

Comparative Osteology of Three Species of Japanese Cormorants of the Genus *Phalacrocorax* (Aves, Pelecaniformes)

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Introduction

Bird fossils are mostly represented by skeletons or bones. Comparative osteology of Recent birds is essential for identification and classification of fossil forms. Although there have been some works on the osteology of the genus *Phalacrocorax* (see RUDOLPHI, 1816; DERSELBE, 1897, 1914; SHUFELDT, 1884, 1889, 1894, 1903, 1915; JEFFRIES, 1883, 1884; LUCAS, 1889, 1896; and GADOW, 1902), these descriptions are not sufficient for researches of paleontological material. Therefore, for the basis of the identification of fossil cormorants, I here describe osteological characters and differences among Recent Japanese cormorants.

The Phalacrocoracidae consist of one genus and 27 species in the world (MAYR, 1979). Among them, four species are distributed in Japan. They are *Phalacrocorax filamentosus* (TEMMINCK & SCHLEGEL), *P. carbo* (LINNAEUS), *P. pelagicus* PALLAS, *P. urile* (GMELIN). *P. filamentosus* is distributed in Japan, Korea, Ussuri and the northern coast of China. *P. carbo* is an Old World cosmopolitan and distributed also in a part of the northwestern New World, etc. *P. pelagicus* is distributed along the coast of the northern Japan, the Bering Sea coast and the Pacific side of North America. *P. urile* is distributed in the Bering Sea coast and islands of the eastern Hokkaido (after the ORNITHOL. SOC. JAPAN, 1974). Another species, *Phalacrocorax niger* (VIEILLOT) is distributed in the southwestern China.

The present writer investigated skeletons of *P. filamentosus*, and compared them with those of *P. carbo*, *P. pelagicus*, and *P. harrisi* which show the extreme aquatic adaptation. Specimens of *P. urile* have not been available.

In Japan, fossil materials which probably belong to the genus *Phalacrocorax* and related forms are found from Miocene beds in Chichibu, and Mizunami (HASEGAWA *et al.*, 1978), and Pleistocene beds in the Shiriyazaki, the Lake Nojiri (ONO, 1979) and Fujisawa (TAKAHASHI & NOKARIYA, 1980). I am planning to report on these materials in future publications.

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Kiyohiko OGAI, Yoshitsugu OKUMURA, Yoshihiko OKAZAKI, and Osamu SAKAMOTO for providing the fossil materials and informations.

Materials and Methods: The data of the Recent specimens studied are listed below.

P. filamentosus: 2 specimens, Miura Peninsula, Kanagawa Pref. and Shimokita Peninsula, Aomori Pref.

P. carbo: 2 specimens, from Ueno Zoo. ♀, bill length, 60 mm, wing length, 320 mm.

P. pelagicus: 2 specimens, offshore of Hyotsu, Hyotsu County, Hokkaido.

All measurements are linear and to the nearest tenth millimeter. Measurement points are illustrated in Fig. 15.

Anatomical nomenclature follows those of HOWARD (1929) and BAUMEL *et al.* (1979).

Osteological Description of Recent Japanese Cormorants

Herein are described and illustrated details of *Phalacrocorax filamentosus*. Specific differences of three species, *filamentosus*, *carbo*, and *pelagicus*, are summarized briefly. The skeletal elements studied are those bones most frequently found as fossils.

A. Description of *Phalacrocorax filamentosus*

Skull (Fig. 1-1)

Premaxillary, slender, deeply hooked, and slightly curved ventrally. External naris, very small and opened at less than 5 mm in front of naso-frontal hinge. From anterior of external naris, nasal groove extended toward tip of bill. No expansion in naris portion. Cranium, especially in posterior portion behind postorbital process, shifted dorsally, elongated, and somewhat expanded laterally. Rostrum, slightly longer than cranium. Lachrymal, thin medially, fused with frontal, ethmoid, and contacted with jugal, forming lachrymal foramen. Jugal, expanded laterally in anterior portion, and vertically in posterior portion. Dorsal rim of orbit, thin. Postorbital process, small and projected ventrally. Supraoccipital, tuberculated medially and articulated with occipital style. Septal foramen, very large, therefore interorbital septum, much reduced. Large foramen, perforates posterior surface of orbit into cranium. Temporal fossa, deep and narrow. Median ridge on parietal and temporal ridge very high. Vomer, small. Palatine, long and narrow, flat, and medially fused with ridge completely. No basipterygoid process. Sphenoidal rostrum, narrow. Basitemporal plate, somewhat large. Anterior margin of plate, makes long, low ridge. Shallow fossa on basioccipital. Exoccipital, tuberculated in lateral and projected ventro-posteriorly. Opisthotic, directed posteriorly. Occipital condyle, slightly notched and somewhat triangular. Foramen magnum, somewhat excavated in lateral margin. Pterygoid, somewhat expanded dorsally, with round ventral ridge. Quadrate, double headed with shallow notch between heads. Otic

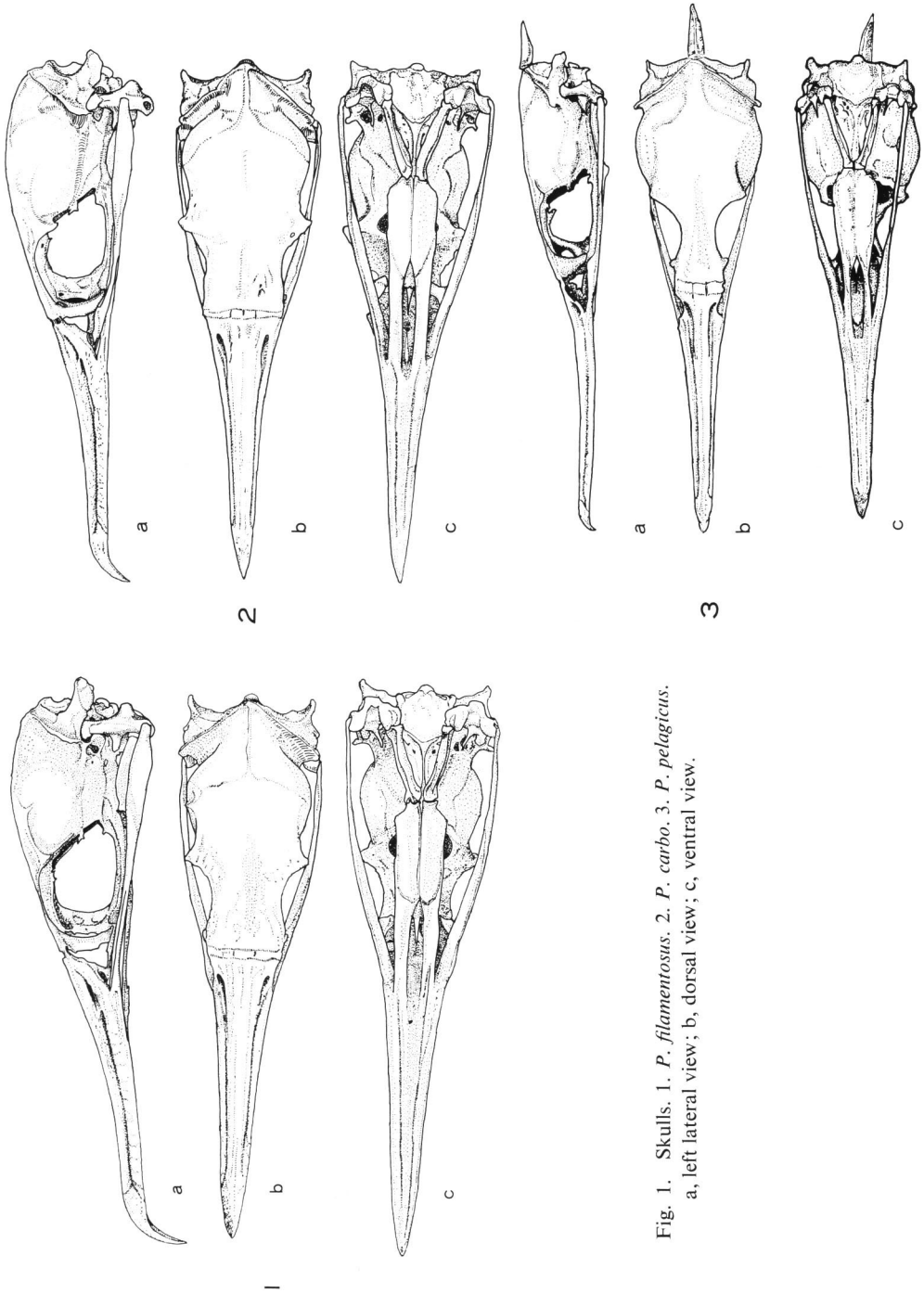


Fig. 1. Skulls. 1. *P. filamentosus*. 2. *P. carbo*. 3. *P. pelagicus*.
a, left lateral view; b, dorsal view; c, ventral view.

process, long.

