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POSTCRANIAL OSTEOLOGY OF THE WATERFOWL

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POSTCRANIAL OSTEOLOGY OF THE WATERFOWL

GLEN E. WOOLFENDEN¹

SYNOPSIS: Postcranial osteology of nearly all the genera of waterfowl of the world is described. On the basis of this study certain changes in the classification within the order are proposed. In comparison with the most recent classification of the waterfowl, that of Delacour, the following changes are proposed: *Anseranas* is placed in a monotypic family; *Stictonetta* is removed from the Anatini and placed tentatively in the Dendrocygnini of the Anserinae; *Cereopsis* is moved from the Tadornini to a monotypic tribe of the Anserinae; *Plectropterus* is moved from the Cairinini to the Tadornini; *Tachyeres* is moved from the Tadornini to the Anatini; the tribe Cairinini is merged with the Anatini; *Merganetta* is moved from the Anatini to a monotypic tribe; *Rhodonessa* is moved from the Anatini to the Aythyini; the tribe Somaterini is merged with the Mergini. The following genera are resurrected: *Olor*, *Nesochen*, *Callonetta*, *Pteronetta*, *Metopiana*, *Mergellus*, *Lophodytes*, and *Nomonyx*, and, tentatively, *Asarcornis* and *Salvadorina*.

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¹ The author, Instructor in Biological Sciences at the University of South Florida, Tampa, completed this work while a graduate student and an instructor at the University of Florida, Gainesville. An earlier version formed his doctoral dissertation and was accepted by the Graduate School in August 1960. Manuscript submitted 19 December 1960.—ED.

INTRODUCTION

It seems logical that the waterfowl, as the Anatidae are commonly known, should be a well-studied group. They have great economic and recreational value, and many species are easily reared in captivity. No living species completely new to science has been discovered since 1894. But, as Delacour and Mayr (1945) point out, their internal anatomy is a completely neglected field. Until Verheyen's osteological work (1955), no modern comparative anatomical study of all the taxa within the family was ever undertaken.

Verheyen bases his classification almost entirely on the number of vertebrae in the different regions of the column and on relative lengths of various limb elements. He admits that structural details of the individual bones are of great importance to paleontologists, but further states, somewhat antithetically, that such features rarely serve to distinguish one waterfowl from another. Previous work with anatic fossil material convinced me that a detailed analysis of the structure of their bones might contribute significantly to better understanding of waterfowl phylogeny.

Many osteological studies emphasize the relative lengths of limb bones. This characteristic may be of significance between closely related species, but in such ancient and diverse groups as the waterfowl, it seems likely that relatively similar proportions could have arisen independently several times. The concept that structural features of the different elements may be more significant than relative sizes underlies this study.

As the skull is treated by other investigators (Verheyen, 1955; Goodman and Fisher, MS), the present study is based primarily on qualitative structural differences in 10 postcranial elements. The relative taxonomic usefulness of these elements is respectively: humerus, carpometaarpus, coracoid, sternum, tarsometatarsus, femur, tibiotarsus, scapula, pelvis, and furculum. Size and other characters of a specific nature variable within the genus are disregarded. The ulna, radius, and fibula are generally considered of lesser taxonomic value and were not studied.

Anatomical nomenclature follows Howard (1929). In a few instances it has been necessary to name other features. When an additional term is first used, it is defined or a reference is cited.

ACKNOWLEDGMENTS

I extend my deep appreciation to Professor Pierce Brodkorb for his valuable and untiring supervision throughout the course of the problem.

Sincere thanks are also due to the other biologists who critically read the manuscript, Oliver L. Austin, Jr., Jean Delacour, J. C. Dickinson, Jr., Hildegard Howard, Roland F. Hussey, and James N. Layne. To Ted T. Allen, who made the drawings, and Robert W. McFarlane and J. Hill Hamon, who did the photographic work, I am also grateful. Finally, I wish to acknowledge financial aid from a grant from the Sigma Xi-RESA Research Fund and also from Lester B. Woolfenden and Gwen S. Woolfenden.

MATERIALS AND METHODS

The skeletal collection of Pierce Brodkorb was supplemented by material borrowed from the American Museum of Natural History, United States National Museum, National Museum of Victoria, Australia, and Peabody Museum of Natural History; these specimens were obtained through the kindness of Dean Amadon, Herbert Friedmann, A. R. McEvey, and Philip S. Humphrey, respectively. Additional material was donated by Richard G. Naegeli, Director of Busch Gardens, Ethel L. Woolfenden, Joseph R. Jehl, Jr., Charles T. Collins, William O. Wirtz II, and Henry M. Stevenson, Jr. Norman L. Ford sent data from specimens in the University of Michigan Museum of Zoology.

Over 85 percent of the currently recognized genera were studied. Only 8 of the 62 genera recognized by Peters (1931) were unavailable, namely *Cyanochen*, *Asarcornis*, *Stictonetta*, *Pseudotadorna*, *Nesonetta*, *Salvadorina*, *Camptorhynchus*, and *Thalassornis*. By Delacour's classification (1954, 1956, 1959) only 5 of his 41 genera were lacking, namely: *Cyanochen*, *Stictonetta*, *Lophonetta*, *Camptorhynchus*, and *Thalassornis*.

The assembled collection of 432 specimens represents 105 of the 167 species of waterfowl recognized by Peters. Those species and subspecies examined and the number of specimens involved are:

<i>Cygnus cygnus</i> 2	<i>Anser anser</i> 1
<i>C. columbianus</i> 24	<i>A. albifrons albifrons</i> 1
<i>C. buccinator</i> 1	<i>A. fabilis</i> 1
<i>C. olor</i> 2	<i>Eulabeia indica</i> 1
<i>C. melancoriphus</i> 3	<i>Cygnopsis cygnoid</i> 2
<i>Chenopsis atrata</i> 4	<i>Philacte canagica</i> 1
<i>Anseranas semipalmata</i> 1 complete +	<i>Branta bernicla hrota</i> 6
1 body skeleton	<i>B. b. nigricans</i> 1
<i>Plectropterus gambensis</i> 2	<i>B. canadensis canadensis</i> 8
<i>Cereopsis n.hollandiae</i> 2	<i>B. c. hutchinsii</i> 2
<i>Chen caerulescens</i> 1	<i>B. ruficollis</i> 1
<i>C. hyperborea</i> 2	<i>Nesochen sandvicensis</i> 1
<i>C. rossii</i> 9	<i>Chloephaga melanoptera</i> 4

- C. leucoptera* 1
C. dispar 3
Chenonetta jubata 2
Dendrocygna viduata 1 complete + 1 body skeleton
D. bicolor bicolor 1
D. javanica 2
D. autumnalis autumnalis 1
D. a. discolor 1 body skeleton
D. arborea 3
Alôpochen aegyptiaca 3
Neothen jubata 1 complete + 1 body skeleton
Sarkidiornis melanota 1
Cairina moschata 4
Coscoroba coscoroba 1
Casarca cana 2
C. tadornoides 1
C. variegata 2
Tadorna tadorna 4
Anas platyrhynchos platyrhynchos 6
A. poecilorhyncha 1
A. luzonica 1
A. melleri 1
A. fulvigula fulvigula 7
A. f. maculosa 1
A. rubripes 6
A. undulata 1
A. cyanoptera cyanoptera 3
A. discors 10
A. querquedula 4
A. castanea 2
A. crecca crecca 1
A. c. carolinensis 10
A. formosa 1
A. falcata 1
A. leucophrys 1
A. brasiliensis 1
A. acuta tzitzihua 5
A. angustirostris 1 body skeleton
A. bahamensis rubirostris 2
Mareca penelope 14
M. americana 4
M. sibilatrix 1
Chaulelasmus streperus 9
Spatula clypeata 5
S. platalea 1
Malacrohynchus membranaceus 1 complete + 1 partial skeleton
Rhodonessa caryophyllacea 1 body skeleton
Aix sponsa 16
Dendronessa galericulata 5
Cheniscus coromandelianus coromandelianus 4
C. pulchellus 1
Nettapus auritus 1
Pteronetta hartlaubii 1
Heteronetta atricapilla 1
Netta rufina 2
Metopiana pepsoca 3
Aythya ("Nyroca") valisineria 3
A. ferina 1
A. americana 5
A. collaris 14
A. fuligula 6
A. nyroca 1
A. marila marila 21
A. m. nearctica 6
A. affinis 25
Tachyeres brachyptera (i.e., *pteneres*) 1
Bucephala clangula clangula 2
B. c. americana 5
B. albeola 7
Clangula hyemalis 5
Histrionicus histrionicus pacificus 1
Somateria mollissima v-nigra 1
S. m. dresseri 7
S. spectabilis 3
Arctonetta fisheri 1
Oidemia nigra nigra 3
O. n. americana 1
Melanitta fusca fusca 1
M. f. deglandi 5
M. perspicillata 1
Polysticta stelleri 1
Hymenolaimus malacorhynchus 1
Nomonyx dominicus 2
Oxyura jamaicensis jamaicensis 11
O. vittata 1
Biziura lobata 1
Mergellus albellus 1
Lophodytes cucullatus 7
Mergus merganser merganser 2
M. m. americanus 2
M. serrator 18
Merganetta armata armata 2

All the ratios presented are intramembral and reflect relative proportions within a given element. Obtained by dividing the width or depth of various portions of the element by its length, the ratios are expressed as percent of the length. Linear measurements are taken to the nearest tenth of a millimeter. The methods of taking the measurements are explained where first mentioned under each element.

DESCRIPTIVE OSTEOLOGY

Listed below are the genera of Anatidae according to Peters (1931), arranged in the subfamilies and tribes of Delacour (1954, 1956, 1959). Two generic changes (*Aythya* for *Nyroca*, cf. American Ornithologists' Union, 1945; *Lampronetta* for *Arctonetta*, cf. Parkes, 1955), and two additions (*Lophonetta* and *Amazonetta* from *Anas*, cf. Delacour and Mayr, 1945) are incorporated. Parentheses enclose the genera not recognized by Delacour, and these follow the genera with which they are synonymized. Asterisks mark the genera not available for this study. Where additional genera are mentioned in the text an authority is listed. I have altered slightly the vernacular names of certain of the tribes and the arrangement of the tribes in the subfamily Anatinae. The latter change allows for clearer presentation of the osteological data which follow this arrangement:

Subfamily Anseranatinae (Pied Goose) *Anseranas*.

Subfamily Anserinae (Whistling Ducks, Swans and Geese).

Tribe Dendrocygnini (Whistling Ducks) *Dendrocygna*.

Tribe Anserini (Swans and Geese) *Coscoroba*; *Cygnus*, (*Chenopsis*); *Anser*, (*Cygnopsis*), (*Chen*), (*Philacte*), (*Eulabeia*); *Branta*, (*Nesochen*).

Subfamily Anatinae (Ducks).

Tribe Tadornini (Sheldrakes) *Cereopsis*; *Chloephaga*; *Cyanochen**; *Neochen*; *Alopochen*; *Tadorna*, (*Casarca*), (*Pseudotadorna*)*; *Lophonetta**; *Tachyeres*.

Tribe Anatini (Dabbling Ducks) *Anas*, (*Nesonetta*)*, (*Chaulelasmus*), (*Mareca*), (*Spatula*), (*Salvadorina*)*; *Rhodonessa*; *Malacorrhynchus*; *Hymenolaimus*; *Merganetta*; *Stictonetta**.

Tribe Cairinini (Perching Ducks) *Amazonetta*; *Chenonetta*; *Aix*, (*Dendronessa*); *Nettapus*, (*Cheniscus*); *Sarkidiornis*; *Cairina*, (*Asarcornis*)*, (*Pteronetta*); *Plectropterus*.

Tribe Aythyini (Pochards) *Netta*, (*Metopiana*); *Aythya*.

Tribe Somateriini (Eiders) *Polysticta*; *Somateria*, (*Lampronetta*).

Tribe Mergini (Sea Ducks) *Melanitta*, (*Oidemia*); *Camptorhynchus**; *Histrionicus*; *Clangula*; *Bucephala*; *Mergus*, (*Mergellus*), (*Lophodytes*).

Tribe Oxyurini (Stiff-tailed Ducks) *Oxyura*, (*Nomonyx*); *Thalassornis**; *Biziura*; *Heteronetta*.

Humerus

Paleontologists and osteologists generally consider the humerus in birds to be extremely useful taxonomically. Of the 10 elements described herein, it shows the greatest number of characters of systematic value.

ANSERANATINAE

The pied goose (*Anseranas semipalmata*) differs from all other Anatidae by three humeral characteristics: (1) The prominent capital shaft ridge (Ashley, 1941) is situated more medially. Correspondingly, the attachment of the external head of the triceps is restricted; it barely extends proximally to the base of the internal tuberosity. In all other waterfowl it extends past the tuberosity toward the head of the humerus. (2) The pneumatic fossa is greatly reduced. The fossa does not extend to the humeral head, and the floor is elevated from the bicipital surface. (3) The facet for the anterior articular ligament is less elevated, particularly along the inner margin.

Because of its superficial resemblance to *Plectropterus*, Delacour and Mayr (1945) treated *Anseranas* as an aberrant member of the perching ducks. Further consideration led Delacour (1954) to place *Anseranas* in a separate subfamily on anatomical evidence presented by Boetticher (1943), who considers several skeletal features important. The structure of its humerus shows *Anseranas* to be a primitive anatid, and completely justifies its removal from the Anatinae.

ANSERINAE

Delacour and Mayr place the whistling ducks and swans and geese in the same subfamily. Similarity in the form of the humeral head in *Dendrocygna* and certain geese has been noted previously (Wetmore, 1924). The prominent capital shaft ridge directed towards the humeral head, coupled with an area of attachment for the external head of the triceps that extends virtually to the humeral head, characterizes the subfamily. In the Anserinae and Anseranatinae the area of pectoral attachment on the external tuberosity is elevated and somewhat circular; in the Anatinae it lies essentially flush with the proximal portion of the shaft and is elongate. In the Anserinae and the Anseranatinae the capital groove is not extensive, whereas in the Anatinae it extends laterally over the anconal surface and undercuts the head considerably.

