrhynchos*	3
		Shiriyanetta hasegawai	128
Procellariidae	**3**	Procellariidae	**90**
Puffinus cf. *puffinus*	2	*Fulmarus* sp.	1
Procellariidae (CBM-PV 8301)	1	*Ardenna tenuirostris*	38
		Ardenna griseus	38
		Puffinus cf. *nativitatis*	11
		Calonectris leucomelas	2
Diomedeidae	**1**	Diomedeidae	**4**
Phoebasteria cf. *albatrus*	1	*Phoebastria* cf. *albatrus*	4
Gaviidae	**4**	Gaviidae	**2**
Gavia pacifica	1	*Gavia* cf. *stellata*	2
Gavia stellata ?	3		
Phalacrocoracidae	**1**	Phalacrocoracidae	**32**
Phalacrocoracidae	1	*Phalacrocorax pelagicus*	19
		Phalacrocorax persicillatus	13
Alcidae	**6**	Alcidae	**264**
Alle cf. *alle*	1	*Uria lomvia*	23
Mancalla sp.	5	*Uria aalge*	5
		Uria onoi	39
		Cepphus columba	3
		Cepphus carbo	3
		Synthliboramphus antiquus	24
		Aethia pusilla	9
		Aethia cristatella	131
		Fraterculini	18
		Mancalla ? sp.	9
		Laridae	**3**
		Laru s magn. *argentatus*	1
		Larinae	1
		Larinae ?	1
		Podicipedidae	**3**
		Podiceps cristatus or *grisegena*	3
		Hydrobatidae	**5**
		Hydrobates leucorhous ?	5

	Diving/swimming locomotion	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene
Ornithurae (Fossil taxa)								
Hesperornithiformes	FPD	■						
Neornithes (modern taxa)								
Podicipedidae	HS-FPD							▨
Gaviidae	HS-FPD						▨	▨
Phalacrocorocidae	FPD				▨	▨	▨	▨
Anhingidae	FPD					▨	▨	
Anatidae	FPD/SS					▨		▨
Alcidae	WPD						■	▨
Procellariidae	WPD				▨	▨		■
Sulidae	WPD				▨	▨		
Diomedeidae	Shorebird (SS)					▨		▨
Hydrobatidae	SS							▨
Laridae	SS							▨
Plotopteridae*	WPD				▨	▨		
Pelagornithidae*	WPD				▨	▨	▨	

Fig. 6-1. Seabird fossil records and the ages in Japan. The black marked part indicates the result of this study. The gray marked part indicates the fossil records. For detailed citation see Table 1-2. * indicates an extinct Neornites. On the basis of Chapters 3 and 6, the Alcidae from the Oligocene and Miocene (Rich et al., 1986; Ono and Hasegawa, 1991; Kohno, 1997) and Gaviidae from the Miocene (Rich et al., 1986) are excluded since the detailed description or citations are unknown. The Miocene Anatidae indicates *Annakacygna* (Matsuoka and Hasegawa, 2022).

Kanto area (Tokyo and Chiba)

Kiyokawa Formation (ca.0.22 Ma)		**Kami-iwakami Formation (Imba-gun)**
Procellariidae	**Anatidae**	**Gaviidae**
● *Puffinus* cf. *puffinus*	● *Melanitta fusca*	●*Gavia pacifica*

Mandano Formation (ca. 0.6 Ma)		
Anatidae		
● *Melanitta fusca*		

Ichijiku Formation (ca. 0.7 Ma)		
Alcidae	**Procellariidae**	**Anatidae**
Alle cf. *alle*	Procellariidae (CBM-PV 8301)	●*Clangula hyemalis*
● *Mancalla* sp.	●*Puffinus* cf. *puffinus*	**Gaviidae**
		●*Gavia stellata* ?
		Phalacrocoracidae
		Phalacrocoracidae

Hirayama Formation (ca. 1.7Ma)		
Diomedeidae	**Anatidae**	
Phoebasteria cf. *albatrus*	Anatidae?	

Shiriya area (Aomori)

Loc.1 and Loc.3 (ca. 0.12 Ma)		
Alcidae	**Procellariidae**	**Anatidae**
Uria lomvia	*Fulmarus* sp.	*Anas* magn. *platyrhynchos*
Uria aalge	*Ardenna tenuirostris*	●*Melanitta fusca*
Uria onoi	*Ardenna grisea*	*Histrionicus histrionicus*
Cepphus columba	● *Puffinus* cf. *nativitatis*	● *Clangula hyemalis*
Cepphus carbo	**Hydrobatidae**	*Shiriyanetta hasegawai*
Synthliboramphus antiquus	*Hydrobates leucorhous* ?	**Podicipedidae**
Aethia pusilla	**Laridae**	*Podiceps cristatus* or *grisegena*
Aethia cristatella	*Larus* magn. *argentatus*	**Gaviidae**
Fraterculini	Larinae	● *Gavia* cf. *stellata*
●*Mancalla* ? sp.		**Phalacrocoracidae**
		Phalacrocorax pelagicus
		Phalacrocorax persicillatus

Loc. 2 (ca. 0.32 Ma)		
Alcidae	**Procellariidae**	**Anatidae**
Uria onoi	*Ardenna grisea*	*Anas* magn. *platyrhynchos*
Cepphus columba	● *Puffinus* cf. *nativitatis*	● *Melanitta fusca*
Aethia cristatella	**Diomedeidae**	*Histrionicus histrionicus*
Fraterculini gen. et sp. indet.	*Phoebastria* cf. *albatrus*	● *Clangula hyemalis*
● *Mancalla? sp.*		*Shiriyanetta hasegawai*
		Podicipedidae
		Podiceps cristatus or *grisegena*
		Phalacrocoracidae
		Phalacrocorax pelagicus

Locality unknown
Procellariidae
Calonectris leucomelas
Laridae
Larinae ?

Fig. 6-2. Taxonomic comparisons of Pleistocene seabirds between the Kanto and Shiriya areas. Taxonomic data compiled Ono et al. (1984), and Watanabe et al. (2018a, 2020). ● indicates a common genus between both areas.

図６-３については、５年以内に雑誌等で刊行予定のため非公開

[redacted]

Fig. 6-3. Estimated distribution routes and methods of Hesperornithiformes.

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