Mandible (Fig. 2-1)

Tip of mandible, not curved downward. Well sutured. Small pneumatic foramina on dentary. No mandibular foramen. Coronoid process, large, and situated more anteriorly. Articular processes, short. Posterior portion of external articular process, strongly concave. Coronoid process, very low, but serves as place for muscular attachment. Prearticular, concave dorsally.

Furcula (Fig. 3-1)

Broad V-shape, and articulated with carinal apex of sternum on furcular process. Scapular tuberosity, very long. Deep and broad fossa present in the space between scapular tuberosity and coracoidal facet. Coracoidal facet, round, large, and smooth articular facet, directed posteriorly. Shaft, expanded dorsoventrally in proximal, slender in distal, and curved strongly to ventral. Symphysis, broad. Furcular process, short. Sternal facet, large. Broad and shallow groove on posterior margin in proximal of shaft.

Coracoid (Fig. 4-1)

Head, thick vertically. Furcular facet, round and flat on ventral of head, situated somewhat medially. Brachial tuberosity, on internal surface of head. Height of brachial tuberosity, 3.6 mm. Lower margin of tuberosity, somewhat excavated. No pneumatic foramina. Triosseal canal, shallow. Coraco-humeral surface, on external surface of ridge between head and glenoid facet. Neck forms broad fossa. Bicipital attachment forms a distinct fossa externally to furcular facet. Glenoid facet, large, even, and oval articular surface on dorso-external surface of head. Scapular facet, flat, and indistinct in boundary. Procoracoid, tuberculated internally. Deep fossa, between procoracoid and scapular facet. No coracoidal fenestra. Shaft, strongly curved dorsally. Intermuscular line, run slightly externally on ventral surface, and terminated on central of upper margin of ventral lip of sternal facet. Attachment of coraco-brachialis, on midpoint of external surface of shaft. Sterno-coracoidal impression forms deep and large oval fossa on ventral surface of distal end. Sterno-coracoidal process, high, and long terminal knob on anterior margin of process. Dorsal lip of sternal facet, straight. Width of ventral lip, equal to that of dorsal one.

Scapula (Fig. 5-1)

Acromion, expanded posteriorly. Furcular articulation, very large. Coracoidal articulation, large and expanded laterally. Glenoid facet forms triangular shaped facet. Fossa on ventral surface of neck. Blade, straight, narrow, and long. Large tubercle on lateral surface of blade. No pneumatic foramen between acromion and coracoidal articulation. Apex, bent inwardly. Deep fossa on internal surface of proximal end.

Sternum (Fig. 6-1)

Somewhat long, and narrow laterally. Carina, slightly expanded ventrally.

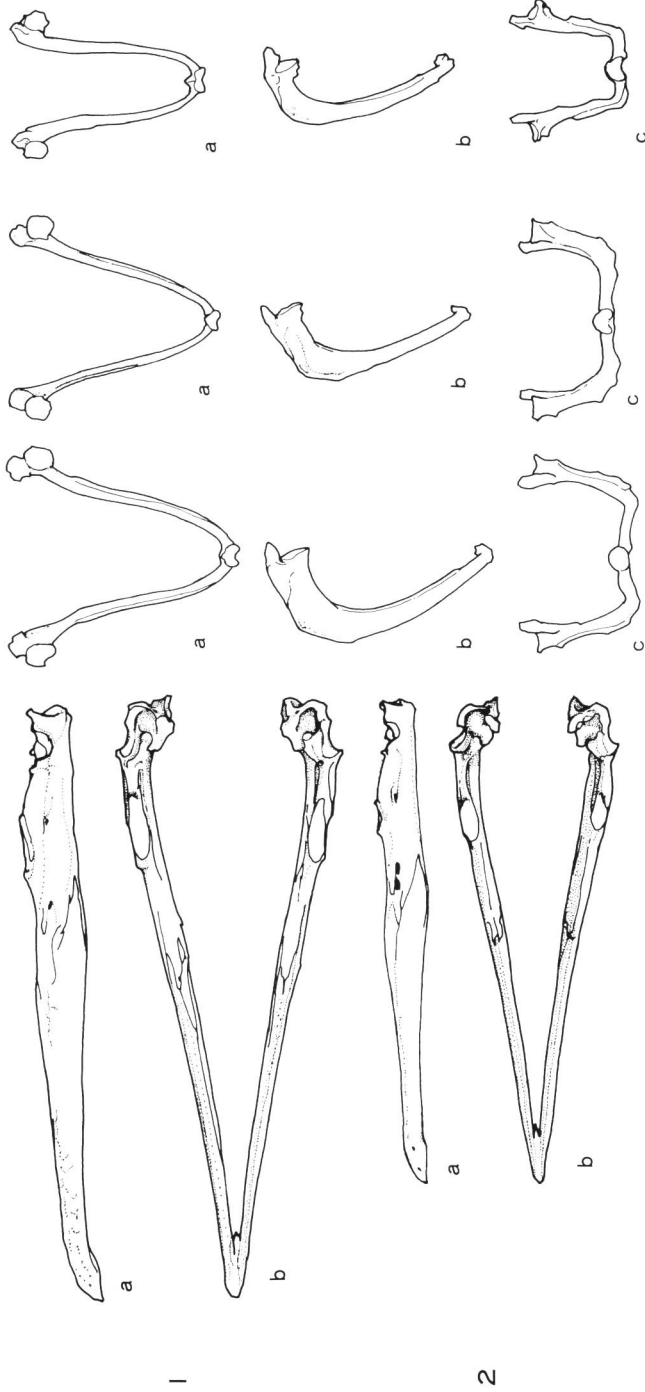


Fig. 3. Furculae. 1, *P. filamentosus*. 2, *P. carbo*. 3, *P. pelagicus*. a, caudal view; b, left lateral view; c, ventral view.

Fig. 2. Mandibles. 1, *P. filamentosus*. 2, *P. carbo*. 3, *P. pelagicus*. a, left lateral view; b, dorsal view.

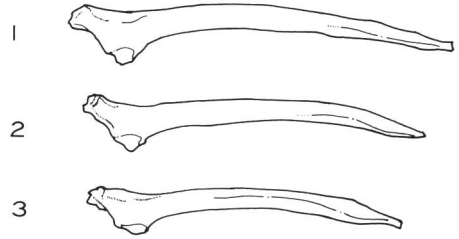
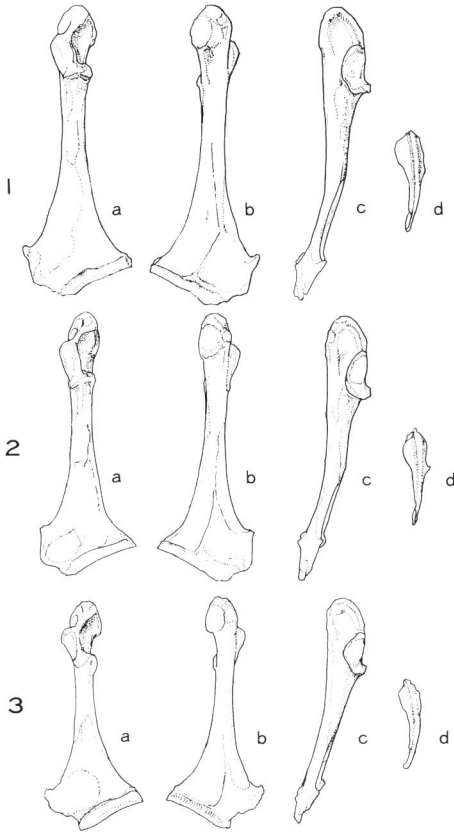


Fig. 5. Scapulae. 1, *P. filamentosus*. 2, *P. carbo*. 3, *P. pelagicus*.

Fig. 4. Coracoids. 1, *P. filamentosus*. 2, *P. carbo*. 3, *P. pelagicus*. a, dorsal view; b, ventral view; c, left lateral view; d, sternal facet.

Anterior carinal margin curved posteriorly. Anterior carinal margin, thin. Carinal apex extended anteriorly. Manibrium weakly developed. No dorsal manibrial spine, and ventral manibrial spine, small. Deep and narrow fossa between large dorsal lip and thin ventral lip of coracoidal sulcus. Sterno-coracoidal process, thick and large square in shape. Costal margin, short. Sternal plate, excavated proximally. Costal process, four. Ventral labial prominence, small. Sternal plate, curved externally, and antero-ventrally. Intermuscular line reaches posterior part of ventral labial process. Xiphial area, short and broad. Post pectoral line runs from distal end of carina to anterior margin of sternal notch. Posterior lateral process, short and broad.