TRIBE DENDROCYGNINI (WHISTLING DUCKS). The humerus of whistling ducks can be distinguished from those of the swans and geese, and also of *Anseranas*, by the width of the space between the external condyle and the facet for the anterior articular ligament in relation to the facet's

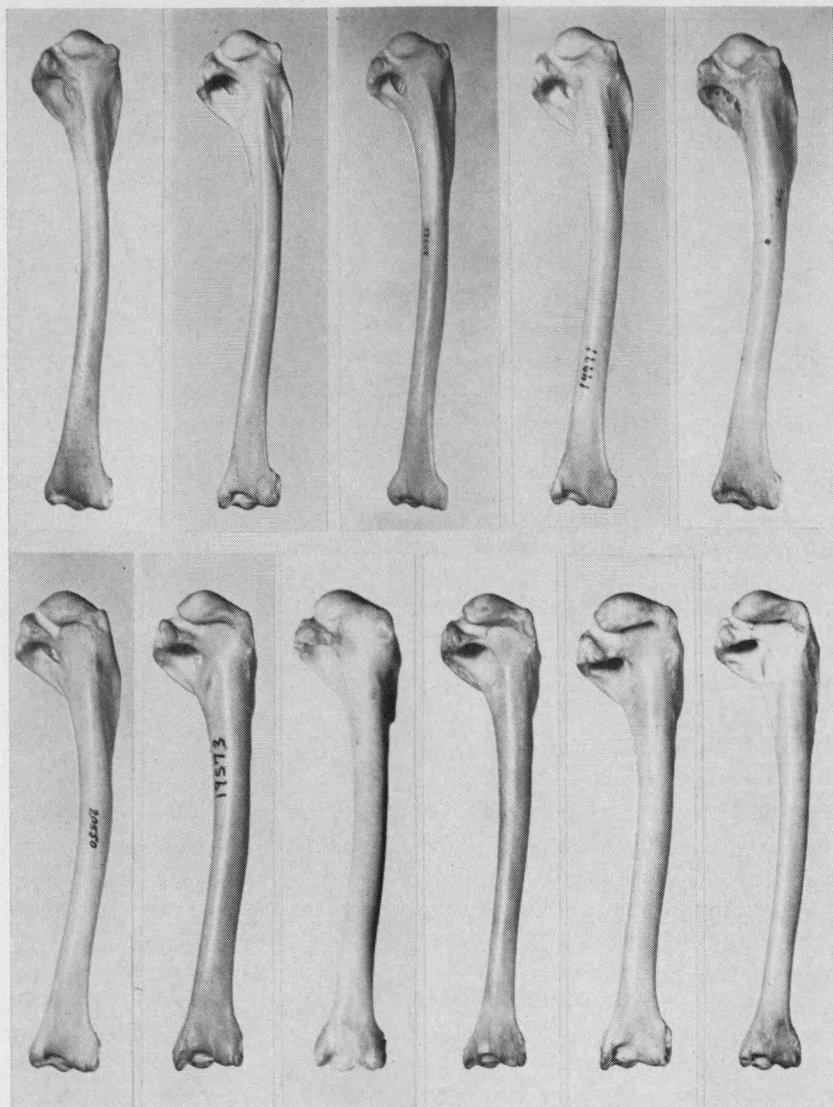


FIGURE 1. Right humerus, anconal view. Top row: *Anseranas semipalmata*, *Dendrocygna autumnalis*, *Cygnus melancoriphus*, *Branta bernicla*, *Cereopsis n. hollandiae*. Bottom row: *Chloëphaga melanoptera*, *Anas platyrhynchos*, *Merganetta armata*, *Aythya marila*, *Clangula hyemalis*, *Oxyura jamaicensis*.

width. In the whistling ducks the space is narrower than the facet, whereas in the swans and geese the reverse is true.

The small size of the humerus and its prominent capital shaft ridge have been considered distinctive of *Dendrocygna*. These two features alone, however, do not separate the genus from the smaller true geese.

TRIBE ANSERINI (SWANS AND GEESE). The prominent capital shaft ridge, the extension of the area of attachment for the external head of the triiceps almost to the humeral head, and narrowness of the facet for the attachment of the anterior articular ligament (narrower than the space between the facet and the external condyle) define this tribe.

Features of the humerus indicate the tribe is comprised of two distinct units, one containing the swans and *Coscoroba*, the other the geese. These two units are distinguishable by the relative width of the distal end of the humerus. In the swans the relatively narrow distal end constitutes 12.2 to 13.9 percent of the total length, and in *Coscoroba* 13.9 percent. In geese the range is from 14.1 to 15.6 percent.

Further characteristics distinguishing these two groups pertain to the configuration of the internal tuberosity and entepicondyle. (1) The entepicondyle is not extended distally as far in swans as in geese. (2) The entepicondylar prominence is more produced laterally in swans, in part the result of the more medially-situated entepicondyle. (3) The internal tuberosity is shorter and more rounded at the tip in swans.

In true swans a short, wide furrow leads transversely from near the proximal end of the capital groove onto the internal tuberosity; this furrow is indistinct in *Coscoroba*.

Neither Peters nor Delacour recognize the genus *Olor* as distinct from *Cygnus*. Other authorities (Wetmore, 1951) consider the separation of the swans into two or more genera warranted. Howard (1946) lists several distinguishing features of the humerus. (1) The intermuscular line on the capital shaft ridge is short, indefinite, and not turned inward below the head in *Cygnus*. In *Olor* the line runs along the ridge and turns inward about $\frac{1}{4}$ inch below the head. (2) The area of attachment of the supraspinatus is clear-cut in outline and situated below the pneumatic foramen; it is bordered by a raised line continuous with the median crest in *Cygnus* (poorly marked in *C. melancoriphus*). In *Olor* the attachment is less clearly marked and spreads past the median crest, and it lacks the raised bordering line at the edge. (3) The ligamental furrow is broad and shallow in *Cygnus olor*, but not in *C. melancoriphus*, whereas in *Olor* it is narrower and deeper. (4) The attachment of the anterior articular ligament is short, broad, and heavily bordered on its outer edge next to the attachment of the pronator

brevis in *Cygnus*. In *Olor* the attachment is long, narrow, and smoothly rounded at the edges. (5) The impression of the brachialis anticus in *Olor* is short, broad (particularly at the proximoexternal edge) clearly outlined, and usually deeply depressed. In *Cygnus* the impression is less clearly outlined. The series of swans available to me confirm these features, the last of which proves particularly useful. *Chenopsis* is similar to *Cygnus* in all these features.

The humeri of the true geese, *Branta*, *Nesochen*, *Anser*, *Cygnopsis*, *Eulabeia*, *Philacte*, and *Chen* are very similar. Two specimens of *Cygnopsis*, both aviary birds, are distinguishable from the other genera through the larger, more rounded and distally extended pneumatic fossa which excavates more of the shaft and the bone forming the median rim of the fossa.

Miller (1937) was unable to distinguish the humeri of *Philacte*, *Anser*, and *Chen* from one another, but found the impression of the external head of the triceps somewhat useful in separating *Nesochen* and *Branta* from these three genera. The impression has a distinct border in *Nesochen* and *Branta*, whereas in *Philacte*, *Anser*, and *Chen* it is most often indistinct. *Cygnopsis* and *Eulabeia* resemble the latter group in this respect. Miller remarks that *Branta* shows greater curvature distally; with my series this feature is not particularly useful. Brodkorb (MS) mentions that the deltoid crest in anconal view shows a distinct bend in the middle in *Branta*, whereas in *Philacte*, *Anser* and *Chen* it is more rounded. In a now larger series of geese we find this feature useful in most cases, but not infallible. *Nesochen* and *Eulabeia* resemble *Branta* in this character.

One feature of the humerus, although not infallible, aids in separating *Chen* from *Anser* and *Philacte*. In *Chen* the humerus, in anconal view, has the head rotated toward the internal side, and thus the lip of bone extending from the head over the capital groove is more prominent. As only two specimens of *Anser* are available it is difficult to assess the value of this character.

ANATINAE

Duck humeri lack the prominent capital shaft ridge directed toward the head that is typical of the Anserinae (*Cereopsis* is an exception, see Tadornini, paragraph 7). A few ducks have a humeral ridge directed toward the external tuberosity, but most lack it. In Anatinae the capital groove extends laterally over the anconal surface and deeply undercuts the head. The differences in size and position of the capital shaft ridge seem to result from a difference in the attachment of the external head of the triceps, which is stronger in the Anatinae. Miller (1937)

postulates that greater strength of the muscle is indicated by the more lateral position of the ridge in *Chloëphaga* (here placed in the Anatinae) as compared with certain true geese.

The structure of the humerus of the Anatinae indicates that the sheldrakes and stiff-tailed ducks are the two most distinct tribes; whereas the dabbling ducks, perching ducks, pochards, eiders, and sea ducks are more closely related to one another.

TRIBE TADORNINI (SHELDRAKES). The sheldrakes have the following humeral characteristics: (1) The capital shaft ridge is fairly prominent as in Anserinae, but is directed towards the external tuberosity. (2) The area of origin of the external head of the triceps is narrower than in other ducks; as a result the area between the attachment of the muscle and the external tuberosity is elevated. (3) The deltoid crest is larger and more flaring than in other ducks. Furthermore, when compared in lateral view, the entire crest tends to be more rounded, and when an abrupt bend is present it lies more posteriad. (4) The deltoid crest extends farther distally (most evident when the distal borders of deltoid and bicipital crests are compared). (5) The head is rotated so that the external tuberosity is usually higher or more anconal in relation to the head than in other ducks. This feature is best seen by viewing the proximal end of the bone with the palmar surface lying on a horizontal plane. The external tuberosity represents more than 89 percent of the height of the head in the sheldrakes, with *Tachyeres* and *Neochen* as exceptions. (The height of the humeral head is the distance between the plane on which the palmar surface lies and a parallel plane touching the anconal surface of the head). In *Neochen* the head is rotated as in other members of the tribe, but a robust head results in the external tuberosity constituting only 87.2 percent of the head height. *Tachyeres* measured 86.2 percent and showed no indication of the rotation present in the other genera assigned to this tribe.

Miller (1937) remarks on the striking modification of *Chloëphaga*, namely the much broader depression of the triceps, which is directly related to the more lateral position of the capital shaft ridge and the external flaring of the deltoid crest. A feature he does not mention that further distinguishes *Chloëphaga* from the true geese and relates it to the other sheldrakes is the greater elevation of the facet for the anterior articular ligament. Miller (1937) felt that *Chloëphaga* would prove to be more closely related to some anserine other than the North American geese. The relationship appears even more distant than he suspected, and more recent monographers place the genus in a subfamily apart from that containing the true geese.

Based on humeral characteristics, the seven available genera of sheldrakes fall into five distinct groups: *Tadorna* and *Casarca* form one, *Chloëphaga* and *Alopochen* another, and *Neochen*, *Cereopsis*, and *Tachyeres* individually the other three.

Tadorna and *Casarca* cannot be separated by features of the humerus. Together they differ from *Chloëphaga* and *Alopochen* as follows: (1) The external tuberosity is less prominent as a result of its distal portion lying almost flush with the shaft. (2) The external head of the triceps is narrower and the capital shaft ridge curves inward toward its external edge. In *Alopochen* and *Chloëphaga*, where the external head of the triceps is wider, the capital shaft ridge is straight and directed towards the median edge of the external tuberosity. (3) The distal end of the humerus possesses characters that tend to distinguish *Tadorna* and *Casarca* from *Alopochen* and *Chloëphaga*, but none is constant. The lack of an anconal protuberance on the entepicondyle is the most reliable of these.

Alopochen differs from *Chloëphaga* as follows: (1) The capital shaft ridge is more prominent in *Alopochen*; correspondingly the area between the ridge and the pneumatic fossa is a much more steeply inclined surface in *Chloëphaga*. (2) The internal tuberosity is less elevated in *Alopochen* (best observed by looking along the shaft towards the pneumatic fossa). (3) The facet for the anterior articular ligament is a rounded knob in *Alopochen*; in *Chloëphaga* the surface is flat.

The humerus of *Neochen* is quite different from those of other sheldrakes, and certain features indicate a relationship to the dabbling ducks. (1) The depression for the external head of the triceps extends laterally to the external tuberosity. This is characteristic of ducks other than sheldrakes; all available sheldrake specimens have a space between the area of muscle attachment and the tuberosity. (2) The lip extending from the head over the impression formed by the external head of the triceps is curved. In most dabbling ducks it is almost straight and perpendicular to the shaft. *Chloëphaga* and *Alopochen* show curvature in this area. (3) The deltoid crest is less flaring and more abruptly bent in the middle as in the dabbling ducks, but extends farther distally, and this is characteristic only of the sheldrakes. (4) The head is rotated as mentioned previously. This feature is unique to the sheldrakes among the ducks. From the characters of the humerus the position of *Neochen* remains uncertain, although its strongest affinities do seem to lie with the sheldrakes.

The humerus of *Cereopsis* is more like that of the swans and geese than any of the sheldrakes. It resembles them in the following ways: (1) The capital shaft ridge is extremely prominent and directed towards

the head. (2) The surface for pectoral attachment on the external tuberosity is elevated from the shaft and, therefore, less elongated than in sheldrakes. (3) The facet for the anterior articular ligament is less elevated than in sheldrakes. (4) The entepicondylar prominence is laterally produced as in swans. *Cereopsis* differs from the swans and geese as follows: (1) The deltoid crest is more evenly curved throughout its length. (2) The head blends in with the shaft instead of being delimited by a depression on the anconal surface. Thus the features of the humerus of *Cereopsis* point toward a strong affinity with the swans and geese.

The humeral feature that best distinguishes the sheldrakes from the other ducks, the rotation of the head, is lacking in the aberrant *Tachyeres*. In sheldrakes the external tuberosity comprises more than 89 percent of the height of the head. In *Tachyeres* the external tuberosity constitutes only 86.2 percent. *Tachyeres* has the following additional characteristics: (1) The excavation for the external head of the triceps is very deep. The depth results in a prominent capital shaft ridge directed towards the external tuberosity. The surface mediad to the ridge upon which the muscle attaches is steeply inclined, and the proximal extent of the muscle forms a deep cavity beneath the head. (2) The internal tuberosity is bent distad so that it considerably overhangs the pneumatic fossa. This striking feature is most evident when the bone is viewed from the internal side. (3) The deltoid crest has the proximal portion concave in anconal view; the distal portion flares widely, and meets the shaft at an abrupt angle. (4) The brachial depression is indistinct, but covers a wide area. (5) The facet for the attachment of the extensor metacarpi radialis (a depression on the external side of the distal end of the humerus immediately proximal to the ectepicondylar prominence) is more mediad than in other ducks.

TRIBE ANATINI (DABBING DUCKS). The humerus of the dabbling ducks can be described as follows: (1) The capital shaft ridge is obsolete, in contrast with the sheldrakes. (2) The pneumatic fossa is ovaloid and unrimmed with heavy bone, in contrast with the perchers (see perching ducks for additional details). (3) The pneumatic fossa is open and contains bony struts (Woolfenden, 1959) instead of being closed as in the pochards (except *Netta* and usually *Metopiana*), eiders, sea ducks (except *Mergus* and *Lophodytes*), and stiff-tailed ducks.

In dabblers the ectepicondyle is equal or subequal in anconal height to the entepicondyle when the humerus is placed on a horizontal flat surface, palmar side down. In the pochards, including *Metopiana* and *Netta*, the entepicondyle is distinctly higher.

Dabblers differ from mergansers in the form of the internal tuberosity. In the mergansers, and this is essentially true of all sea ducks, it is shorter and the length (measured perpendicular to the shaft from the ligamental furrow to the tip) is less than the width (measured from the capital groove to the area of attachment of the infraspinator).

No humeral features have been found that enable the separation of *Chaulelasmus*, *Mareca*, and *Spatula* from the genus *Anas*. Specimens of *Mareca* frequently display a robust shaft and a compressed distal condylar area, but these features do not seem consistent enough in large series to merit generic distinction.

On the basis of the humerus alone the species *Anas leucophrys* deserves segregation in a separate genus. The distal condylar area is grossly different from that of the 22 available species of typical dabblers (*Anas*, *Chaulelasmus*, *Mareca*, *Spatula*). The name *Callonetta*, proposed as a subgenus by Delacour (1936) for this little-known species can be used (Delacour spells it *Calonetta* in later publications [1945, 1956]). Its humerus differs from those found in the aforementioned genera as follows: (1) The shaft is more sigmoid than in *Anas*. (2) The distal end is rotated so that the ectepicondyle is much more elevated than the entepicondyle. (3) In anconal view the entepicondyle appears distally elongated. In typical dabblers the entepicondyle is generally as high as the ectepicondyle and is never distally elongated. (4) The deltoid crest is more rounded distally from the bend, instead of being angular as in typical dabblers. Features 1, 2, and 3, and also a robust shaft (8.0 percent of total length) strongly oppose Delacour's suggestion (1956) of the possible affinities of *Callonetta* to the pochards (wherein the shaft varies from 6.0 to 7.0 percent). In certain perching ducks (*Nettion*, *Cheniscus*, and *Amazonetta*), and sea ducks (*Histrionicus* and *Clangula*), however, the rotation of the condyles and thickness of the shaft resemble that of *Callonetta*. Of these two tribes only the perching ducks have the open fossa found in *Callonetta*.