Humerus (Fig. 7-1)

Head, low and wide. Deltoid crest, low, and tuberculated strongly on distal end. Ligamental furrow, deep and broad. Bicipital furrow, very deep and narrow but broad on distal margin of head, and getting narrower distally and terminated on a half of deltoid crest. Bicipital surface, expanded anteriorly. Bicipital crest, somewhat expanded distally. External tuberosity, low but large on innermost of proximal end.

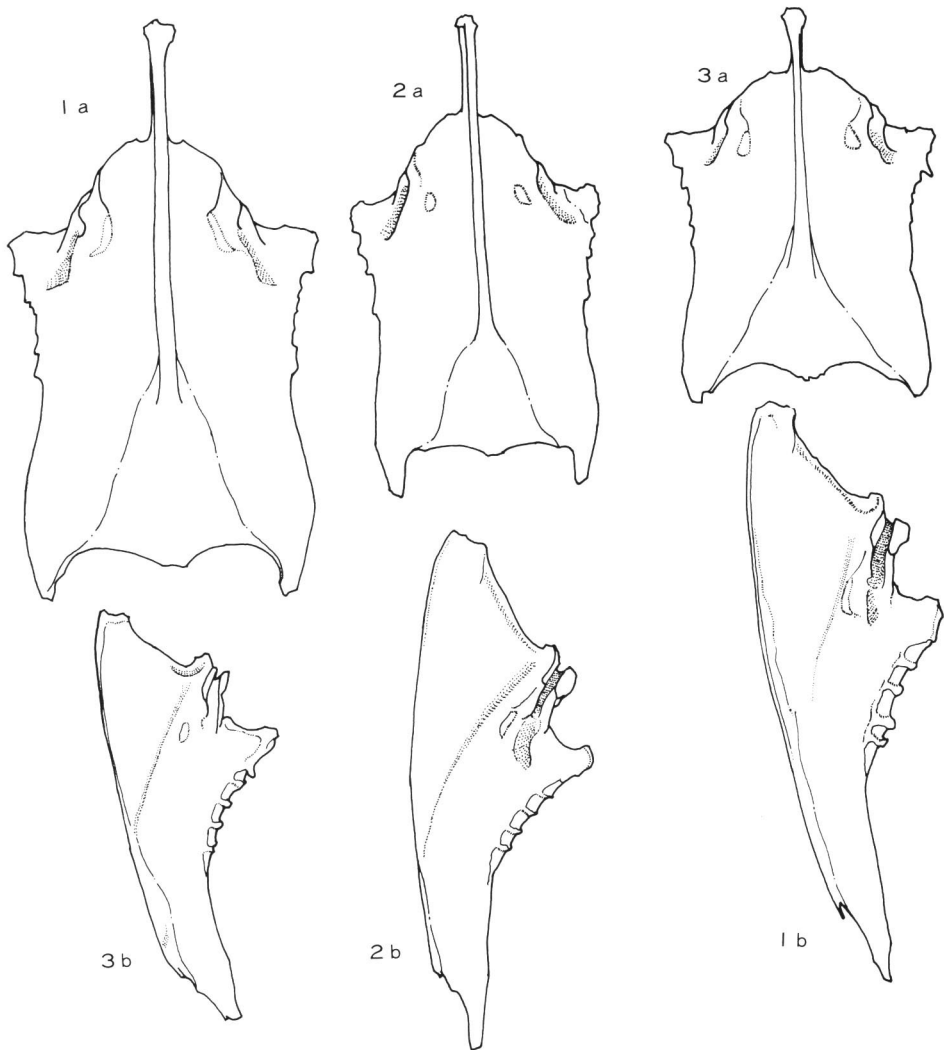


Fig. 6. Sterna. 1, *P. filamentosus*. 2, *P. carbo*. 3, *P. pelagicus*. a, ventral view; b, left lateral view.

Internal tuberosity, large and situated more internally. Capital groove, broad. No pneumatic foramen. Pneumatic fossa, large. Capital-shaft ridge, well developed. Attachment of infraspinatus, large. Attachment of supraspinatus, situated on internal margin of median crest. Median crest, short. Attachment of latissimus dorsi posterioris, short and tuberculated in proximal part. Attachment of latissimus dorsi anterioris, long, broadened distally, and terminated at a half of shaft dorsally. Shaft, slightly flattened, and somewhat curved posteriorly in distal. Expansion of shaft, at distal end of deltoid crest. Impression of brachialis anticus, shallow and situated on

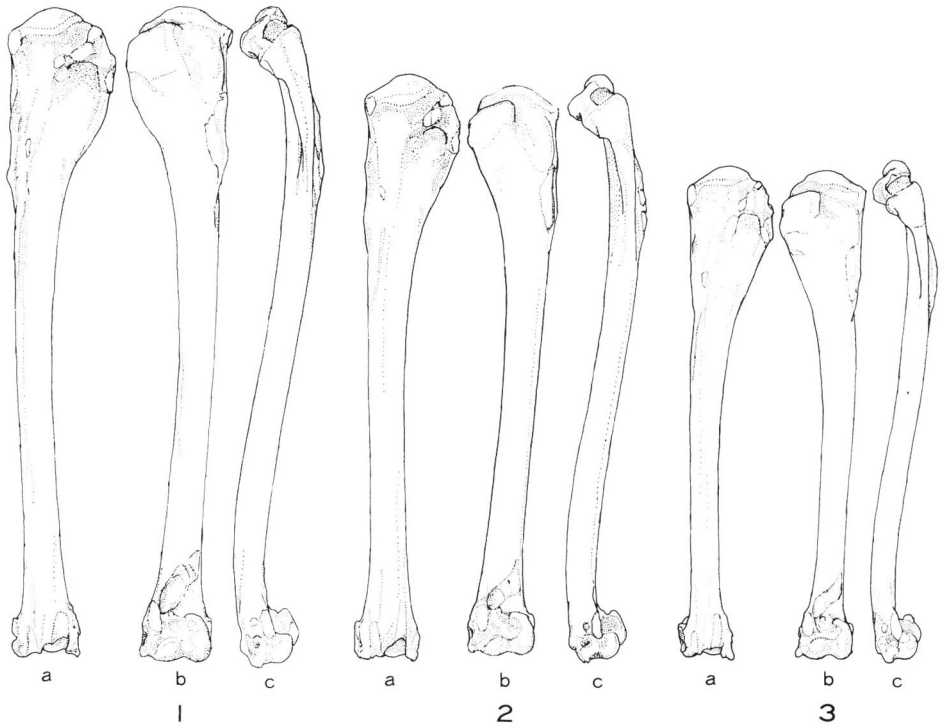


Fig. 7. Humeri. 1, *P. filamentosus*. 2, *P. carbo*. 3, *P. pelagicus*. a, caudal view; b, cranial view; c, ventral view.

dorsoproximal margin of attachment of anterior articular ligament, and dorso-proximally extended in oval shapes. Brachial depression, shallow, narrow, and extended only dorsally. External condyle, bulbous, inflated, and hooked at proximal end. Internal condyle, round and narrow. Intercondylar furrow, shallow and wide. Entepicondyle, expanded ventrally. Attachment of anterior articular ligament, very large and long. Attachment of pronator brevis form deep fossa behind attachment of anterior articular ligament. Ectepicondyle, large. Ectepicondylar prominence, expanded dorsally. External and internal tricipital groove, shallow and broad. Olecranal fossa, broad and somewhat deep.

Olecranon, low and terminated more ventrally. Olecranal fossa, deep and wide. Dorsal lip of external cotyla, developed distally. Ventral margin of internal cotyla, expanded ventrally. Deep and wide fossa, between internal cotyla and prominence for anterior articular ligament. Impression of brachialis anticus, long, but shallow. Prominence for anterior articular ligament, situated medially. Proximal of shaft, slightly compressed antero-posteriorly. Shaft, moderately curved posteriorly. Anterior intermuscular line runs medially in proximal, and more ventrally in half of shaft. Proximal radial depression, indistinct. Carpal tuberosity, large and flattened dorso-

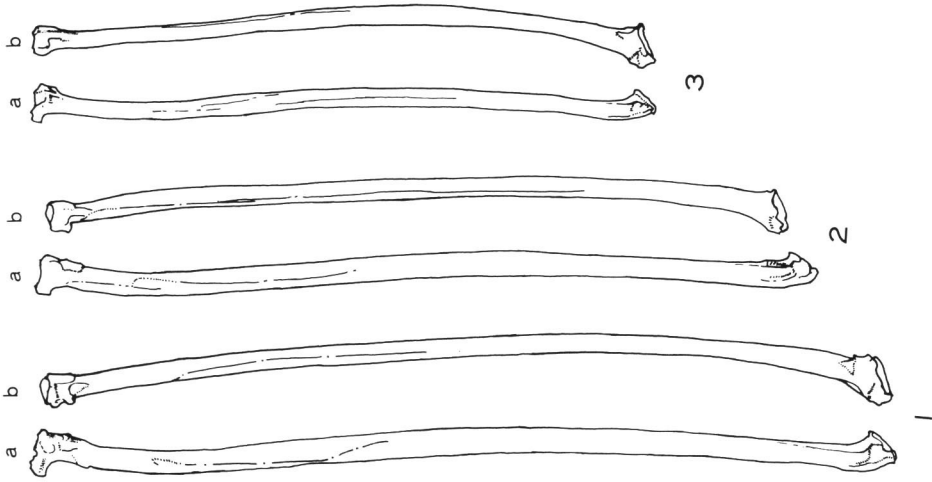


Fig. 9. Radii. 1, *P. filamentosus*. 2, *P. carbo*. 3, *P. pelagicus*. ca, cranial view; b, ventral view.

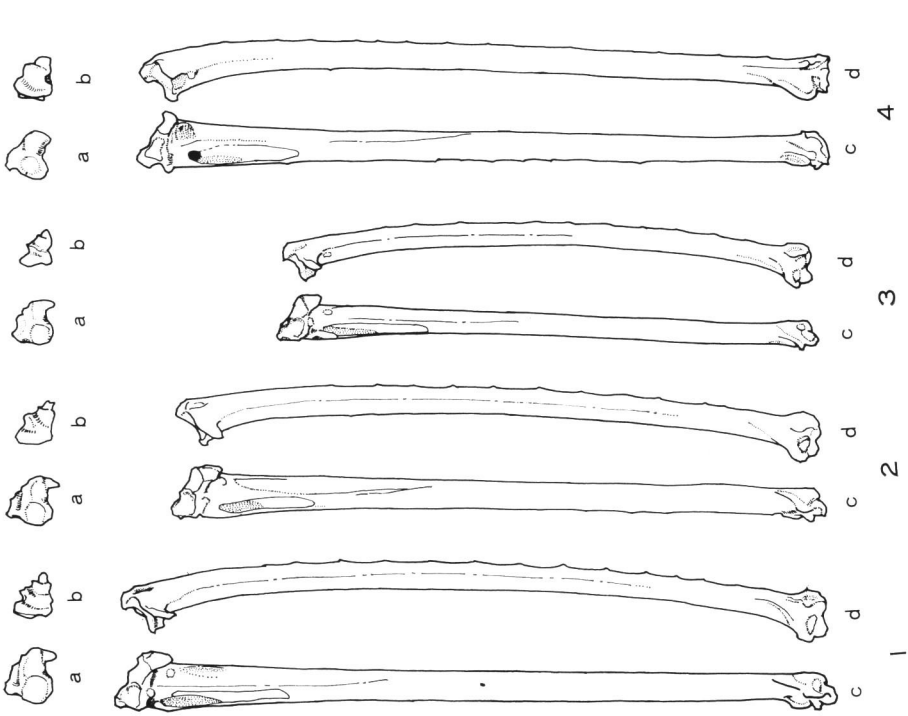


Fig. 8. Ulnae. 1, *P. filamentosus*. 2, *P. carbo*. 3, *P. pelagicus*. 4, *Sula leucogaster*. a, proximal view; b, distal view; c, cranial view; d, dorsal view.

ventrally. Anterior margin of external condyle, elongated anteriorly and forms articular surface for radial carpus. Ventral margin of external condyle, reduced in length and forms tubercle. Distal radial depression forms deep triangular-shaped fossa in dorsal surface of distal end. Tendinal groove, indistinct. Tendinal pit, deep. Distal radial depression, large. External condyle, expanded ventrally. Proximal of shaft, slightly compressed antero-posteriorly. Olecranal fossa, large and extended to apex of olecranon. Ventral margin of internal cotyla, expanded ventrally. Impression of brachialis anticus, long distally, but shallow. Tendinal groove, shallow. Tendinal pit, deep. Distal radial depression, large. External condyle, expanded ventrally.

Radius (Fig. 9-1)

Capital tuberosity, high and rotated dorsally. Ligament papilla, large. Bicapital tubercle, short. Ulnal facet, long triangular shape. Shaft, curved anteriorly in proximal, and posteriorly in medial. Tendinal groove, indistinct. Anterior margin of distal end, expanded anteriorly. Tubercle, on posterior margin of distal end. Scapho-lunar facet, broad.

Carpometacarpus (Fig. 10-1)

Ventral carpal trochlea, expanded posteriorly. Large tubercle, on distal end of dorsal carpal trochlea. Anterior carpal fossa, shallow, and extended posteriorly. Ventral surface of extensor attachment, excavated. External ligamental attachment, excavated. Internal ligamental fossa, broad and shallow. Anterior margin of pliciform process, excavated deeply. Pliciform process, high. Extensor attachment, rotated proximally. Process of metacarpal I, curved proximally, and concave on dorsal

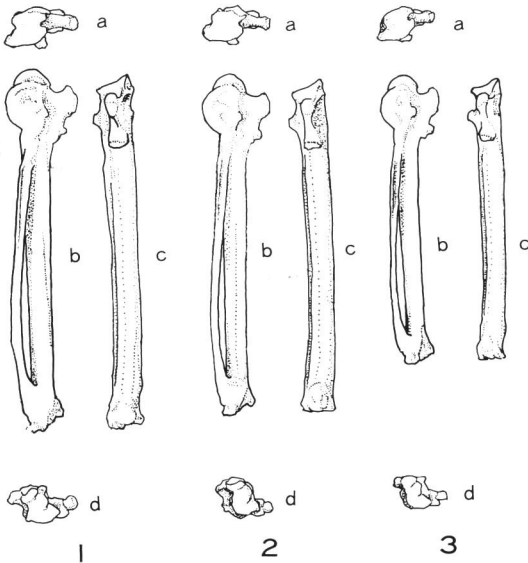


Fig. 10. Carpometacarpi. 1, *P. filamentosus*. 2, *P. carbo*, 3, *P. pelagicus*. a, cranial view; b, distal view.

surface. Metacarpus I, concave strongly between process of metacarpal I and pollical facet. Fossa, between pollical facet. Metacarpal II, slender, and straight in anterior margin, but curved dorsally. Groove, on posterior surface of proximal end of metacarpal III. Flexor attachment, on proximal symphysis of metacarpus III and III. Intermetacarpal tuberosity, on proximal end of metacarpal II. Tendinal groove, indistinct, but forms groove only on distal end. Intermetacarpal space, narrower in proximal end. Distal symphysis, long. Triangular fossa, on ventral surface of distal end of metacarpus II. Deep groove, on facet for digit II medially. Facet for digit III, more projected distally. Deep fossa, between facet for digit II and digit III.

Pelvis (Fig. 11-1)

Thoracics, 2. Lumbar, 4. Sacral, 3. Caudal, 8 (+1). Subiliac space, not so expanded anteriorly and overlapped on anterior articular facet of 1st synsacral vertebra. Median dorsal ridge, expanded dorsally to distal end of synsacral vertebrae. Apex of median dorsal ridge, flattened. Shield, less developed. Canals among transverse section on shield, very large. Centrum of thoracic and lumbar vertebrae, very flattened laterally, with 3-4 hypapophyses. Parpophysis, small. Shallow groove, on ventral surface of centrum of lumbar, sacral and anterior caudal vertebrae. Ilium, strongly concave at lumbar vertebral portion. Anterior iliac crest, developed, but posterior iliac crest, indistinct. Pectoral process, not developed. Acetabulum, not so thick. Obturator foramen, long. Antitrochanter, flat, horse bean shaped, and external margin of antitrochanter, expanded laterally. Large tubercle on dorsal surface of ilium. Postacetabular ischia, expanded inwardly. Preacetabular ilium expanded. Pubis, slightly attenuated in its anterior two third, and somewhat expanded in area of contact with ischium. Posterior iliac crest, developed. Ischio-pubic fenestra, not closed distally by ischium and pubis. Ilioischiatric fenestra, large, and shield of ilium, very narrow. Ischial angle, acute, and expanded posteriorly. Distinct notch, on posterior margin of area of fusion of ilium and ischium, and resulting spine at posterior-most end of ilium. Renal depression, not so distinct, but only recognizable on area behind ilioischiatric fenestra. Renal bar, less projected internally.

Femur (Fig. 12-1)

Head, somewhat short and extended internally. Attachment of round ligament, large and somewhat posteriorly on dorsal surface of head. Neck, flat. Iliac facet, flat. Shallow fossa on posterior margin of iliac facet. Trochanter, indistinct. Trochanteric ridge, strongly expanded anteriorly. Large fossa on external surface of trochanteric ridge. Lower margin of trochanteric ridge, thickened. Fossa between trochanter and trochanteric ridge. Anterior intermuscular line, from distal margin of trochanteric ridge, to center of shaft. Obturator ridge, slightly expanded internally. Distinct tubercle, on internal surface posteriorly as same level as distal end of trochanteric ridge. Shaft, compressed laterally and curved anteriorly toward distal end. Anterior intermuscular line, curves externally at a third from distal end. Posterior intermuscular line, distinct only externally on proximal, and internally on distal.