The affinities of *Malacorhynchus* are inconclusive from its humeral characteristics, which are: (1) The pneumatic fossa is closed as in the diving tribes. (2) The rim of the pneumatic fossa is ovaloid and lacks heavy bone, thus contrasting with typical perching ducks. (3) The facet for the anterior articular ligament is elevated as in dabbling and perching ducks. (4) The rotation of the condyles, which results in the ectepicondyle being slightly higher than the entepicondyle, contrasts with the pochards. (5) The position of the pits for the muscles that attach to the internal surface of the entepicondyle resembles that found only in dabbling and perching ducks.

Hymenolaimus and *Merganetta* have several features in common that distinguish them from all other dabbling ducks. The fact that both genera habitually dive may account for their similarities: (1) The entepicondyle is less flaring and less extended distally. (2) The area for the attachment of the external head of the triceps is more deeply and broadly excavated. (3) The deltoid crest is reduced and more rounded and thus less angular at the bend. (4) The bicipital crest joins the shaft at a much wider angle than in other dabblers, particularly in *Merganetta*. (5) The internal tuberosity is less produced anconally, and possesses a distally directed flexure.

These two genera are best distinguished from each other by comparing the depth of the ligamental furrow. In *Merganetta* this is extremely shallow, more so than in any other anatid, whereas in *Hymenolaimus* it appears to be of normal depth. The brachial depression, although not deep in *Merganetta*, covers a larger area than is characteristic of the tribe. Lastly, *Merganetta* has the facet for the anterior articular ligament less elevated than *Hymenolaimus*.

Rhodonessa has humeral characteristics intermediate between those of the dabbling ducks and the closely related pochards. The following features are worth noting: (1) The shaft is intermediate in width (7.0 percent of total length) between dabbling ducks (average 7.44 percent) and pochards (average 6.33 percent). (2) The facet for the anterior articular ligament is less elevated than in dabblers, but more elevated than in pochards. (3) The entepicondyle has a more prominent process on the anconal surface than in any other dabbling duck. In this respect *Rhodonessa* resembles the pochards, for when the humerus is viewed from this distal end with the palmar surface lying flat, the entepicondyle is more elevated than the ectepicondyle. The reverse is true of the dabbling duck.

TRIBE CAIRININI (PERCHING DUCKS). The most trenchant feature of perching duck humeri is the rim of the open pneumatic fossa. This tribe shows a definite trend toward a reduction of the fossa to a restricted, circular opening rimmed with heavy bone. In the extremely similar humeri of dabbling ducks the fossa becomes ovaloid by an upward extension into the internal tuberosity. The shaft of the humerus in many perching ducks tends to be more robust so that the range for the available genera (all but *Asarcornis*) is from 6.7 to 8.7 percent of the total length, with an average of 7.81. The ratio in the aberrant *Plectropterus* is 5.7 and 6.3 percent.

Chenonetta, *Nettapus*, and *Cheniscus* are similar and can be distinguished from other perching ducks in several ways: (1) The proxi-

mal end of the humerus is inflected to give a more sigmoid appearance of the shaft. (2) The prominent deltoid crest is more flaring and the head is seemingly less prominent. (3) The pneumatic fossa is more restricted. When the humerus is viewed from the internal side down a line perpendicular to the shaft and passing through the internal tuberosity, the fossa can scarcely be seen. In other perching ducks one can normally see into the fossa when the humerus is so orientated. (4) The distal condyles are rotated so that in distal view the ectepicondyle is elevated above the entepicondyle. *Sarkidiornis* and *Amazonetta* also have this feature.

Nettapus and *Cheniscus*, whose humeri are indistinguishable on qualitative features, have the entepicondylar prominence distally produced and the facet for the anterior articular ligament more flush with the shaft than does *Chenonetta*. Otherwise the similarity between these three genera is striking.

Chenonetta, *Nettapus* and *Cheniscus* share with *Aix*, *Dendronessa*, *Cairina*, and *Pteronetta* a difference in the form of the head as compared with other perchers. In these genera the depression formed by the external head of the triceps is indistinct along the internal edge of the external tuberosity, and blends with the external portion of the head. In *Amazonetta* and *Sarkidiornis* the depression is distinct and extends to the external tuberosity, as in the dabbling ducks.

Aix, *Dendronessa*, *Cairina*, and *Pteronetta* have additional similarities in the form of the humerus. The shaft is curved in these genera in contrast to *Sarkidiornis*, but the head is not inflected, in opposition to *Chenonetta*, *Nettapus*, *Cheniscus*, and *Amazonetta*.

Cairina and *Pteronetta* differ from *Aix* and *Dendronessa* through greater overhang of the lip over the capital groove. Otherwise the humeri of these four genera are qualitatively extremely similar. Furthermore, all would be difficult to separate from the typical dabblers if it were not for differences of the fossa and the area of attachment of the external head of the triceps. The humeri of *Aix* and *Dendronessa* are indistinguishable.

A few minor differences in the proximal end exist between *Pteronetta* and *Cairina*. (1) In *Pteronetta* the depression for the external head of the triceps extends farther laterally, whereas *Cairina* shows an elevated area immediately medial to the external tuberosity. (2) In *Pteronetta* the deltoid crest extends farther out the shaft than in *Cairina*. This is best seen by comparing its distal extent with that of the bicipital crest.

The humerus of *Amazonetta* can be distinguished from those of typical dabblers quite easily. *Amazonetta* has the same pronounced

sigmoid curvature of the shaft, with the flaring deltoid crest and inflected head as do *Chenonetta* and *Nettapus*. In *Amazonetta* the distal condyles tend to be rotated so that in distal view the ectepicondyle is elevated above the entepicondyle, as in *Callonetta*.

Certain features of the humerus of *Amazonetta* show greater resemblance to the dabbling ducks than to the perching ducks. (1) The pneumatic fossa is ovaloid. (2) The depression for the external head of the triceps is excavated to the external tuberosity instead of blending with the head laterally. The humeral characteristics of *Amazonetta* leave its position in the Anatinae somewhat in doubt, but certainly it is generally distinct from *Anas*.

Sarkidiornis has the constricted, round pneumatic fossa that characterizes the tribe, but differs from typical perching ducks in having the depression for the external head of the triceps distinct and extending to the external tuberosity as in the dabbling ducks. *Sarkidiornis* differs from all other perching ducks in that the shaft of the humerus is very straight. The species also has the distal portion of the external tuberosity elevated so that the plane which passes through the area of pectoral attachment almost parallels the plane of the shaft. Furthermore, the bicipital crest is more rounded and meets the shaft at almost a right angle.

Several humeral features of *Plectropterus* suggest its closer affinity to the sheldrakes than the perching ducks. The head is rotated as in the sheldrakes, although the external tuberosity measures less than 89 percent of the total height of the head in the two specimens available. Another sheldrake feature is the rather prominent capital shaft ridge directed towards the external tuberosity. The shaft of the humerus, thick in the perching ducks, is thin in *Plectropterus* (5.7 to 6.3 percent of the total length), not only thinner than in the perchers, but even thinner than in the sheldrakes.

TRIBE AYTHYINI (POCHARDS). The important differences between the pochards and the closely similar eiders and sea ducks are associated with the distal end of the element. The pochards have the following characteristics: (1) The impression for the brachialis anticus is usually a well-formed depression with the distal medial rim sharply defined. Stettenheim (1958) uses this feature to distinguish *Aythya* from similar-sized *Clangula* and *Lophodytes*. (2) The distal condyles are rotated so that the entepicondyle is higher than the ectepicondyle when the palmar surface is lying flat. As a result the palmar floor of the olecranal fossa lies almost parallel to the flat surface in the pochards, whereas in the eiders and sea ducks a considerable angle is formed. The angle in

eiders and sea ducks results from pronounced rotation of the condyles in the opposite direction from that in pochards. (3) In pochards the intercondylar furrow is essentially confluent with the olecranal fossa without the transverse ridge that separates them in the eiders and sea ducks.

With the exception of the closed pneumatic fossa, the humerus of *Aythya* is similar to dabbling duck humeri. However two additional features seem useful: (1) The shaft is relatively thinner (6.0 to 6.9 percent of total length, average 6.33) than in typical dabblers (6.7 to 8.4 percent, average 7.44). (2) The facet for the anterior articular ligament is less elevated.

Humeri of species in the genus *Aythya* are extremely similar, varying significantly only in total length. The width of the shaft and the width through the distal end, given as percentages of the total length, range from 6.0 to 6.9 and from 13.9 to 15.3 respectively for 27 specimens of *Aythya marila*. The ranges for 45 specimens of seven other species of *Aythya* fall within those obtained for the one species.

Metopiana and *Netta*, which possess open fossae, show their affiliations to the genus *Aythya* in the shape and elevation of the anconal portion of the entepicondyle. As previously mentioned, in distal view the entepicondyle is higher than the ectepicondyle. In *Metopiana* (6.8 to 6.9) and *Netta* (6.7 to 7.0), the shaft is intermediate in width between *Aythya* (6.33 average) and the typical dabblers (7.44 average). Elevation of the facet for the anterior articular ligament is also intermediate between the low one found in *Aythya*, and the high one of typical dabblers.

The differences between the humeri of *Metopiana* and *Netta* are of generic magnitude. In *Metopiana* the bicipital crest arises more abruptly from the shaft, and the head is more robust than in *Netta*. In *Metopiana* the head comprises from 7.6 to 7.8 percent of the total length, whereas both specimens of *Netta* have a percentage of 6.6.

TRIBE SOMATERIINI (EIDERS). Delacour and Mayr (1945) placed the eiders and sea ducks in one tribe. In his later work Delacour (1956) states that the affinities of the eiders lie more with the dabbling ducks and places them in a separate tribe near this group. Humphrey (1958a) published evidence in support of the change.

Structurally the humeri of eiders and sea ducks are very similar. They differ from those of the dabbling ducks in a number of significant characters. (1) The pneumatic fossa is closed in the eiders, and with two exceptions, in the sea ducks. (2) The internal tuberosity is short and deep. (3) The facet for the anterior articular ligament is lower.

(4) The pit for the origin of the pronator longus (the distal pit nearest the anterior articular ligament) extends farther proximally. (5) The pit for the origin of the pronator brevis (the most proximal of the three pits situated on the internal side of the entepicondyle, also see Howard [1929, fig. 21]) is situated farther distally. The last three features reduce the area occupied by the entepicondylar prominence, a trait characteristic of sea ducks.

Delacour and Mayr (1945) place the four eider species in one genus, *Somateria*. Humphrey (1958a) agrees that *Lampronetta* should be synonymized, but maintains that *Polysticta* is generically distinct, a judgment followed by Delacour (1959). The form of the humerus supports this conclusion. No features of the humerus were found to separate *Lampronetta* from *Somateria*, but in *Polysticta* the distal end is much more strongly rotated. As a result the anconal portion of the external condyle is elevated above the entepicondyle. The only other ducks with a similar degree of rotation of the distal end are *Clangula* and *Histrionicus* of the sea ducks. Thus the distinctness of *Polysticta* brought forth by Humphrey also points to a close relationship of the genus to certain sea ducks. Because eiders and sea ducks are similar in the form of the humerus, the eiders are included in the discussion of the sea ducks which follows.

TRIBE MERGINI (SEA DUCKS). The humerus shows much variation in form in sea ducks. Two quite obvious features which seem to have phylogenetic significance are the degree of rotation of the distal condyles and the shape of the deltoid crest.

Histrionicus and *Clangula*, which Delacour and Mayr believe occupy a central position among sea ducks—"they lead to the scoters and eiders on one side and to the goldeneyes and mergansers on the other"—and *Polysticta* of the eiders are the only genera in the group that show extreme rotation of the distal condyles. In distal view even the anconal portion of the external condyle is elevated above the entepicondyle.

Polysticta differs from *Clangula*, and particularly from *Histrionicus*, in having greater excavation of the humeral head for the external head of the triceps. The degree of excavation in *Polysticta* is matched only in *Bucephala*.

Clangula differs from *Histrionicus*, and most other genera, in that the entepicondyle is produced distally.

The deltoid crest in scoters (*Melanitta* and *Oidemia*) and in mergansers (*Lophodytes*, *Mergellus*, and *Mergus*) is characteristic in each group. In scoters, in distinction to eiders and other sea ducks, the deltoid crest extends farther distad, and its distal portion is more flaring;

the crest maintains a sharp edge to the most proximad point of the external tuberosity, whereas in other genera, and particularly the eiders, the crest ends before reaching the external tuberosity. In lateral view the crest in scoters is gently curved and lacks the more proximal, sharp bend found in other genera.

Oidemia differs from *Melanitta* only in the relative width through the distal condyles. In *Oidemia* this measurement varies from 13.9 to 14.4 percent of the total length; in *Melanitta* the range is 14.5 to 15.8 percent.

In mergansers the deltoid crest is large and sharply angular. Typically, when the humerus of a merganser is placed palmar surface down on a flat surface, only the angle in the middle of the crest touches the surface. This contrasts sharply with the humerus of the closely related *Bucephala*, in which the deltoid crest is small and rounded at the bend.

Mergellus is the most distinct of the merganser genera in qualitative features of the humerus. The deltoid crest, although angular, is not as large as in *Mergus* and *Lophodytes*. The pneumatic fossa is closed, whereas it is always open (*Mergus*), or almost always open (*Lophodytes*) in the others. *Mergellus* differs from the similarly-sized *Lophodytes* in still other ways. The relative width of the shaft is 6.4 percent of the total length in *Mergellus*, from 7.1 to 7.7 percent in *Lophodytes*. The relative width of the distal condyles in *Mergellus* is 14.4 percent of the total length, in *Lophodytes* 15.6 to 17.3 percent.

Other than size the most obvious feature separating *Lophodytes* and *Mergus* is the shape of the humeral shaft. In *Lophodytes* the shaft is distinctly more sigmoid in anconal view than in *Mergus*, in which it is straighter than in most other ducks.

The humeri of the two species of *Mergus* examined are separable by the width of the shaft relative to its total length (Wetmore, 1948). Four specimens of *M. merganser* range from 7.0 to 7.3 percent. In 17 specimens of *M. serrator* the range is 5.6 to 6.9 percent.

Bucephala differs from *Somateria* and *Lampronetta* in having greater curvature of the shaft, and a more restricted, closed pneumatic fossa. In *Somateria*, although the fossa is closed, it is rather deep.

TRIBE OXYURINI (STIFF-TAILED DUCKS). The humerus of the stiff-tailed ducks shows the tribe to be very distinct among the Anatinae. Howard (1946) commented on the ease with which *Oxyura jamaicensis* can be distinguished from all other (i.e. North American) ducks, and this species has many features in common with the other genera assigned to the tribe. The tribe is unique in the following ways: (1) The pneumatic fossa is shallow, barely reaching the head, and has numerous fora-

mina piercing the walls. In other ducks the fossa may be closed or open, but if closed it is not as shallow, nor is it pierced by an abundance of foramina. (2) The scar for the latissimus dorsi posterioris lies essentially in line with the outer edge of the pectoral attachment. In all other Anatidae the scar lies far mediad to the outer edge of the pectoral attachment. (3) The entepicondyle is reduced, as is the pit for the flexor carpi ulnaris (the distal pit farthest from the anterior articular ligament).

Oxyura possesses the following identifying features: (1) The surface for the external head of the triceps is deep, and broadly excavated. (2) The distal portion of the external tuberosity is elevated so that the surface for pectoral attachment lies in a plane that almost parallels the plane of the shaft. (3) The shaft is thin (5.2 to 6.0 percent of the total length). (4) The facet for the anterior articular ligament is only slightly elevated from the shaft, and is distinctly turned towards the internal edge of the element. (5) The external condyle has a ridge extending toward the brachial depression.