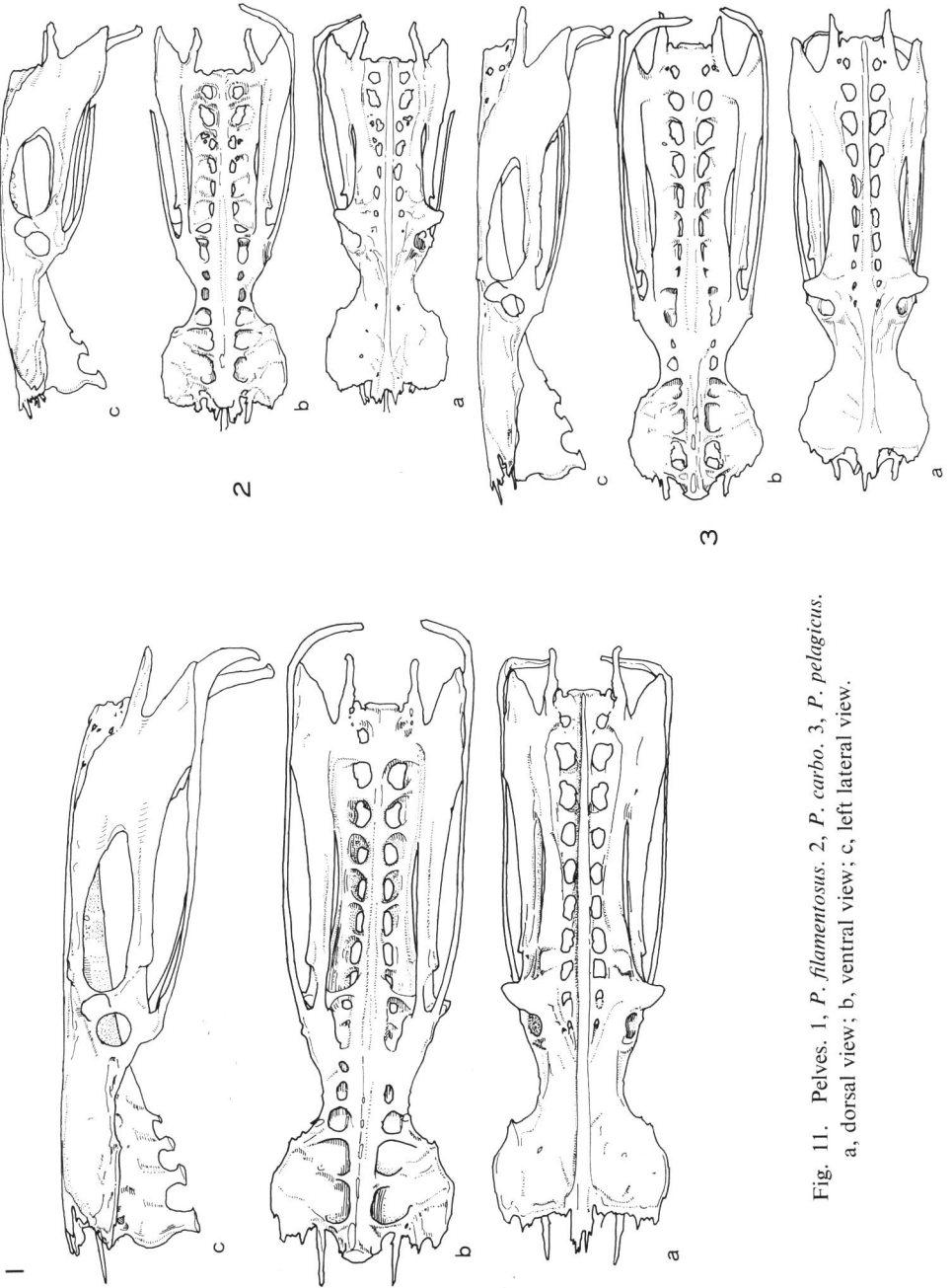


Fig. 11. Pelves. 1, *P. filamentosus*. 2, *P. carbo*. 3, *P. pelagicus*.
a, dorsal view; b, ventral view; c, left lateral view.

Dorsal margin of fibular condyle, broad, and expanded laterally. Fibular groove, broad and deep. Dorsal margin of external condyle expanded externally. Articular surface of internal condyle, horse bean like in shape. Anterior ridges of external and internal condyles, low. Rotular groove, shallow, and broadened. Pit for tibialis, on center of lower surface of external condyle.

Patella

Anterior crest large, in *pelagicus*, and *filamentosus*, but small in *carbo*. Trihedral in form, with an extensive, squarish base. A large foramen, above its middle. Remarks: such a large patella, possessed by grebes and cormorants corresponds with underwater adaptation of pelvic limb diving. Small size in *carbo*, reflects its' habitat, estuaries of rivers, and inland waters.

Tibiotarsus (Fig. 13-1)

Flat, and short. Internal articular surface, low and expanded externally. Prominence of external articular surface, directed posteriorly. Interarticular area, wide anteriorly. Inner cnemial crest, high, and large articular facet for patella on proximal margin of inner cnemial crest. Outer cnemial crest, large. Rotular crest, high, but lower than cnemial crests and deep tendinal fossa on rotular crest external. Ligament attachment, small tubercle. Flexor attachment, slightly externally. Fibular crest, high and long. Intermuscular line, internally in proximal. Shaft, flat. Tendinal groove, situated externally. Distal end of tendinal groove, externally. Fossa, between distal, external margin of shaft and supratendinal bridge. Groove for proneus profundus, broad and shallow. Prominence, on anterior margin of groove for proneus profundus. Internal ligamental prominence, small. Trochlea, situated internally. Internal condyle, narrow and more expanded distally than external condyle. Indistinct fossa on posterior margin of internal condyle. External condyle, slightly wide. Anterior intercondylar fossa, narrow but deep. External ligamental prominence, large and elongated proximally to make attachment for spine of fibula. Posterior intercondylar sulcus, distinct.

Tarsometatarsus (Fig. 14-1)

Internal cotyla, deep and long oval shape. External cotyla, flat and square in shape. No fossa on anterior margin of external cotyla. Intercotylar depression, shallow and extended to inner calcaneal ridge. Intercotylar prominence, high, but not expanded anteriorly. Proximal ligamental attachment forms large tubercle on internal margin of anterior metatarsal groove. Attachment of external ligament, oval fossa with small ridge anteriorly. Outer proximal foramen, equal to inner one in size, and perforated to posterior surface at level of distal margin of 1st calcaneal ridge. Inner proximal foramen, slightly higher than outer one, and perforated to posteriorly at equal level of outer one. Four calcaneal ridges of hypotarsus and 4 tendinal canals. First ridge, largest, and forms tuberosity at posterior end. Second, high and fused with 1st one. Third, low and somewhat wide. Fourth ridge, expanded proximally, not