Nomonyx appears less specialized than *Oxyura*. It may be distinguished from *Oxyura* as follows: (1) The internal tuberosity is elongate instead of very short. (2) The facet for the anterior articular ligament is more elevated and faces palmarad instead of internally. (3) The depression for the external head of the triceps is less excavated. (4) The distal portion of the external tuberosity is less elevated and therefore less distinct from the shaft. The one available complete humerus has the shaft thin (6.0 percent of total length), but thicker than in most of the 13 specimens of *Oxyura*.

The humerus of *Biziura* shows it to be definitely a stiff-tailed duck: (1) The pneumatic fossa is shallow and perforated. (2) The distal portion of the external tuberosity is elevated from the plane of the shaft. (3) The shaft is thin (5.5 percent of the total length). (4) The facet for the anterior articular ligament is turned towards the internal edge of the element.

Many features of generic magnitude occur on the humerus of *Biziura*: (1) The depression for the external head of the triceps is restricted to an area well below the head and mediad to the capital shaft ridge. Thus the head blends in with the shaft instead of being delimited by a distinct lip as in *Oxyura*. (2) The external tuberosity has the distal portion even more elevated than in *Oxyura*, and as a result the area of pectoral attachment is more rounded and less elongate than in other genera. The external tuberosity is further accentuated because the proximal portion of the deltoid crest bends inward under the tuberosity. (3) The scar for the latissimus dorsi posterioris lies largely distal

to the bicipital crest. (4) The ectepicondyle is greatly reduced, without the groove between it and the external condyle present in all other ducks. (5) The entepicondyle is very small, and on the internal edge only one large pit is evident. (6) The brachial depression is broad and rounded distally. In other stiff-tails the distal end of the depression is usually pointed. (7) The ridge extending from the palmar tip of the external condyle, described above for *Oxyura*, is indistinct.

Strong evidence supports placing the genus *Heteronetta* with *Oxyura*, *Nomonyx*, and *Biziura*. The humerus has the trenchant characteristics of the tribe, namely the shallow, abundantly perforated pneumatic fossa and the laterally situated scar for the latissimus dorsi posterioris. The degree of development of certain features of *Heteronetta* suggest it to be the least specialized member of the tribe: (1) The entepicondyle is reduced, but not to the extreme exhibited by *Oxyura* and *Biziura*. (2) The shaft is thin (6.3 percent of total length), but thicker than in any other stiff-tail. (3) The facet for the anterior articular ligament is low, but not as low as in other stiff-tailed ducks. (4) The plane of the surface for the pectoral attachment is inclined to the plane of the shaft, more as in Anatinae other than the stiff-tailed ducks. (5) The area of attachment of the external head of the triceps is reduced and blends in with the head, and it lacks the depression and overhanging lip of the other stiff-tails. (6) The scar for the latissimus dorsi posterioris is situated laterad, but not as far as in other stiff-tails. The humerus of *Heteronetta* indicates this genus to be a link between the quite distinct stiff-tails and some other tribe, possibly the dabbling ducks.

Carpometacarpus

The carpometacarpus is very useful taxonomically because of its many articulating surfaces and muscular attachments:

ANSERANATINAE

The carpometacarpus of *Anseranas* has several characteristics that distinguish it from those of all other waterfowl: (1) The carpal trochlea has the lower portion of the external rim unnotched. In all other anatids the outer rim is distinctly notched below. (2) A large pneumatic foramen is present in the internal ligamental fossa. A similarly situated foramen is present in other waterfowl, but none has it as large. (3) The process of metacarpal I is small. (4) Metacarpal II curves upward distally more than in other waterfowl. (5) The facet for digit II is wider and has a more extended lower, lateral process in correspondence with feature 4. (6) Metacarpal III is more curved

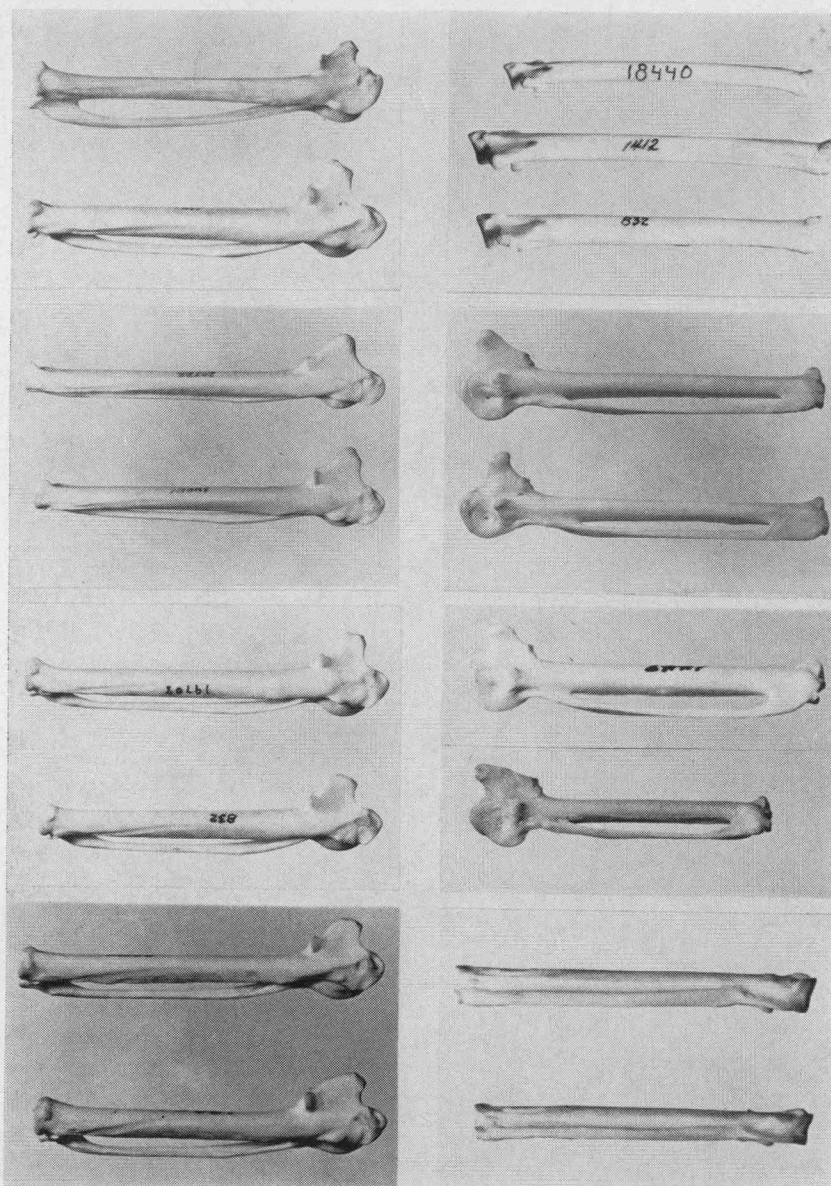


FIGURE 2. Left carpometacarpus. Row 1: external view *Anseranas semipalmata* and *Cairina moschata*; dorsal view *Dendrocygna autumnalis*, *Branta bernicla*, and *Anas rubripes*. Row 2: external view *Cygnus melancoriphus* and *Branta canadensis*; internal view *Branta canadensis* and *Cereopsis n.hollandiae*. Row 3: external view *Tadorna tadorna* and *Anas rubripes*; internal view *Anas crecca* and *Merganetta armata*. Row 4: external view *Aythya affinis* and *Clangula hyemalis*; ventral view *Bucephala albeola* and *Oxyura jamaicensis*.

throughout its length, particularly distally. (7) Metacarpal III is ungrooved on the lower proximal surface. (8) The facet for digit III protudes farther distally. In most other anatids this facet does not extend beyond that for digit II.

ANSERINAE

Two traits seem characteristic of the Anserinae: (1) The upper surface of metacarpal II, and particularly the distal half, is flat and the angle formed with the external surface is correspondingly rather sharp. In the Anatinae the upper surface is rounded, without sharp angles. (2) The extensor attachment is confined to the tip of the short, but high, process of metacarpal I. In the Anatinae the extensor attachment is longer and extends distally onto the distal edge of the process.

TRIBE DENDROCYGNINI (WHISTLING DUCKS). The thin, elongate carpometacarpus of whistling ducks has the following three features to distinguish it from all other anatids: (1) Metacarpal II in dorsal view is strikingly incurved. (2) The external rim of the carpal trochlea is only slightly notched. In all other waterfowl, except *Anseranas*, the external rim is notched distinctly. This character may be evidence of the primitive position of the whistling ducks. (3) A prominent neck is present between the carpal trochlea and metacarpal III.

TRIBE ANSERINI (SWANS AND GEESE). The carpometacarpi of swans and geese agree in: (1) Metacarpal III has a distally progressive rotation toward the medial side. (2) The pollical facet has a small lateral articulating surface.

Swans may be distinguished from geese by several carpometacarpal features: (1) In lateral view the external rim of the carpal trochlea slopes sharply downward from the process of metacarpal I. In geese the angle between the posterior edge of the process of metacarpal I and the upper, external rim of the carpal trochlea is smaller. (2) The pit on the internal side below and distal to the pisiform process is separated by a raised area from the intermetacarpal space. (3) The process of metacarpal I is lower and has a proximal edge that usually slopes toward the carpal trochlea. In geese the process is higher and the proximal edge is nearly perpendicular to the shaft. (4) Metacarpal II has only a slight depression on the external surface immediately proximal to the facet for digit II; in geese the depression is deeper. (5) The external rim of the facet for digit II is widely rounded; in geese this edge is almost straight.

Coscoroba resembles the true swans in all five of these characteristics. It can be separated from them by differences in the lower,

distal portion of the carpal trochlea. (1) The cuneiform fossa (Brod-korb, 1958b), which lies between the rims of the carpal trochlea distally, is delimited proximally by a ridge that extends medially from the external rim of the carpal trochlea. In true swans the ridge is lacking and the fossa extends proximally between the two rims.

Howard (1946) lists three criteria for separating the carpometacarpus of *Olor* and *Cygnus*; all seem weak in the series of specimens I have studied. Listed in a sequence of decreasing usefulness these are: (1) *Cygnus* has the external crest of the trochlea short, and the lobe at its distal edge appears aborted in comparison with *Olor*. (2) *Cygnus* has the process of metacarpal I straighter and more evenly swollen at the tip, whereas in *Olor* the process inclines more definitely toward the inner side. (3) *Cygnus* has the area below the pisiform process excavated into a distinct pitlike depression, the posterior rim of which is prominent. In *Olor* the area is roughened, sometimes depressed, but it tends to slope away toward the posterior face without an intervening rim.

Additional criteria were found more useful in my series: (4) The cuneiform fossa is deeper, and has a distinct proximal and medial rim in *Cygnus*. In *Olor* the rim is indistinct, the fossa gradually inclining to the surrounding areas. (5) Metacarpal I has a deeper depression on the external surface immediately proximal to the facet for digit II in *Cygnus*, and thereby more closely resembles geese. In *Olor* this area is noticeably shallower. *Chenopsis* is similar to *Cygnus* in all of the characteristics discussed above.

No criteria of the carpometacarpus are apparent to enable qualitative separation of the several genera of true geese (*Anser*, *Cygnopsis*, *Chen*, *Philacte*, *Eulabeia*, *Branta*, *Nesochen*). The shorter, broader facet for digit III attributed to *Chen* (Miller, 1937) is not constant.

Externally the true geese strongly resemble several genera assigned to the sheldrake tribe by Delacour and Mayr (1945). A number of carpometacarpal features support the allocation of these superficially gooselike species of the genera *Chloëphaga*, *Neochen*, and *Alopochen* to a position near the sheldrakes *Tadorna* and *Casarca*, as well as nearer the other duck genera. The following four characteristics of true geese serve to separate them from the sheldrakes: (1) The external rim of the carpal trochlea has the upper portion extending proximally before curving downward. (2) The external rim of the carpal trochlea is shallowly notched below. In sheldrakes the notch is noticeably deeper, as is generally true of all ducks. (3) The internal rim of the carpal trochlea is less rounded and usually grades more smoothly into the ridge of bone lying distal to it. In sheldrakes the more round-

ed rim falls off sharply. (4) The process of metacarpal I in lateral view is lower; the height through the process ranges from 19.7 to 24.4 percent of the total length of the carpometacarpus. In sheldrakes the process is typically higher (23.3 to 28.6 percent), a feature that Miller (1937) uses to separate *Chloëphaga* from the North American genera of true geese.

The process of metacarpal I frequently has a rugose cap in both geese and sheldrakes. Shufeldt (1892) attributes this condition to disease; Miller (1937) thinks its frequency of occurrence makes a pathological origin unlikely. Many waterfowl commonly fight with their wings, and the occurrence of the knob may well be correlated with this behavior. *Chloëphaga*, *Alopochen*, and *Neochen* almost always have the knob, and all are listed as very quarrelsome by Delacour and Mayr. Caps also occur on the carpometacarpi of *Cygnus*, *Chenopsis*, *Branta*, *Anser*, *Tachyeres* (large), *Hymenolaimus* (large), *Merganetta* (large), and *Sarkidiornis*.

Two genera, *Merganetta* and *Plectropterus*, have developed carpal spurs (Rand, 1954), and the latter is known to be aggressive in captivity. In addition to a metacarpal I process seemingly designed for a spur, one specimen of *Merganetta*, labelled a juvenile male (U.S.N.M. 346808) possesses a sharp claw 3 mm. in length on the tip of the pollex, a fact apparently unrecorded in the literature (Fisher, 1940).

ANATINAE

The Anatinae can be distinguished from the Anseranatinae and Anserinae by two carpometacarpal features: (1) The upper surface of metacarpal II is rounded, without sharp angles. (2) The extensor attachment on the tip of the process of metacarpal I is longer and extends distally onto the anterior edge of the process (a weak character for sheldrakes).

With the ducks the most critical region of the carpometacarpus is the external surface of the trochlea. The shape and location of the attachments for two ligaments and the ridges on the bone associated therewith are particularly significant. Howard (1929) labels an external ligamental attachment on her drawings. In waterfowl the ligament attached thereon extends to the cuneiform (ulnare). Another place of ligamental attachment from which a ligament extends to the scapholunar (radiale) lies distal to the one labelled in Howard. The external scapholunar ligament crosses over the external cuneiform ligament.

Delacour (1954, 1956, 1959) divides the Anatinae into seven tribes. Features of the carpometacarpus separate the subfamily into five groups: (1) sheldrakes, (2) dabbling and perching ducks, (3) pochards,

(4) eiders and sea ducks, and (5) stiff-tailed ducks. Although the carpometacarpi of dabbling and perching ducks (group 2), pochards (group 3), and eiders and sea ducks (group 4) are very similar, combinations of the characteristics listed at the beginning of each should make possible the proper determination of all specimens, assuming comparative material is available.

TRIBE TADORNIINI (SHELDRAKES). Sheldrakes have three features of the carpometacarpus that distinguish them from other ducks; all three features are common to the true geese, perhaps an indication of an intermediate position of the sheldrakes between the geese and ducks: (1) The external scapholunar ligamental attachment is broad, usually prominent, and situated higher and more distal than in other ducks. It always lies distal to the ridge that extends from the external cuneiform ligamental attachment to the proximal fornix (the point of fusion of metacarpal II and III proximally). (2) The lobe at the distal end of the external rim of the carpal trochlea is larger. (3) The process of metacarpal I is higher, shorter, and frequently has a rugose cap.

The carpometacarpus of *Cereopsis* resembles those of the Anserini of Delacour and Mayr (1945). Two unique features distinguish the species: (1) In the process of metacarpal I the proximal edge slopes forward, and the distal edge is more concave so that the tip is more pointed. (2) The distal metacarpal symphysis is approximately twice as long as that found in geese.