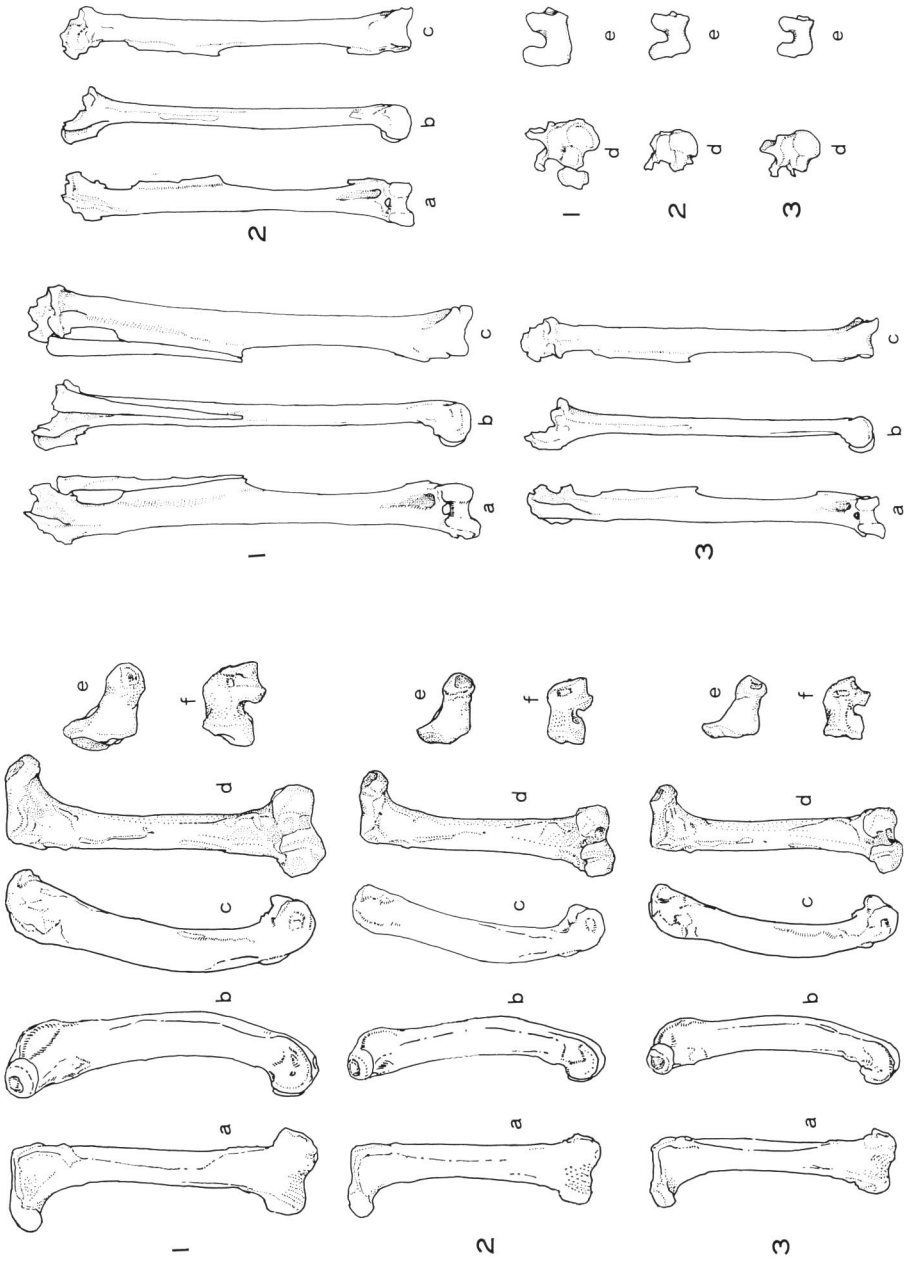


Fig. 13. Tibiotarsus. 1, *P. filamentosus*. 2, *P. carbo*. 3, *P. pelagicus*. a, cranial view; b, lateral view; c, caudal view; d, proximal view; e, distal view.

Fig. 12. Femora. 1, *P. filamentosus*. 2, *P. carbo*. 3, *P. pelagicus*. a, cranial view; b, medial view; c, lateral view; d, caudal view; e, proximal view; f, distal view.

posteriorly like other 3 ridges. First canal, small, and situated more posteriorly and closed by second ridge. Second canal, large and separated into anterior part and posterior part by prominence on internal surface of second canal. Third canal, broad. Fourth canal, incompletely closed but forms shallow fossa. Arrangement of tendons of tarsal flexors, type II (KIYOSUMI, 1948). Tubercle for tibialis anticus, large, and closely to proximal foramina. Shaft, narrow and high, externally. Anterior metatarsal groove, shallow, and continued at distal foramen. Inner extensor groove, very deep and situated more proximally. Posterior metatarsal groove, indistinct. Outer extensor groove, narrow but deep. Distal foramen, large. Anterior surface of distal end of shaft, round. Trochlea for digit 3, deep groove. External intercotylar notch, larger than internal one. Wing of trochlea for digit 2, tuberculated internally.

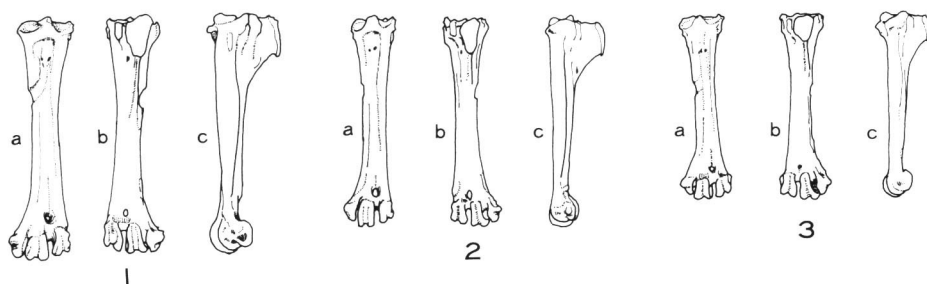


Fig. 14. Tarsometatarsi. 1, *P. filamentosus*. 2, *P. carbo*. 3, *P. pelagicus*. a, cranial view; b, caudal view; c, lateral view.

Vertebrae (Presacral vertebrae)

Cervicals—18 Thoracis—5

Neural spine, from 2nd (axis) to 8th cervical, developed. Especially the 7th, the 8th ones, very high. No neural spine on the 9th, 10th, 11th (only muscular line). On the 12th cervical, low and tubercular, neural spine. The 13th, and 14th cervicals slightly higher than the former. Spine of 15th cervical, stout. Spine of 16th, 17th 18th, large and quadrate-shaped in lateral view. No fusion among thoracics.

Hypapophysis

On atlas (1st), axis (2nd), 3rd cervical, very long hypapophysis. On 4th, 5th, 6th cervicals, low hypapophysis. On 7th–13th cervicals, no hypapophysis. Parapophysis especially on 13th cervical, strongly developed. Largest hypapophysis developed on the 14th cervical. Size of hypapophyses, reduced gradually from 15th cervical to 18th.

Costae

Presacral portion—5

Sacral portion—3

Dorsal costae somewhat long. 1st costa without uncinat process, from 2nd to 5th costa with large uncinat process. 6th costa with large uncinat process.

B. Comparison

Japanese Recent cormorants, *P. filamentosus*, *P. carbo*, *P. palagicus*, are distinguishable by osteological characters. Following bones distinctly show specific differences.

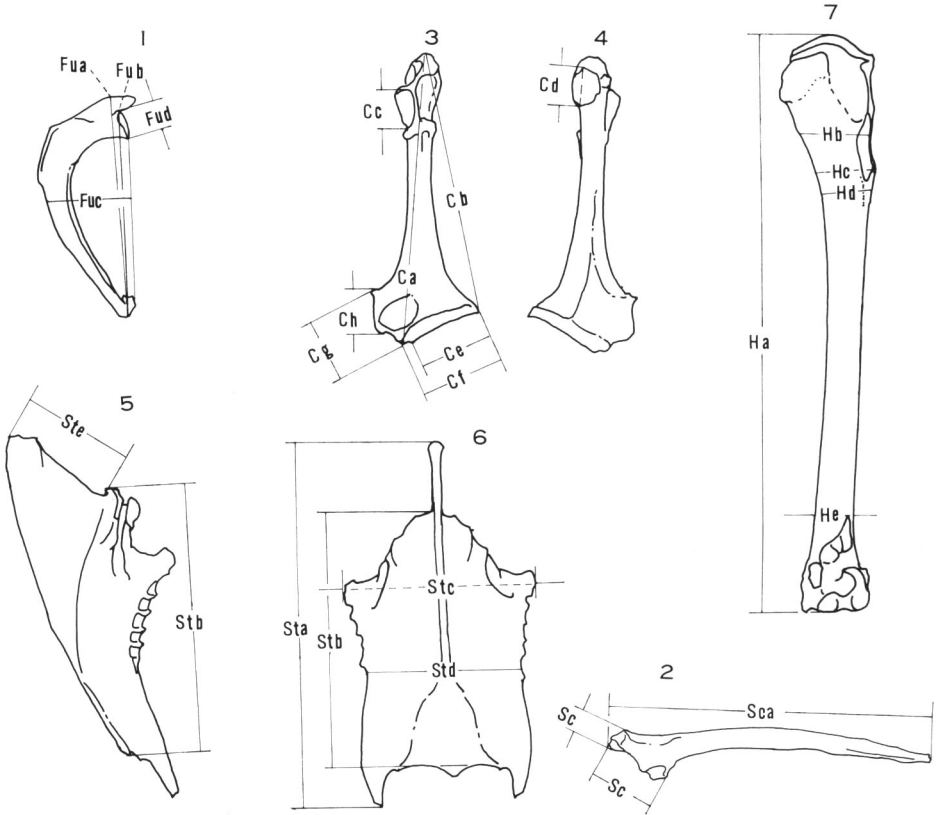
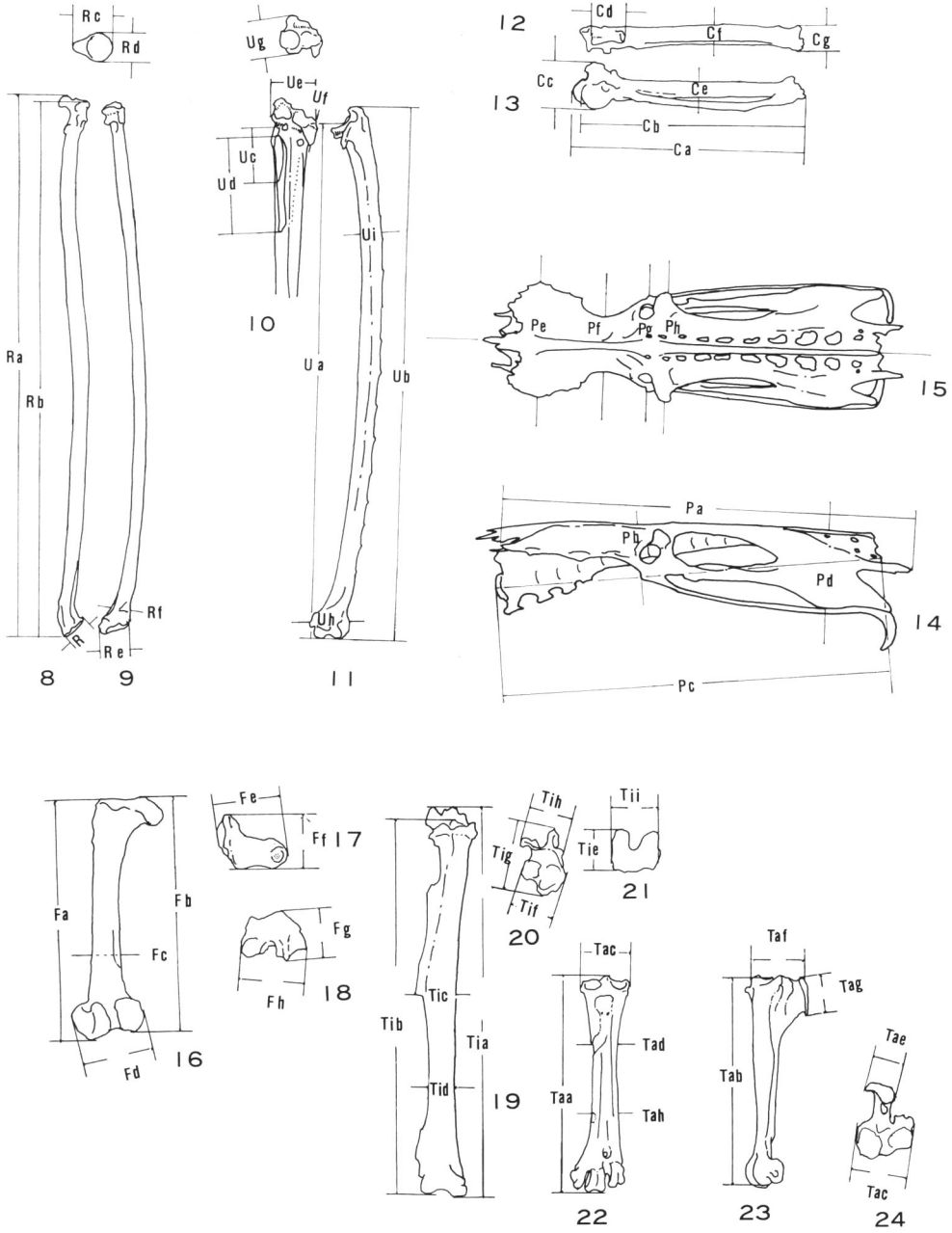


Fig. 15. Measurement points of Recent Japanese cormorants and related species of Pelecaniformes. 1, furcula in left lateral view. 2, left scapula in lateral view. 3, left coracoid in dorsal view. 4, left coracoid in ventral view. 5, 6, sternum, 5: left lateral view, 6: ventral view. 7, left humerus in cranial view. 8, 9, left radius, 8: proximal view, 9: ventral view. 10, 11, left ulna, 10: proximal view, 11: dorsal view. 12, 13, left carpometacarpus, 12: cranial view, 13: ventral view. 14, 15, pelvis, 14: left lateral view, 15: dorsal view. 16, 17, 18, left femur, 16: caudal view, 17: proximal view, 18: distal view. 19, 20, 21, left tibiotarsus, 19: caudal view, 20: proximal view, 21: distal view. 22, 23, 24, left tarsometatarsus, 22: cranial view, 23: lateral view, 24: proximal view.



Skull (Fig. 1)

In *filamentosus*, premaxillary, deeply hooked. Cranium, orientated ventrally.

Table 1. Measurements of Recent Japanese cormorants.
(Measurement points are shown in Fig. 15).

		Phalacrocorax					filamen-	carbo	pelagi-
		filamen-	carbo	pelagi-			tosus	tosus	cus
		tosus		cus					
furcula	Fua	68.3	66.2	56.8	carpometacarpus	Caa	74.8	71.4	60.4
	Fub	65.4	63.2	54.2		Cab	71.4	68.9	58.5
	Fuc	26.5	21.0	17.5		Cac	15.4	14.3	12.5
	Fud	8.2	7.2	6.9		Cad	11.4	10.2	10.0
	Fue	58.1	56.0	40.0		Cae	4.7	4.2	4.0
						Caf	4.9	4.8	4.3
coracoid	Ca	80.1	72.9	63.4	pelvis	Pa	154.2	130.3	107.1
	Cb	73.8	65.4	57.8		Pb	21.8	22.9	18.7
	Cc	13.2	13.3	11.9		Pc	144.8	126.4	94.5
	Cd	11.0	9.6	8.3		Pd	31.5	30.5	26.8
	Ce	18.3	21.4	19.0		Pe	42.5	43.9	35.2
	Cf	21.5	23.2	18.8		Pf	22.2	18.0	15.4
	Cg	13.9	14.9	19.8		Pg	22.6	28.0	15.7
	Ch	11.6	13.3	8.8		Ph	42.5	35.7	31.4
scapula	Sca	92.0	82.3	74.7	femur	Fa	66.8	54.9	54.3
	Scb	19.2	19.0	16.6		Fb	65.0	53.4	52.7
	Scd	7.8	7.6	6.5		Fc	7.4	7.2	6.2
sternum	Sta	124.3	111.0	93.5		Fd	18.7	15.3	13.7
	Stb	84.7	74.4	64.6		Fe	18.3	15.3	13.8
	Stc	69.4	57.1	61.0		Ff	15.0	11.1	11.0
	Std	54.5	46.8	48.4		Fg	12.3	9.8	9.7
	Ste	35.9	37.3	28.0		Fh	18.6	15.3	13.6
humerus	Ha	160.0	159.0	131.0		tibiotalarsus	Tia	126.6	99.9
	Hb	17.9	17.1	14.6	Tib		118.6	93.8	93.2
	Hc	16.2	14.7	13.5	Tic		13.4	10.2	9.9
	Hd	11.5	11.4	10.6	Tid		8.1	6.7	6.2
	He	9.0	9.2	7.1	Tie		12.9	11.2	9.8
	Hc-Hd				Tif		13.8	11.1	10.9
		0.40	0.29	0.27	Tig		20.4	17.0	13.6
	Hd				Tih		14.0	11.0	11.0
					Tii		14.2	11.6	10.5
ulna	Ua	172.0	159.0	131.0	tarsometatarsus	Taa	68.0	59.3	52.1
	Ub	163.8	152.3	126.0		Tab	66.4	58.2	51.2
	Uc	19.6	12.7	15.2		Tac	15.1	12.3	11.8
	Ud	32.6	23.6	25.9		Tad	7.4	6.2	5.7
	Ue	13.7	12.2	11.2		Tae	7.2	5.4	5.8
	Uf	7.1	7.1	5.1		Taf	18.6	16.1	14.4
	Ug	12.4	11.4	10.0		Tag	11.8	9.9	8.0
	Uh	10.7	10.0	9.0		Tah	8.1	7.1	6.5
	Ui	6.5	6.8	6.1					
		×8.0	×8.3	×6.8					
radius	Ra	165.9	153.2	128.2					
	Rb	161.0	148.9	124.1					
	Rc	9.0	8.0	7.7					
	Rd	6.9	6.3	5.3					
	Re	10.3	9.0	8.0					
	Rf	5.8	5.6	4.8					

Table 2. Proportions in skeletal elements of Recent Japanese cormorants and Harriss flightless cormorant (*Phalacrocorax harrisi*).