With *Cereopsis* removed because of its resemblance to the true geese, three major groups remain within the sheldrakes: *Chloëphaga*, *Alopochen*, and *Neochen* form one group; *Tadorna* and *Casarca* another; and *Tachyeres* the third.

No qualitative features separating *Casarca* from *Tadorna* are evident, but the two as a unit can be distinguished from *Chloëphaga*, *Alopochen*, and *Neochen* by a combination of characteristics: (1) The process of metacarpal I is lower, thinner in proximal view, nearly perpendicular to the shaft, and usually without a rugose cap. In the other three genera the process is higher, thicker, bent proximally, and frequently it possesses a rugose cap. (2) The cuneiform fossa is longer and extends proximally beyond the lobe that marks the distal extent of the external rim of the carpal trochlea. In the others the fossa ends rather abruptly at a point opposite the lobe. (3) The tuberosity of metacarpal II is more prominent in dorsal view, and does not rise so high up from the shaft in the three gooselike genera. (4) The facet for digit III falls decidedly short of the facet for digit II. In the other three genera the two facets are almost equal in distal extent.

Alopochen seems the most distinct of the three gooselike genera. The following features set it apart from the other two: (1) The external surface situated below the external cuneiform ligamental attachment is deeply grooved. (2) The anterior carpal fossa is shallow. In *Chloëphaga* and *Neochen* the anterior carpal fossa forms an obvious pit at the edge of the carpal trochlea. (3) The flexor attachment is more distal. In the other two genera the flexor attachment lies farther proximad. A ratio of the distance to the midpoint of the flexor attachment from the proximal end divided by the carpometacarpal length ranges from 27.5 to 30.3 percent with only 1 specimen of 8 having a greater percentage than 29.3. The same ratio ranges from 29.5 to 31.4 in 3 specimens of *Alopochen*.

Although the 3 genera of gooselike sheldrakes are very similar, *Neochen* seems slightly closer to *Chloëphaga*. The flexor attachment ratio is 28.6 percent for the one specimen, and the anterior carpal fossa is deep. The groove below the external cuneiform ligamental attachment, however, seems deeper than in most specimens of *Chloëphaga*.

Delacour (1954) includes *Tachyeres* in the sheldrakes, but it differs from that tribe in two diagnostic features of the carpometacarpus: (1) The external scapholunar ligamental attachment lies on the diagonal ridge that passes from the external cuneiform ligamental attachment to the proximal fornix. In sheldrakes the attachment lies distal to the ridge. (2) The lobe at the distal end of the external rim of the carpal trochlea is essentially lacking. All true sheldrakes have a prominent lobe. In *Tachyeres* the process of metacarpal I is long as in most ducks. The process appears high, as in sheldrakes, but this may be due to foreshortening of the element, correlated with a flightless condition. Although a rugose cap is present as is typical of sheldrakes, this condition is found sporadically throughout the Anatidae.

TRIBES ANATINI AND CAIRININI (DABBING AND PERCHING DUCKS). (1) The distal portion of the external rim of the carpal trochlea has a noticeable prominence, but it is usually smaller than that found in eiders and sea ducks. The lateral outline of the area is convex. (2) The cuneiform fossa is deeper than in pochards, but usually shallower than in eiders and sea ducks. (3) The external scapholunar ligamental attachment is prominent and larger than in pochards, and usually lies on a conspicuous ridge that extends from the external cuneiform ligamental attachment to the proximal fornix. (4) The flexor attachment extends distally beyond the proximal fornix. The extent of the proximal end of the flexor attachment is variable. (5) The process of metacarpal I is higher and straighter than in eiders and sea ducks.

TRIBE ANATINI (DABBING DUCKS). Features of the carpometacarpus do not support the recognition of *Chaulelasmus*, *Mareca*, and *Spatula* as distinct genera. Some differences do occur, but none was found that has a high constancy. Many characters that appear useful in a small series break down when additional specimens are compared. In comparing 16 specimens of *Mareca* with 7 of *Chaulelasmus*, 5 of *Spatula*, and over 40 of numerous species of *Anas*, *Mareca* proved the most distinct of the three, some specimens being assignable without comparative study. The straight, robust shaft and the recessed condition of the facet for digit III are the best criteria. However, not all the specimens could be identified, even with the aid of comparative material.

Wetmore (1944) and Brodkorb (1958a) mention that the carpometacarpus of *Anas* (*Nettion*) *carolinensis* can be separated from that of *Anas* (*Querquedula*) *discors* as follows: (1) *Nettion* has the anterior carpal fossa very shallow, whereas it is deeply excavated in *Querquedula*. (2) In *Nettion* the length of the distal metacarpal symphysis is 6.0 mm. or less, whereas in *Querquedula* it is approximately 7 mm. or more. The feature pertaining to the depth of the anterior carpal fossa readily separates 17 of 25 specimens (*Nettion* 9, *Querquedula discors* 10, *Q. cyanoptera* 3, *Q. querquedula* 3), but for 3 (*Nettion* 2, *Q. discors* 1) the character is reversed, and in 5 others it appears intermediate. Just how Wetmore measured the distal metacarpal symphysis is uncertain, but some of the available specimens of *Querquedula* apparently measure less than 7 mm., so even this character is not entirely constant.

Qualitative features of the carpometacarpus indicate that 4 of the available genera of dabbling ducks are distinct from *Anas*, namely *Callonetta*, *Malacorhynchus*, *Hymenolaimus*, and *Merganetta*.

Callonetta has three distinctive features: (1) The process of metacarpal I has its distal edge sloping sharply proximally, and has only a small attachment surface at the tip. (2) The base of metacarpal III is narrower in ventral view. (3) The external rim of the carpal trochlea is slightly longer and narrower.

Malacorhynchus also has three criteria that distinguish it from typical dabblers: (1) The process of metacarpal I appears decidedly shorter in lateral view and has only a small extensor surface. (2) The proximal end of metacarpal III is very narrow and does not extend laterally around the cuneiform fossa. (3) The shaft of metacarpal II is noticeably thinner in dorsal view.

Hymenolaimus is very different from other dabbling ducks: (1) The internal rim of the carpal trochlea is enlarged; it curves farther downward and is thicker. (2) The groove between the rims of the carpal trochlea and the cuneiform fossa is very deep. (3) The external scapho-

lunar ligamental attachment is larger and situated farther distally. In this respect *Hymenolaimus* resembles the sheldrakes. (4) The external portion of the proximal end of metacarpal III fuses with metacarpal II farther distad. (5) The tuberosity of metacarpal II is reduced. (6) The facet for digit III is enlarged with the lateral end bent downward and both ends extended distally. (7) A rugose knob is present on the process of metacarpal I. Although present in many distantly related waterfowl, a knob is most typical of the sheldrakes.

The very short carpometacarpus of *Merganetta* resembles that of *Hymenolaimus* in a number of features. As both are inhabitants of mountain streams, convergence of some features might be expected. The following characteristics distinguish *Merganetta*: (1) Both rims of the carpal trochlea are enlarged, and especially the internal one; they curve farther downward, and the internal rim is thickened. (2) The groove between the rims of the carpal trochlea and the cuneiform fossa is very deep. (3) The proximal end of metacarpal III is narrower and does not extend so far laterad. (4) The tuberosity of metacarpal II is greatly reduced. (5) The facet for digit II has the external edge more rounded. (6) The facet for digit III is distally produced. (7) The process of metacarpal I is larger, curves sharply proximad, and sometimes has a large knob.

TRIBE CAIRININI (PERCHING DUCKS). The perching ducks are only weakly differentiated from the dabblers. Two features of the carpometacarpus are somewhat useful in separating the tribes: (1) The external scapholunar ligamental attachment tends to be obscure. (2) The process of metacarpal I tends to be higher, shorter, and straighter.

Features of the carpometacarpus of *Plectropterus* indicate the genus is a sheldrake and not a perching duck: (1) The external scapholunar ligamental attachment is situated distal to the ridge that passes from the external cuneiform ligamental attachment to the proximal fornx. This feature is typical of the sheldrakes. (2) The lobe at the distal end of the external rim of the carpal trochlea is large. In ducks other than sheldrakes, the lobe is relatively small or even absent.

Although *Plectropterus* does not have the enlargement of metacarpal I typical of the sheldrakes, a process of the scapholunar (figured in Rand, 1954) serves its quarrelsome nature.

On the basis of carpometacarpal features, the two most distinct of the remaining genera are *Sarkidiornis* and *Pteronetta*. *Cairina*, *Chenonetta*, *Aix*, and *Dendronessa* are all very similar to one another.

Sarkidiornis can be characterized as follows: (1) Metacarpal I is located farther distad with the highest point of its process opposite the

pisiform process. In other perchers the peak is proximal to the pisiform, and the anterior carpal fossa is more extensive. (2) The external rim of the carpal trochlea is rounded proximally. In the others the rim tends to be acuminate, the point occurring immediately proximal to the external cuneiform ligamental attachment. (3) The groove on the external surface below the external cuneiform ligamental attachment is deeper.

Pteronetta is rather easily distinguished from other perching ducks, including *Cairina*: (1) The process of metacarpal I is higher. (2) The curve of the internal rim of the carpal trochlea is situated so that the lowest point underlies the pisiform process, whereas in the others the lowest point is more proximal.

The large, robust carpometacarpus of *Cairina* has one distinctive feature: The process of metacarpal I is slightly excavated by a depression that lies along the external edge of the base.

No qualitative features useful in distinguishing *Aix*, *Dendronessa* and *Chenonetta* were found.

Nettapus and *Cheniscus*, for which I find no mutually exclusive characteristics, differ from other perching ducks in the following way: (1) The prominence proximal to the external cuneiform ligamental attachment is higher and extends proximally to the posterior rim. In other perchers it is lower and it terminates distal to the proximal rim.

Features of the carpometacarpus of *Amazonetta* strongly support its recognition as a genus distinct from *Anas*. The process of metacarpal I is higher and straighter, a feature characteristic of the perching ducks. In addition, the external rim of the carpal trochlea appears longer and narrower than in *Anas*. Separating *Amazonetta* from other perchers, and the dabblers, is the facet for digit III that is reduced in size and recessed; thus it does not extend distally as far as the facet for digit II.

TRIBE AYTHINI (POCHARDS). The carpometacarpus of pochards is quite distinct with the following characteristics: (1) The distal portion of the external rim of the carpal trochlea is usually without a swelling, and generally so greatly reduced that the outline in lateral view is concave. (2) The cuneiform fossa is shallow. (3) The external scapholunar ligamental attachment is usually prominent, but small. The diagonal ridge from the external cuneiform ligamental attachment to the proximal fornix is usually obscure. (4) The flexor attachment always lies entirely proximal to the proximal fornix. (5) The process of metacarpal I is high and straight as in the dabblers.

Metopiana and *Netta* are near *Aythya*, especially as indicated by the position of the flexor attachment, but certain features of the carpometacarpus indicate an intermediate position between *Aythya* and the dabblers: (1) The bone is shorter and more robust than in *Aythya*. (2) The process of metacarpal I is straighter. In *Aythya* the process curves more proximad. (3) The distal portion of the external rim of the carpal trochlea is more prominent. The area is more reduced in *Aythya*. (4) The region on the external surface, situated proximal to the external cuneiform ligamental attachment, is larger. In *Aythya* this area is much reduced.

The carpometacarpi of *Metopiana* and *Netta* are very similar, but most individuals can be separated by the tuberosity of metacarpal II and the external rim of the facet for digit II which, in dorsal view, are produced farther laterally in *Metopiana* than in *Netta*.

It is unfortunate that no carpometacarpus of *Rhodonessa* is available because its humeral features indicate this genus belongs with the pochards and not with the dabblers.

TRIBES SOMATERIINI AND MERGINI (EIDERS AND SEA DUCKS). Eiders and sea ducks form a group easily distinguished from the pochards. The two as a unit seem more like the dabblers, and particularly the perchers, in carpometacarpal features. The following distinguishing characteristics were noted: (1) The distal portion of the external rim of the carpal trochlea has a prominent swelling that is usually larger than in dabblers and perchers. (2) The cuneiform fossa is deeper than in the other groups, and it frequently excavates under or around the internal rim of the carpal trochlea. (3) The external scapholunar ligamental attachment is obscure, and the diagonal ridge is frequently absent. (4) The flexor attachment is variable with the genera. (5) The process of metacarpal I is lower, wider, and curved proximally. This feature is not useful for separating *Bucephala*, *Lophodytes*, or *Mergellus*, but is extremely useful for the other genera.

Examination of the carpometacarpi of 70 specimens of eiders and sea ducks reveals two basic facts: (1) The eiders show greater similarity to the sea ducks, and particularly to the scoters and *Histrionicus*, than to the dabblers; (2) the most obvious division of the genera is into two units, one containing *Bucephala* and the mergansers, the other the eiders, scoters, *Histrionicus*, and *Clangula*. This same division is also evident from features of the humerus.

The important features for separating the two units are found in the process of metacarpal I, and in the position and shape of the pollical facet. In *Bucephala* and the mergansers the process tends to be higher,

and the extensor attachment on the tip is shorter. In the other group of genera the process is lower, longer in lateral view, and the extensor attachment extends down the sloping distal edge of the process. These features are most distinct in *Bucephala*, *Lophodytes*, and *Mergellus* at one extreme, and *Clangula* at the other. Some specimens of *Mergus* are very similar to certain scoters and eiders, but in *Bucephala* and the mergansers the pollical facet lies in line with or proximal to the internal rim of the carpal trochlea. In the other genera the pollical facet lies distal to the internal rim of the carpal trochlea. Furthermore, *Bucephala* and the mergansers have only a small lateral lobe on the pollical facet, best compared in proximal view. In the other genera the lobe is larger and has a prominent pit or groove between it and the shaft of metacarpal II. These characteristics permit 100 percent separation between *Bucephala* and the mergansers and the remaining sea ducks.

With some features the division within the *Bucephala* and merganser group appears to lie between *Bucephala* and the mergansers, but with others the break occurs between *Mergus* and the other three genera. This is the case with humeral features, which indicates that *Bucephala* and the mergansers have been previously placed in separate taxa only because of such plastic features as the shape of the bill.

A basic difference in the shape of the process of metacarpal I divides the sea ducks into two groups. One of these groups, *Bucephala* and the mergansers, shows significant differences in the relative height of the process. In 18 specimens of *Bucephala*, *Lophodytes*, and *Mergellus* the range for the height through the process of metacarpal I is 22.5 to 23.9 percent of the total length of the bone. In 19 specimens of *Mergus* (17 *M. serrator*, 2 *M. merganser*) the range is from 21.0 to 22.6 percent, except for one adult *M. serrator* which measures 17.9 percent. Only one individual of the latter group overlaps the minimum for the other genera. Of the 17 available specimens of *M. serrator*, 14 are from Florida and all are immature birds. It seems likely from comparison with adult birds that the ratio would be more significant if the sample were not biased in respect to age.

The small size of the lobe at the distal end of the carpal trochlea separates *Bucephala* from the mergansers. In *Lophodytes*, *Mergellus*, and *Mergus* the lobe is relatively large. An additional feature useful for separating *Bucephala* from *Mergus* is the structure of the pisiform process. In proximal view it curves sharply upward in *Bucephala*, forming a deep groove for the flexor digitorum profundus. In *Mergus* the pisiform process is directed medially, forming more of a shelf than a groove. Specimens of *Lophodytes* and *Mergellus* are intermediate for this feature.

With *Mergus* distinguished by the relative height of the process of metacarpal I, the best characters for separating *Bucephala* from *Lophodytes* and *Mergellus* are: (1) the feature pertaining to the external rim of the carpal trochlea mentioned above, and (2) the shape of the facet for digit II. In *Bucephala* the external portion of the facet for digit II is larger and extends farther down into the groove between the facets for digits II and III. In *Lophodytes* and *Mergellus* it is smaller and does not extend down as far. No valid feature for separating *Mergellus* from *Lophodytes* was found on the carpometacarpus.

Of the remaining members of the eider and sea duck group, *Clangula* seems the most distinct. It has the following characteristics: (1) The process of metacarpal I is very low, with the distal edge thick and curving sharply proximally. (2) The carpal trochlea is depressed; its external rim forms only a slight angle with the trend of the shaft; the internal rim has only a relatively small depression between it and the base of metacarpal III. (3) The pit distal to and below the pisiform process is very deep. (4) The tuberosity of metacarpal II is situated more medially, and as a result the external edge of the facet for digit II appears more rounded. (5) The shaft of metacarpal II is robust (7.8 to 8.8 percent of the total length). The range for the others is 6.5 to 7.9, except for *Histrionicus* which measures 8.0 percent.

Two characteristics of the eiders separate them from the scoters and *Histrionicus*: (1) The flexor attachment is nearly twice as long as in the others, and is situated farther distad. (2) The upper surface of the shaft of metacarpal II in medial view is arched.

The carpometacarpus of *Lampronetta* appears indistinguishable from that of *Somateria*, but *Polysticta* differs from both in: (1) The notch in the external rim of the carpal trochlea is smaller in ventral view. (2) The lobe immediately distal to the notch is smaller. (3) The cuneiform fossa is shallower.

The carpometacarpus of *Oidemia* is slimmer than that of *Melanitta* (width of metacarpal II relative to the total length 6.5 to 7.1 percent in *Oidemia*, 7.0 to 7.9 percent in *Melanitta*), but otherwise it appears indistinguishable from that genus. *Histrionicus* has a thick shaft of metacarpal II (8.0 percent of the total length), and a larger lobe at the distal end of the external rim of the carpal trochlea.

TRIBE OXYURINI (STIFF-TAILED DUCKS). The stiff-tailed ducks are the easiest of the Anatinae to define on the basis of the carpometacarpus: (1) The distal margin of the internal rim of the carpal trochlea appears nearly parallel to the shaft in ventral view. In the others the rim is deflected laterally. (2) Metacarpal III is narrower at the proximal end.

In members of the other four groups metacarpal III widens at the proximal end and thus reaches, or virtually reaches, the external side of the element. (3) The area on the external surface below the external ligamental attachments is deeply grooved. Although a groove is present in other ducks it is not nearly as deep. (4) The facet for digit II is narrow, crescent-shaped, and has the lower margin concave (*Heteronetta* is an exception). In the other ducks the facet is broader, and the lower margin is nearly straight.

Features of the carpometacarpus strongly support the close relationship of *Heteronetta*, *Nomonyx*, *Oxyura*, and *Biziura* pointed out by Delacour and Mayr (1945). *Heteronetta* is the least specialized member of the tribe. The features that separate it from the other stiff-tails are generally those found in ducks of other tribes: (1) The process of metacarpal I is higher, and in lateral view, noticeably narrower. (2) The distal margin of the internal rim of the carpal trochlea is deflected laterally in ventral view. In other stiff-tails the process is nearly parallel to the shaft; in other tribes it is even more deflected than in *Heteronetta*. (3) The facet for digit II is broadly rounded externally and has the lower margin straight. (4) The tuberosity of metacarpal II is smaller. (5) The prominence on the internal edge at the proximal end of metacarpal III is situated nearer to the proximal fornx. In other stiff-tails it lies more proximad.

Nomonyx resembles *Oxyura* less than it does *Biziura* in features of the carpometacarpus. It can be separated from these two genera by the following features, all of which seem to indicate a lesser degree of specialization: (1) The process of metacarpal I is noticeably narrower in lateral view. (2) The distal margin of the internal rim of the carpal trochlea in ventral view has a slight lateral deflection greater than that found in *Oxyura* and *Biziura* but less than in *Heteronetta*. (3) The tuberosity of metacarpal II is smaller. (4) The external rim of the carpal trochlea is not as deeply grooved as in other stiff-tails.

The following carpometacarpal features separate *Biziura* from *Oxyura*: (1) The external rim of the carpal trochlea is extremely deeply grooved, more so than in all other anatids, so that the bottom of the cuneiform fossa can be seen in lateral view. (2) The distal portion of the internal rim of the carpal trochlea is thickened. In *Oxyura* the rim is of uniform thickness throughout. (3) The tuberosity of metacarpal II curves more laterad.

Sternum

The sternum has received an exaggerated amount of attention from avian taxonomists. It is not as useful as the humerus, carpometacarpus,

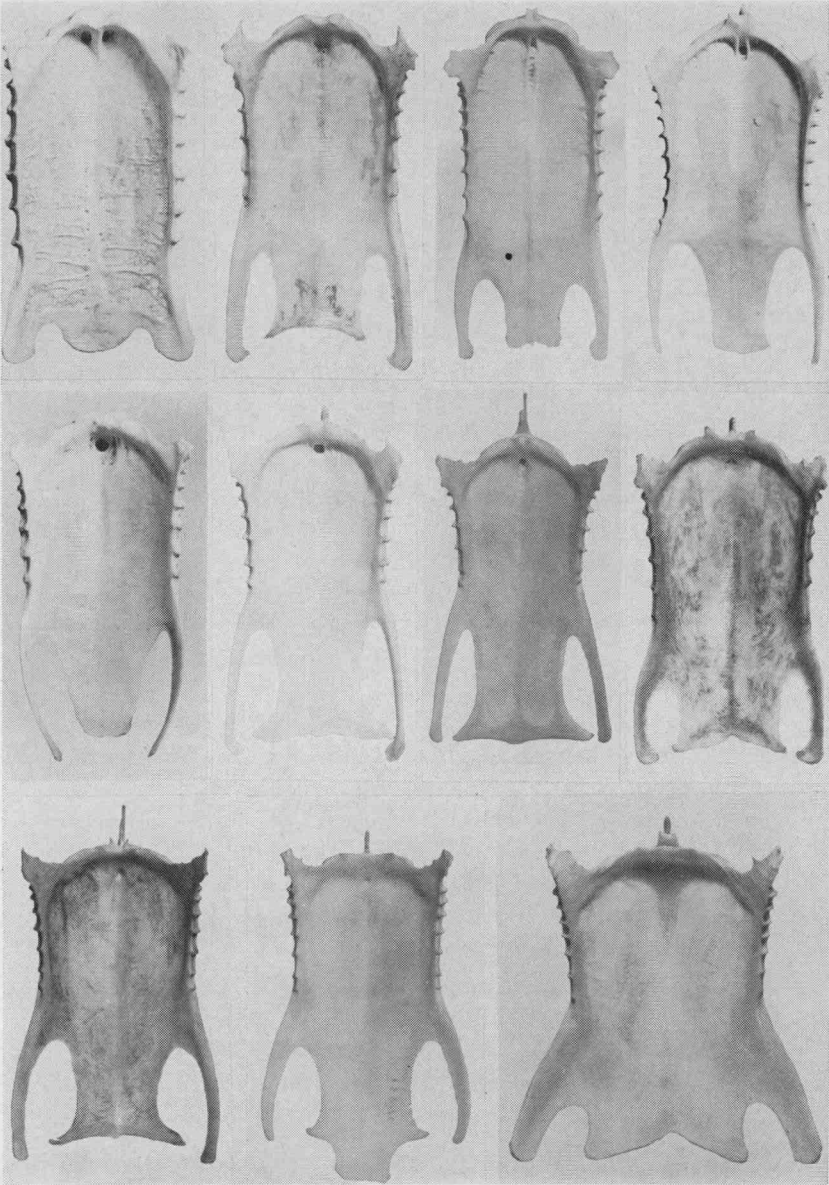


FIGURE 3. Sternum, dorsal view. Top row: *Anseranas semipalmata*, *Dendrocygna autumnalis*, *Cygnus olor*, *Branta canadensis*. Middle row: *Cereopsis n.hollandiae*, *Alopochen aegyptiaca*, *Anas fulvigula*, *Merganetta armata*. Bottom row: *Aythya valisineria*, *Clangula hyemalis*, *Oxyura jamaicensis*.

or coracoid; however, some features of phylogenetic significance do occur. Certain structural features of the sternum and pectoral girdle may be better understood by reference to the ligaments described in the Appendix.

The posterior margin of the sternum varies considerably. Most Anatidae have sternal notches, but in a few genera the notches are characteristically ossified posteriorly to form fenestrae. Other genera may, on occasions, have one or both notches so enclosed.

ANSERANATINAE

The primitive *Anseranas* is easily distinguished from all other anatids by the following criteria, the first five of which are unique among the waterfowl: (1) The costal margin is over 50 percent of the length of the basin (measured from the dorsal sulcal lip to the postpectoral line). (2) The sternal basin is deep. (3) The dorsal surface of the sternal plate is pierced by numerous foramina and crossed by transverse ridges. (4) The sternum is trilobed posteriorly, because of very shallow sternal notches and a rounded xiphisternum. (5) A stout median bar extends from the dorsal sulcal lip into the basin. (6) The dorsal and ventral manubrial spines are lacking.

ANSERINAE

The Anserinae can be distinguished from the Anseranatinae in the following ways: (1) The costal margin is shorter, always less than 50 percent of the basin length. (2) The sternal basin is shallower. (3) The pneumatic foramina are confined to the area posterior and ventral to the dorsal sulcal lip, and to the anterior median portion of the basin. (4) The xiphisternum flares laterally; its posterior margin is truncate or slightly concave, and the sternal notches are deeper. (5) There is no stout bar as described for *Anseranas*.

The Anserinae can be distinguished from the Anatinae as follows: The dorsal sulcal lip overhangs the sternal basin medially, and forms a large concavity at the anterior end of the sternal plate. The overhanging lip and the rather prominent costal margins cause the sternal basin to appear deeper. This character is least developed in *Nesochen*.

TRIBE DENDROCYGNINI (WHISTLING DUCKS). The sternum of whistling ducks shares the greatest number of similarities with that of the pied goose. The costal margin is almost as long as in *Anseranas*, the sternal basin is almost as deep, and the manubrial spines are lacking. *Dendrocygna* differs from *Anseranas* in the characteristics listed for the Anserinae; numbers 1, 4, and 5 are particularly useful. The whistling

ducks can be distinguished from the swans and geese by their lack of a ventral manubrial spine.

TRIBE ANSERINI (SWANS AND GEESE). Swans and geese can be separated into two very distinct units on the basis of the sternum. Swans and *Coscoroba* form one group, and geese form the other. The sterna of these two units are so different as to suggest they might be treated as separate tribes.

The sternum of swans is unique in the position of the intermuscular line delimiting the supracoracoideus from the pectoralis superficialis as noted by Stejneger (1882). In swans the line extends along the sternal plate only a short distance, usually less than 75 percent of the carinal length, before it curves down onto the carina. In all other waterfowl the intermuscular line extends along the plate essentially to the posterior end of the carina. The reduction in the relative length of the line is indicative of the reduction of the supracoracoideus muscle. Further indication of a reduction in this muscle is apparent when the sternum is viewed in ventral aspect. In swans the intermuscular line angles sharply toward the carina; in geese the line essentially parallels the carina throughout its length.

The supracoracoideus functions to raise the wing. In the Cathartidae, Fisher (1946) associates a reduced supracoracoideus with a decrease in speed of wing flapping. It seems likely that the same principle applies to the swans, which also have a slow wing beat.

The swans are further distinguished as follows: (1) The sternal notches are shallow. (2) The posterior lateral processes rarely extend beyond the xiphisternum. (3) The posterior lateral processes are nearly in a line with the costal margin. (4) The costal margin is elongate, forming from 40 to 50 percent of the basin length. (5) A ventral manubrial spine is present which serves to distinguish swans from *Anseranas* and *Dendrocygna*. (6) A pit is present in the dorsal portion of the anterior carinal margin in some specimens of all species. In *Olor columbianus*, *O. buccinator*, *O. cygnus*, and *O. bewickii* the pit becomes a huge cavern for a loop of the trachea. In *Cygnus olor*, *C. melanocoryphus*, and *Chenopsis* the pit is small or absent, and does not contain the trachea.

Only one feature of the sternum, additional to the cavern for the tracheal loop, supports the recognition of *Olor* as distinct from *Cygnus*, and this may be a result of widening of the carina in *Olor*. The posterior portion of the pectoralis superficialis lies close to the carina in *Cygnus*, but far laterad to the carina in *Olor*.

The sternum of *Coscoroba* indicates it is closely related to the swans. The intermuscular line, although more extensive than in the true swans, curves down onto the carina well anterior to its posterior termination. In ventral view the line gives additional indication of a reduction of the supracoracoideus by distinctly angling toward the carina throughout its length as shown in Stejneger (1882). Further evidence for considering *Coscoroba* near the swans comes from the fact that some specimens possess a pit in the dorsal portion of the carinal margin. *Coscoroba* can be distinguished from the true swans by the following criteria: (1) The intermuscular line extends beyond 75 percent of the carinal length (usually about 90 percent). (2) The posterior lateral processes extend well beyond the xiphisternum. Both features are figured in Stejneger (1882).

Of all the Anserinae, the true geese are closest to the Anatinae. Geese may be distinguished from *Anseranas* and other Anserinae by: (1) The costal margin is less extensive (usually less than 40 percent of the basin length). (2) The sternal notches are deeper (more than 33 percent of the basin length). (3) The posterior lateral processes flare from the costal margins. (4) The xiphisternum is normally widened posteriorly. (5) A dorsal manubrial spine is present. In other Anserinae and in *Anseranas* the notch is enlarged and eliminates the spine. These characters, except the last, are also present in the Anatinae.

The sterna of geese show little generic variation. Miller (1937) in his comparison of *Nesochen* with *Branta*, *Anser*, *Chen* and *Philacte* found several features to distinguish *Nesochen*, but no constant characters to separate the remaining four genera from one another.

Nesochen is characterized by the following features: (1) The sternum is narrower, the width (narrowest extent between the costal margins) varying from 27 to 40 percent of the basin length. In all other geese the minimum is over 41 percent. (2) The carina is visibly lower. As Miller states, the difference in carinal height is evident only posterior to the apex where no fixed points for measurements can be selected. (3) The ventral manubrial spine is a transverse ridge less thick than the buttonlike prominence of other genera. (4) The pneumatic foramen is very small, less than a millimeter wide. (5) In addition to these features, which have been verified in the present series, the one available *Nesochen* has a less prominent intermuscular line, especially posteriorly. Possibly all of the above features, and certainly 1, 2, and 5, can be attributed to curtailed flight.

One character that allows the separation of *Branta* from *Anser*, *Chen*, *Philacte*, and *Nesochen* is the shape of the ventral manubrial spine. In *Branta* the spine is compressed into a vertically spatulate

process, whereas in the other four it is of the normal peglike shape. Two specimens of *Cygnopsis* and one of *Eulabeia* are intermediate in this respect.

ANATINAE

In the ducks the sternal basin is distinctively flattened. The reduced posterior surface of the dorsal sulcal lip and the less prominent costal margins eliminate the large concavity at the anterior end of the sternal plate. Miller found this character the best means of distinguishing *Chloëphaga*, here considered in the Anatinae, from the true geese.

All the duck tribes cannot be separated by sternal characters alone, but a number of sternal features aid in distinguishing some tribes or parts of tribes. For those tribes that cannot be characterized by the sternum alone, the various genera are discussed under the tribal units of Delacour (1954, 1956, 1959). Similarities to genera in other tribes are mentioned.