	Phalacrocorax						Phalacrocorax	
	filamentosus		carbo		pelagicus		harrisi	
	length	(%)	length	(%)	length	(%)	(GADOW, 1902) length	(%)
humerus	160.0	39.3	145.1	30.6	123.9	39.3	101	39.6
ulna	172.0	42.3	159.0	42.3	131.0	41.5	82	32.2
carpometatarsus	74.8	18.4	71.4	19.0	60.4	19.2	72	28.2
Total (W)	406.8		375.5		315.3		255	
femur	67.5	25.8	54.9	25.6	54.3	26.1	73	25.8
tibiotarsus	126.6	48.3	99.9	46.7	101.5	48.8	140	49.5
tarsometatarsus	68.0	25.9	59.3	27.7	52.1	25.1	70	24.7
Total (H)	262.1		214.1		207.9		283	
W/H	1.55		1.75		1.52		0.90	
Fa/Tib	0.533		0.550		0.535		0.521	
Taa/Tib	0.537		0.59		0.513		0.50	

	Phalacrocorax			Phalacrocorax harrisi
	filamentosus	carbo	pelagicus	
Std/Stb	0.64	0.64	0.75	0.73
Sta/Pa	0.838	0.846	0.874	—
Fuc/Fua	0.388	0.317	0.308	0.158
Ph/Pa	0.276	0.274	0.293	0.246
Pd/Pa	0.204	0.207	0.250	0.190

Rostrum, slightly longer than cranium. Postorbital process, small. Lateral fossa of foramen magnum, shallow. In *carbo*, same as *filamentosus*, but postorbital process, somewhat large. Fossa on basioccipital, slightly deep. Lateral fossa of foramen magnum, slightly deep. In *pelagicus*, skull, very compressed vertically. Premaxillary, slightly hooked. No postorbital process. Cranium, as long as rostrum. Fossa on basioccipital, somewhat deep. Lateral fossa of foramen magnum somewhat deep.

Mandible (Fig. 2)

In *carbo*, coronoid process very low, but made in relatively narrow muscular attachment. Pre-articular, excavated somewhat dorsally. In *pelagicus*, Compressed vertically. Coronoid process, vestigial and made in small. Post-external articular process, narrow. Pre-articular fossa, shallow. Post-articular process, narrow and long.

Furcula (Fig. 3)

In *filamentosus*, broad V-shape. Curve ratio: 0.388 (see Table 2-2, and Fig. 15). In *carbo*, somewhat broad V-shape. Curve ratio: 0.317. In *pelagicus*, narrow V-shape. Curve ratio: 0.308.

Coracoid (Fig. 4)

In *filamentosus*, sterno coracoidal process, high (11.6 mm). Shaft strongly curved. In *carbo*, sterno coracoidal process, high (13.3 mm), less curved. In *pelagicus*, sterno coracoidal process, low (8.8 mm), less curved.

Sternum (Fig. 6)

In *filamentosus*, carina and sternal plate somewhat long. Sternocoracoidal process, large. In *carbo*, sternocoracoidal process, slender. In *pelagicus*, carina and sternal plate short.

Humerus (Fig. 7)

In *filamentosus*, large tubercle on distal end of deltoid crest. Long and very deep bicipital furrow. Bicipital crest, somewhat expanded distally. Impression of brachialis anticus, shallow and extended proximally. In *carbo* no tubercle on distal end of deltoid crest. Long bicipital furrow, but its distal margin, indistinct. Bicipital crest, less expanded. Impression of brachialis anticus, deep but short. In *pelagicus*, no tubercle on distal end of deltoid crest. Bicipital furrow, short but relatively deep. No expansion of bicipital crest. Impression of brachialis anticus, shallow and somewhat long.

Ulna (Fig. 8)

In *filamentosus*, ventral margin of internal cotyla, expanded ventrally. Impression of brachialis anticus, long but shallow. In *carbo*, ventral margin of internal cotyla, not so expanded dorsally. Impression of brachialis anticus, somewhat short. In *pelagicus*, ventral margin of internal cotyla, not expanded dorsally. Impression of brachialis anticus, long.

Radius (Fig. 9)

In *filamentosus*, tendinal groove, indistinct. Anterior margin of distal end, expanded anteriorly. In *carbo*, tendinal groove, distinct, broad and situated more posteriorly. In *pelagicus*, tendinal groove, separated into anterior one and posterior one.

Femur (Fig. 12)

In *filamentosus*, trochanteric ridge, strongly expanded anteriorly. Fossa between trochanter and trochanteric ridge. Shallow fossa on posterior margin of iliac facet. In *carbo* trochanteric ridge, less expanded. No fossa between trochanter and trochanteric ridge. In *pelagicus* trochanteric ridge, strongly expanded. No fossa between trochanter and trochanteric ridge. Deep fossa on posterior margin of iliac facet.

Patella

Size, *filamentosus*→*pelagicus*→*carbo*. And no canals in *pelagicus*.

Tibiotarsus (Fig. 13)

In *filamentosus*, external margin of internal articular surface, low. Rotular crest, lower than cnemial crest. Tendinal fossa, deep. Fossa, indistinct on posterior margin of internal condyle. In *carbo*, external margin of internal articular surface, low.

Rotular crest, lower than cnemial crests. Tendinal fossa, deep. Deep fossa, on posterior margin of internal condyle. In *pelagicus*, external margin of internal articular surface, high. Rotular crest, higher than cnemial crests. Tendinal fossa, shallow. Deep fossa on posterior margin of internal condyle.

Tarsometatarsus (Fig. 14)

In *filamentosus*, proximal ligamental attachment, large. Calcaneal tuberosity of first calcaneal ridge, expanded. Second and 3rd ridge, high. First calcaneal canal, closed by second ridge. Second calcaneal tuberosity of first calcaneal ridge, expanded. Second, third ridges, high. First calcaneal canal, closed by second ridge. Second canal, deep and separated to anterior part and posterior part by prominence on internal surface of second canal. Third canal, somewhat broad. In *carbo* proximal ligamental attachment, indistinct. Calcaneal tuberosity of first ridge, expanded distally. Second ridge, indistinct. Third ridge, high. First calcaneal canal, closed by perichondrium. Second canal, broad but separated. Third canal, narrow. In *pelagicus*, proximal ligamental attachment, long. Calcaneal tuberosity of first ridge, low distally. Second ridge, high. Third ridge, low. First calcaneal canal, closed by second ridge. Second canal, broad and separated anterior part and posterior part. Third canal, narrow.

Vertebrae

P. carbo

Cervicals . . . 18 Thoracics . . . 5

There are no distinct differences between vertebrae of *P. filamentosus* and *P. carbo*. Hypapophysis of 14th cervical, shorter than that of 15th one.

P. pelagicus

Cervicals . . . 18 Thoracics . . . 5

Cervicals are relatively slender, compared with those of *P. filamentosus* and *P. carbo*. Hypapophysis of 14th cervical, shorter than that of 15th. On 17th, 18th cervicals, 1st and 2nd thoracics.

Costae

P. carbo

Presacral portion . . . 5

Sacral portion 2

1st costa with long shaft and large uncinat process. 2nd to 5th costa with large uncinat process. 6th costa with large uncinat process.

P. pelagicus

Presacral portion . . . 5

Sacral portion 2

1st costa with relatively large uncinat process. 2nd to 5th costa with large uncinat process. 6th costa with small uncinat process.

Phalacrocorax urile, which was not available, has been mentioned about osteological characters by SHUFELDT (1915). The skeleton of *P. urile* is quite similar to that of

P. pelagicus. In *Phalacrocorax urile*, "the skull is smaller than in the others, of a lighter and more delicate structure. The superior mandible (maxilla) is rather lengthy, and the cranium compressed from above downward. The occipital line and crest is somewhat reduced, and the occipital style small. Over the parietal region, in the mid-longitudinal line, the surface is smooth and the crest absent. At its medial inferior angle the lacrymal is connected with the mesethmoid by a slender, bent bar of bone, which is larger and stronger in remaining three types. The foramen magnum is very large in proportion to the size of skull. The occipital line and crest meet in the middle line at the site where the occipital style articulates."

Genus *Phalacrocorax* is the under water swimmer, and has the ability of flight. *Phalacrocorax harrisi* (*Nannopterum harrisi*) loses the ability of flight, but has adapted to the extreme aquatic life (GADOW, 1902, SCHUFELDT, 1915). MAYR (1979) classified *Nannopterum harrisi* (Harriss flightless cormorant) into genus *Phalacrocorax* with the other species of *Phalacrocorax*. *Phalacrocorax harrisi* is distributed in Isabela and Fernandia (Narborough), Galapagos Archipelago. *Phalacrocorax harrisi* obtained distinct modifications in the pectoral girdles and wing bones. The wing bones are reduced extremely compared with the leg bones (Table 2). The carina of sternum and the curvature of fulcula are reduced. Coracoid is much reduced in length and strength. The reduction of scapula is extreme (SCHUFELDT, 1915). The leg bones are relatively longer (Table 2). SCHUFELDT (1915) wrote, "Differences between *Phalacrocorax* and *Nannopterum*, generic distinction, so far as its skeleton is concerned, are upon those morphological changes which have taken place in its osseous and other systems, due to the gradual loss of the power of flight. In other respects *Nannopterum* is a true cormorant." Future problems lie in this region.

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