TRIBE TADORINI (SHELDRAKES). Within the Anatinae the sheldrakes are most like the true geese in features of the sternum, particularly in the rather prominent dorsal sulcal lip and the numerous pneumatic foramina in the sternal basin. In addition to lacking a distinct concavity beneath the dorsal sulcal lip, the sheldrakes may be separated from the closely similar true geese as follows: (1) the costal facets number six or less, except in the aberrant *Cereopsis* and *Tachyeres* (in geese a minimum of seven is present). (2) The costal margin typically tapers posteriorly. The sternum of sheldrakes is narrowest immediately adjacent to the last costal process; whereas in geese the narrowest point, which is sometimes difficult to establish, always lies anterior to at least two costal processes. The difference is undoubtedly a manifestation of the above characteristics.

Miller uses the shape of the sterno-coracoidal process to aid in separating *Chloëphaga* from the true geese; in *Chloëphaga* it is longer and projects more anteriorly. Although the process is variable, the differences between *Chloëphaga* and true geese are generally those between Anatinae and Anserinae, and therefore it serves to separate the two subfamilies. Miller's other criterion for separating *Chloëphaga* from the true geese is the relative length of the posterior lateral processes, extending well beyond the xiphisternum. As a few goose specimens show the same feature, this character is not infallible.

The sheldrakes form a fairly distinct tribe. The sternal basin is deeper than in other ducks, although there is overlap with some dabblers and perchers. The shape of the pneumatic fossa is also of limited

use. The fossa is typically a large opening bordered laterally by stout bars, which frequently are fused with the sternal plate. The resulting fossa does not have the round or elliptical shape of other ducks, but instead it is a constricted opening that is either oval or somewhat rectangular in outline. The sterno-coracoidal process is shorter and has a more prominent posterior extension in the sheldrakes than in other ducks.

Tachyeres differs strongly from other sheldrakes in its broad, flat sternum. (1) The width is 55.6 percent of the basin length. (2) The ventral manubrial spine barely protudes beyond the ventral sulcal lip. (3) The carina is greatly reduced, with the posterior two-thirds of its margin virtually a straight line. (4) The posterior lateral process curves mediad more than in other sheldrakes. (5) The pneumatic fossa is elliptical and small. (6) The sterno-coracoidal process is longer and lacks a prominent posterior extension. The very shallow basin, ducklike sterno-coracoidal process, possibly the elliptical fossa, and the seven costal processes suggest that *Tachyeres* may be incorrectly located in the sheldrake tribe.

Characteristics of the sternum of *Cereopsis* disclose little more than the fact that it is aberrant. The element has qualities of both the sheldrakes and the true geese. The following features were noted: (1) The sternal basin is deeper than in sheldrakes, but lacks the concavity beneath the dorsal sulcal lip found in geese. (2) The dorsal manubrial area is notched as in many sheldrakes, whereas no geese have a distinct notch. (3) The ventral manubrial spine is lacking. All geese have such a spine, as do most sheldrakes. (4) The xiphisternum is not flared posteriorly as is true of all sheldrakes and most geese. (5) The costal processes number 6 or 7; a minimum of 7 was counted for geese, a maximum of 6 for sheldrakes, *Tachyeres* excluded. (6) The carinal margin is more curved throughout its length than in members of either of the two tribes.

Among the more typical sheldrakes, *Chloëphaga* has the widest sternum (46.9 to 50.8 percent of basin length), *Tadorna* and *Casarca* the narrowest (40.1 to 45.1 percent), whereas *Alopochen* (44.9 to 49.8) and *Neochen* (45.3 to 45.8) are intermediate. *Chloëphaga* usually has abundant pneumatic foramina; *Tadorna* and *Casarca* have only the large, centrally located one; *Alopochen* and *Neochen* are intermediate, but nearer *Chloëphaga*. In *Chloëphaga*, *Alopochen* and *Neochen* the posterior lateral processes extend well beyond the xiphisternum. In *Tadorna* and *Casarca*, where they are shorter, they normally extend less than 5 mm. beyond.

Chloëphaga has a narrower xiphisternum (its least width divided by the least width between costal margins, 31.3 to 44.8 percent) than *Alopochen* (66.5 to 66.9), and *Neochen* (50.5 to 54.6), but in *Tadorna* and *Casarca* the structure varies greatly in width with the different species. *Chloëphaga* has a higher carina than *Alopochen*, and it extends farther back on the sternal plate. *Neochen*, *Tadorna*, and *Casarca* are more like *Chloëphaga* in this respect.

TRIBE ANATINI (DABBING DUCKS). The sternum of dabbling ducks shows the following characteristics: (1) The sternal basin is shallower than in the sheldrakes. (2) The single pneumatic foramen is elliptical or round. (3) The ventral manubrial spine is usually present and typically long, thin, and peglike. (4) The sternum is narrow (*Anas*, *Chaulelasmus*, *Mareca*, *Spatula*, 37.5 to 48.9 percent of total length; *Callonetta*, 43.3; *Malacorhynchus*, 44.4; *Hymenolaimus*, 44.5), narrower than in most members of the four diving-duck tribes. *Rhodonessa* and *Merganetta* are exceptions. (5) The posterior lateral processes are straighter than in divers and only occasionally fused with the xiphisternum.

Within the tribe the sterna of all genera except *Rhodonessa* and especially *Merganetta* are very similar. *Callonetta* has two weak features that support generic status: (1) The costal processes number six, whereas the vast majority of specimens of typical dabblers have seven, although the range is from six to eight. (2) The ventral manubrial spine is thinner, with a weak dorsal area for the ligamental attachment.

Malacorhynchus has the ventral manubrial spine large and strong as in typical dabblers but differs in having six costal processes. *Hymenolaimus* is also very similar to the typical dabblers, surprising when one considers its habits. It has the following differences: (1) The costal processes number six. (2) The ventral manubrial spine is reduced to a weak projection. (3) The dorsal manubrial area has a prominent notch. (4) The carina is slightly reduced with its ventral edge only slightly curved.

Rhodonessa can be distinguished at once from the typical dabblers by several good sternal features: (1) The sternum is wider (50.8 percent of basin length). (2) The dorsal manubrial area is notched. (3) The ventral manubrial spine is lacking. The one available specimen (USNM 344802) lacks the spine as apparently did the one used by Verheyen (1955). Though occurring also in certain perching ducks, this feature is generally limited to the species with diving habits, but *Rhodonessa* does not habitually dive (Delacour, 1956).

In *Merganetta* the sternum has the following features: (1) It is wide, 52.7 to 52.9 percent of the basin length. (2) The ventral manubrial spine is lacking. (3) The carina is greatly reduced, the margin being straighter than in typical dabblers. (4) The posterior lateral processes curve more mediad. (5) The sternal notches are reduced to $\frac{1}{4}$ of the basin length (they measure approximately $\frac{1}{3}$ in other dabbling ducks). (6) The dorsal manubrial area is deeply notched, and has two prominent lateral projections. The sternum of *Merganetta* diverges from those of typical dabblers to the extent that tribal status for the species may be justified.

The sternum of *Salvadorina* was studied by Mayr (1931), who found the element somewhat narrower than in *Anas platyrhynchos*, especially caudally, and with the intermuscular line less clearly marked. In sternal characteristics he concluded that *Salvadorina* is closer to *Anas platyrhynchos* than to *Aythya*.

TRIBE CAIRININI (PERCHING DUCKS). As the sternum of perching ducks does not differ significantly from that of the dabbling ducks, it is impossible to characterize the tribe as a whole on the basis of this element. Within the tribe, *Cairina*, *Aix*, and *Dendronessa* have the ventral manubrial spine greatly reduced, whereas in *Amazonetta*, *Chenonetta*, *Nettapus*, and *Cheniscus* it is prominent. *Pteronetta* and *Sarkidiornis* are intermediate in this respect.

Cairina has numerous pneumatic foramina beneath the dorsal sulcal lip and costal margins, and along the midline of the basin. In other perching ducks, with the exception of the aberrant *Plectropterus*, only the large, anteriorly and centrally located foramen is present. *Plectropterus* resembles the sheldrakes more closely than the perching ducks in the structure of the sternum: (1) The sternal basin is deeper than in all ducks except certain sheldrakes. (2) The pneumatic foramen is bordered laterally with struts as described for the sheldrakes. (3) The dorsal manubrial area is deeply notched and has the lateral processes found in certain sheldrakes.

TRIBE AYTHYINI (POCHARDS). Sterna of the three genera of pochards are easily separable; *Metopiana* is the least specialized, *Aythya* the most specialized, and *Netta* is intermediate.

Metopiana has the following sternal characters: (1) The ventral manubrial spine is present as a prominent, single, peglike process. When compared with dabbling ducks the spine of *Metopiana* is shorter and thinner. (2) The dorsal manubrial area is notched as in all pochards. This character separates the sternum of *Metopiana* from the similar nondiving ducks. (3) The width is less (43.2 to 47.4 percent

of the basin length) than in all other pochards, and also it is less than in *Rhodonessa* and *Merganetta* of the dabblers. (4) The pneumatic foramen is large (4 mm. wide), as in typical dabblers; it is much smaller in *Aythya*. (5) The posterior lateral processes are longer, thinner, and straighter than in other pochards.

Netta, which is osteologically intermediate between *Metopiana* and *Aythya*, has the following features: (1) The ventral manubrial spine is lacking. (2) The width is intermediate (51.5 to 52.1 percent) between *Metopiana* and *Aythya*. Only two of 71 specimens of *Aythya* had a relative width less than 53.0 percent. (3) The pneumatic foramen is large (3 mm. wide) as in *Metopiana*.

Aythya possesses the following sternal characteristics: (1) The ventral manubrial spine is usually a short, two-pronged structure with the prongs flaring laterally. The length of the prongs varies as does the depth of the notch between them. This feature is the best means of separating the sternum of *Aythya* from those of all other ducks. (2) The relative width is greater (51.3 to 66.7 percent) than in other pochards. (3) The pneumatic foramen is reduced (less than 3 mm. wide) but almost always present. (4) The posterior lateral processes are shorter and wider, and curve farther mediad than in *Metopiana*.

TRIBE SOMATERIINI (EIDERS). The sternum of eiders is typical of diving ducks. The element is wide (53.0 to 58.6 percent of the basin length), the dorsal manubrial area is widely notched, and the posterior lateral processes are wide and curve toward the midline. The sternum is most like that of the scoters, from which it can be separated by: (1) The posterior lateral processes are wider, and more in line with the long axis of the element. (2) The notches are usually shallower. (3) There is less curvature throughout the entire element. In *Polysticta* a small ventral manubrial spine is present as noted by Shufeldt (1909), possibly indicative of a relationship with *Clangula*. In *Somateria* and *Lampronetta* the spine is a short, bilobed protuberance.

TRIBE MERGINI (SEA DUCKS). As with other elements, the sternum of sea ducks exhibits great structural variation. Several sternal structures occur nowhere in the Anatidae except in certain members of this tribe: The genera *Bucephala*, *Lophodytes*, *Mergellus*, and *Mergus* are the only waterfowl that regularly have sternal fenestrae instead of notches. These genera and *Clangula* are the only ducks with a pronounced abdominal plate extending beyond the postpectoral line.

Though *Bucephala* and the mergansers agree in the presence of sternal fenestrae instead of notches, they can be separated by the dis-

tance the carina extends anteriorly beyond the dorsal sulcal lip. In order to obtain a measurement, a straight edge was laid along the midline, from the posterior margin over the dorsal sulcal lip, and a perpendicular was extended from this line to the carinal apex. The distance along the straight edge from the perpendicular to the dorsal sulcal lip is considered the amount of carinal overlap. The results are given as a percentage of the basin length. In *Mergus* the range is 25.6 to 35.6 (average, 31.59); in *Bucephala* the range is 11.4 to 22.0 (average, 16.13). *Mergellus* (18.5) and *Lophodytes* (18.5 to 19.9, average 19.39) are intermediate, but closer to *Bucephala*. Most taxonomists confronted with the sterna of *Mergellus* or *Lophodytes* would probably place them with *Bucephala* and not *Mergus*.

The pneumatic fossa is of limited use in distinguishing the mergansers from *Bucephala*. In *Mergus* the foramen is large, approximately 5 mm. wide. Some specimens lack openings for the foramen into the carina as mentioned by Shufeldt (1909), but usually these are present. In *Bucephala* the foramen is smaller, under 4 mm. Sometimes it is only a slight depression and frequently lacks openings into the carina. *Lophodytes* has a wide pit, usually without openings into the carina, and the one specimen of *Mergellus* has a prominent foramen.

The relative width of the sternum in *Bucephala* (50.5 to 56.1 percent), *Mergellus* (52.3), *Lophodytes* (49.5 to 55.2), and *Mergus* (47.7 to 54.2) is of little use for identification. The basin length used to figure the above percentages does not include the variable abdominal plate. The postpectoral line is used as the point from which the measurement is taken.

The sternum of *Clangula* is easily distinguished from that of all other waterfowl by the combination of a large abdominal plate and sternal notches. The plate is relatively larger than in *Bucephala* and the mergansers. The ventral manubrial spine varies from a short peg-like process to a small bifid protuberance. The relative width of the sternum varies from 50.3 to 55.0 percent.

Histrionicus has a relatively wide sternum (59.3 percent) and a bifid ventral manubrial spine.

A greater curvature throughout the entire element characterizes the sternum of the scoters (*Melanitta* and *Oidemia*). There is no fixed point from which to measure the curvature, but it can be seen by comparing the ventral edge of the carina or the juncture of the carina with the sternal plate. The sternal basin appears significantly deep in the scoters, because of the curvature of the element and

the more abruptly rising dorsal sulcal lip. The posterior lateral processes are thinner, and more flared laterally than in the eiders. Furthermore, the notches are usually deeper. The sternal width (48.8 to 55.9 percent of basin length) and the diameter of the pneumatic fossa (less than 0.5 mm. to over 4 mm.) are poor taxonomic criteria. Scoters possess either a very short, bifid ventral manubrial spine or none at all. The dorsal sulcal area is broadly notched.

The sternum of the extinct *Camptorhynchus* is illustrated in ventral and lateral views in Rowley (1877). The specimen from which the drawing was made, including the coracoids and furculum, is still extant and is the only one known (Humphrey and Butsch, 1958). The sternum resembles that of the eiders in that the posterior lateral processes are wide, and in line with the long axis of the element, and it lacks the basin curvature possessed by scoters. However, the sternum appears less specialized than in the eiders, for the posterior lateral processes approach the xiphisternum, as in *Histrionicus*.

TRIBE OXYURINI (STIFF-TAILED DUCKS). The sternum in the stiff-tailed ducks has the following features: (1) The pneumatic foramen is lacking or minute. (2) The ventral manubrial spine is present, and points more dorsad than in other ducks (except in *Biziura*, which lacks the spine). (3) The basin is very shallow.

Oxyura, one of the most specialized of the stiff-tails, has these sternal characters: (1) The width varies from 59.5 to 68.4 percent of the basin length. (2) The ventral manubrial spine is wide and bifurcate distally. (3) The sternum has shallow notches in *O. jamaicensis* (12 specimens), fenestrae in *O. vittata* (1 specimen). (4) The posterior lateral processes are short, wide, and flaring. (5) The xiphisternum is wide. (6) The costal processes number 7, or rarely 8.

The sternum of *Nomonyx* is much less specialized. (1) It is relatively much narrower (48.0 to 54.1 percent) than in *Oxyura*. (2) The ventral manubrial spine is long, thin, and peglike. (3) The notches are deeper than in *Oxyura*. (4) The posterior lateral processes are thinner and curve farther mediad. (5) The xiphisternum is narrower than in *Oxyura*. (6) The costal processes number six. (7) The carina is reduced, as is typical of the tribe.

The sternum of *Heteronetta* has the large, dorsally directed ventral manubrial spine that characterizes the tribe, but otherwise is much less specialized than those of other members: (1) It is relatively narrower (43.9 percent) than in *Oxyura* and *Nomonyx*. (2) The ventral manubrial spine is wide basally but becomes thin distally.

(3) The notches are deeper than in *Oxyura* and *Nomonyx*. (4) The posterior lateral processes are thin and straight. (5) The xiphisternum is narrower than in *Oxyura* and *Nomonyx*. (6) The costal processes number six, as in *Nomonyx*.

The aberrant sternum of *Biziura* has the following features: (1) The dorsal and ventral manubrial areas are widely and deeply notched. (2) The carina is greatly reduced, the posterior $4/5$ of the margin being virtually a straight line. (3) The carinal apex does not extend beyond the sulcal lips. (4) The posterior lateral processes flare and then curve mediad. (5) The sternal notches are shallow. (6) Two 5-mm. foramina are present on either side of and adjacent to the carina, approximately $1/3$ the basin length from the posterior end (only 1 specimen is available and this may not be a normal feature). (7) The width is apparently great, but only 41.4 percent of the basin length, because of reduction in the area posterior to the costal margin. (8) The costal processes number seven.

Coracoid

The coracoid is an important taxonomic element. The angles between certain parts of the bone, as well as proportions and structural details, are useful.

ANSERANATINAE

The coracoid of *Anseranas* is vastly different from those of all other waterfowl: (1) A coracoidal foramen is present as a circular opening in the large procoracoid. The fenestra not only pierces the bone but opens into the shaft as well. (2) A pneumatic foramen is present on the dorsal surface anterior to the sternal facet. (3) The dorsal portion of the sternal facet has a prominent medial lip that is essentially perpendicular to the shaft. (4) The sternocoracoidal process has a prominent knoblike extension. (5) The surface of the triosseal canal is inflated, rather than depressed as in most other waterfowl, and lacks the pneumatic foramina found in geese and swans. (6) The angle formed between the axis of the head, best seen in anterior view, and the plane upon which the dorsal surface lies is 88 to 93 degrees. Swans are the only other waterfowl that have an angle greater than 87 degrees. (7) The head is wider, and (8) the neck is less constricted than in other waterfowl. (9) Depth through the scapular facet at its narrowest point is 16.3 to 17.5 percent of the length

(measured from the head to the internal distal angle), greater than in all other waterfowl except certain swans and geese.

ANSERINAE

Although no single character of the coracoid distinguishes the Anserinae from the Anatinae, a combination of features proves diagnostic: (1) The angle between the axis of the head and the plane upon which the dorsal surface lies is 79 to 93 degrees, greater than in most Anatinae. (2) The angle between the sternal facet and the shaft is small, with a range from 70 to 83 degrees (measured with one straight edge touching the internal distal angle and the median portion of the head,

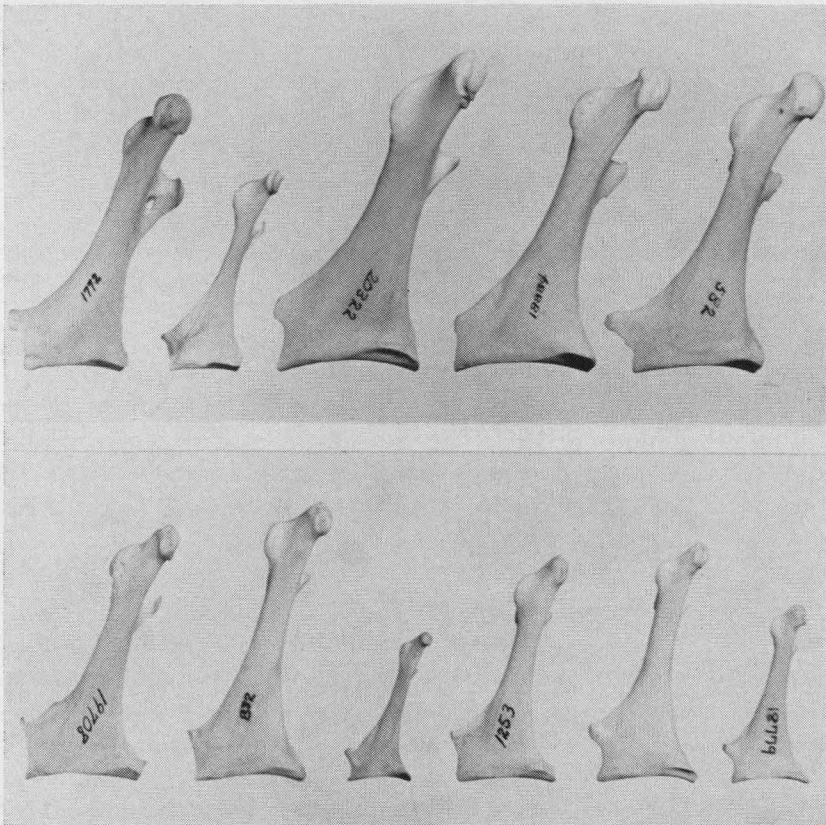


FIGURE 4. Right coracoid, ventral view. Top row: *Anseranas semipalmata*, *Dendrocygna autumnalis*, *Cygnus melancoriphus*, *Branta canadensis*, *Cereopsis n.hollandiae*. Bottom row: *Tadorna tadorna*, *Anas rubripes*, *Merganetta armata*, *Aythya affinis*, *Clangula hyemalis*, *Oxyura jamaicensis*.

and the other lying along the posterior border of the element). (3) The ventral lip of the sternal facet is wide and concave, with the external edge essentially perpendicular to the shaft. (4) The median edge of the sternal facet is typically broad and blunt, partially a result of the wide lips to the sternal facet.

TRIBE DENDROCYGNINI (WHISTLING DUCKS). The coracoid of whistling ducks resembles that of swans and geese in most characteristics, but its slender shaft gives it a decidedly ducklike appearance. *Dendrocygna* can be distinguished from the swans and geese by the following coracoidal features: (1) The depth is 12.6 to 14.1 percent of the length. A minimum of 15.0 is recorded for the swans and geese. (2) The width is 8.3 to 10.3 percent of the length (measured at the narrowest point posterior to the procoracoid with the caliper legs perpendicular to the plane of the dorsal surface). Its minimum width is 12.4 percent in the swans and geese. (3) The pneumatic foramina beneath the furcular facet are minute or absent. (4) The ventral surface has a pronounced depression immediately anterior to the sternal facet and medial to the intermuscular line. This character makes the coracoid of *Dendrocygna* separable at a glance from that of any other bird.

TRIBE ANSERINI (SWANS AND GEESE). Although the coracoids of whistling ducks and swans and geese show basic similarities, these tribes can be separated easily. Swans and geese have the following coracoidal properties: (1) The depth is 15.0 to 22.1 percent of the length. (2) The width varies from 12.4 to 16.4 percent. (3) The pneumatic foramina beneath the furcular facet are large and numerous.

The coracoid supports the distinction of two groups within the Anserini, one being swans and *Coscoroba*, the other the geese, previously defined by other skeletal elements. The major difference between the two is in the form of the triosseal canal: (1) In swans the triosseal canal has no deep depression between the procoracoid and the brachial tuberosity. In geese the depression is deep. (2) In swans pneumatic foramina are small and extend under the entire furcular facet. In geese, where they are larger, the foramina are normally restricted to the area beneath the brachial tuberosity. (3) The angle between the axis of the head and the plane of the dorsal surface ranges from 83 to 93 degrees in swans. In geese the range is 80 to 85 degrees. (4) The depth through the scapular facet ranges from

16.4 to 22.1 percent of the length in swans. In geese the range is 15.0 to 17.6 percent.

Coscoroba resembles the swans in the size and location of pneumatic foramina and the depth through the scapular facet (18.2 percent). It is intermediate between swans and geese in the depth of the triosseal depression and the angle of the head (83 degrees). From the swans, to which it seems more closely allied, *Coscoroba* differs as follows: (1) The ventral edge of the shaft in internal view is virtually straight, whereas it is curved toward the ventral prominence of the head in swans. (2) The sternal facet in posterior view is straighter, less arched, than in swans. (3) The width below the procoracoid is 13.7 percent of the length; swans range from 13.6 to 16.4, but only three of 36 specimens are narrower than *Coscoroba*.

Four coracoidal features that aid in separating *Olor* from *Cygnus* are listed by Howard (1946): (1) The furcular facet is undercut for its full extent in *Olor*. In *Cygnus* the facet is flattened against the shaft ventrally with only a slight undercut near the brachial tuberosity. *Chenopsis* resembles *Cygnus* in this respect, although 1 of 4 specimens is intermediate. (2) The procoracoid is larger in *Olor* and smaller in *Cygnus* and *Chenopsis*. (3) The coracoidal notch is absent in *Olor*, although Howard notes some exceptions. In *Cygnus* there is a more (*C. olor*) or less (*C. melanoriphus*) distinct notch located where the coracoidal fenestra occurs. Two of four specimens of *Chenopsis* have the notch sealed off as an elongate fenestra. This opening does not appear to be homologous with the foramen in the procoracoid of *Anseranas*. (4) The scapular facet is broad and shallow in *Olor*. In *Cygnus olor* and *Chenopsis* the area is more evenly rounded. *Cygnus melanoriphus* is intermediate.

The coracoid exhibits a feature that allows for a separation of the geese. Miller (1937) uses it to separate *Branta* from *Anser* and *Chen*, but with the present series it has wider application. In *Branta* and *Nesochen* the furcular facet is undercut for its full extent. In *Anser*, *Chen*, *Cyanopsis*, *Philacte*, and *Eulabeia* the furcular facet is deeply undercut dorsally, flattened against the shaft in the middle, and only slightly excavated ventrally. Pneumatic foramina frequently occur under the ventral portion of the facet in *Branta* and *Nesochen*, but are absent in this area in the other genera.

Nesochen differs from other geese as follows: (1) The depression in the triosseal canal between the procoracoid and the brachial tuberosity is shallower. (2) The angle of the coraco-humeral surface is

more nearly transverse to the shaft. Miller also mentions that pneumatic foramina beneath the brachial tuberosity are greatly reduced, but this is not the case with my one specimen.

ANATINAE

The following features when compared with those listed for the Anserinae should identify coracoids of the many members of the Anatinae: (1) The angle between the axis of the head and the plane of the dorsal surface varies from 61 to 81 degrees, except in *Cereopsis* and *Plectropterus*. (2) The angle between the sternal facet and the shaft varies from 80 to 96 degrees, except in the gooselike sheldrakes. (3) The ventral lip of the sternal facet is less prominent and slopes sharply toward the shaft. Certain sheldrakes are exceptions. (4) The flattened sternal facet has the ventral lip projecting medially; thus, the median edge is pointed. Again certain sheldrakes are exceptions. (5) The prominent depression on the ventral surface in *Dendrocygna* is lacking. (6) The depth through the scapular facet (10.1 to 14.6 percent of the total length) is usually less than in swans and geese. *Cereopsis* and *Plectropterus* are the exceptions.

When studying duck coracoids, difficulty arises from the extensive individual variation exhibited by such features as the depth of the depression in the triosseal canal, the length of the procoracoid, and the length of the sterno-coracoidal process. Although other features of the element are rather useful, it is not possible to characterize all of the tribes as defined by Delacour (1954, 1956, 1959). Reallocation of certain genera discussed below alleviates much of the difficulty.

TRIBE TADORNINI (SHELDRAKES). Compared with those of other Anatinae, the typical sheldrake coracoids have the following properties: (1) The procoracoid averages larger than in other ducks. (2) The triosseal depression averages deeper. (3) The surface of the furcular facet has a depression ventral to the brachial tuberosity. (4) The furcular facet is undercut extensively near the brachial tuberosity. (5) The angle between the sternal facet and the shaft is smaller, 75.5 to 81 degrees, the range for other ducks being 79 to 96 degrees.

Chloephaga, *Neochen*, and *Alopochen* are all rather similar and agree in the following criteria: (1) The depression in the furcular facet joins the undercut of the brachial tuberosity to form a notch in the facet. (2) Pneumatic foramina are usually prominent beneath the brachial tuberosity. The shape of the anterior end of the coracoid

differentiates these three genera. *Alopochen* has the deepest triosseal depression. *Neochen* has the widest furcular notch, which occupies most of the facet, and it also has the most prominent ventral tuberosity on the head. *Chloëphaga* has the shallowest triosseal canal, essentially lacking in some specimens, and the largest lateral protuberance on the head, located at the termination of the coraco-humeral surface.

Tadorna and *Casarca* can be characterized by the following features: (1) The furcular facet is entire because the depression and undercutting are less than in the three genera previously discussed. (2) Pneumatic foramina are minute or lacking under the furcular facet. The genus *Casarca* cannot be distinguished from *Tadorna* by coracoidal features.

Cereopsis is an exception in all five properties of the coracoid that aid in separating the Anserinae from the Anatinae, and the genus is easily separated from the typical members of the sheldrake tribe: (1) The angle between the axis of the head and the plane upon which the dorsal surface lies is 83 to 85 degrees. A maximum of 81 degrees is found in the true sheldrakes. (2) The depth through the scapular facet varies from 16.6 to 18.5 percent of the length. The other genera range from 12.9 to 14.5 percent. (3) The width posterior to the procoracoid varies from 14.0 to 15.8 percent of the length; true members of the tribe vary from 11.0 to 12.8. (4) The furcular facet is undercut for its full extent. In the others the facet is undercut only dorsally. (5) Pneumatic foramina are present under the entire length of the furcular facet. In the true sheldrakes they are either absent, or present only under the brachial tuberosity.

The coracoid of *Cereopsis* shows much greater resemblance to that of the swans and true geese. From the swans *Cereopsis* differs in having the head of the coracoid wider and shallower. It differs from the geese in having the depression in the triosseal canal between the procoracoid and the brachial tuberosity reduced.

Tachyeres can be distinguished from the typical sheldrakes as follows: (1) The angle between the axis of the head and the plane of the dorsal surface is 71 degrees. In the remaining sheldrakes the range is 72 to 81 degrees. (2) The depth through the scapular facet is 11.0 percent of the length. The range for the typical sheldrakes is 12.0 to 14.5 percent. (3) The width posterior to the procoracoid is 10.6 percent. The range for the true sheldrakes is 11.0 to 12.8 percent. (4) The angle between the sternal facet and the shaft is 87

degrees. (5) The internal end of the sternal facet is elongated and pointed. In the other genera assigned to the tribe the area is short and blunt. (6) The dorsal and ventral lips of the sternal facet are essentially flush with the shaft, whereas in sheldrakes they are prominent. All of these features of *Tachyeres* indicate a relationship to other Anatinae than the sheldrakes.

TRIBE ANATINI (DABBING DUCKS). The one feature that seems characteristic of the coracoid of the dabbling ducks is the angle between the axis of the head and the plane of the dorsal surface. This varies from 61 to 71 degrees. Exceptions are found in *Merganetta* and *Rhodonessa*, the two genera that also differ significantly from the typical members of the tribe in other properties.

Merganetta can be distinguished by two features: (1) The angle between the axis of the head and the plane of the dorsal surface is 74 degrees. (2) The head is deflected ventrally in medial view.

Rhodonessa resembles the pochards in the form of the coracoid. It differs from the dabblers in the following ways. (1) The angle between the axis of the head and the plane of the dorsal surface is 72.5 degrees, above the maximum recorded for the typical dabblers but within the range of *Aythya* (72 to 75 degrees). (2) The head is similar to that of the pochards (see description under pochard tribe).

The coracoids of the remaining genera of dabbling ducks show no qualitative distinguishing features.

TRIBE CAIRININI (PERCHING DUCKS). The coracoids of perching ducks are so similar to those of the dabblers, the two tribes cannot be differentiated on the basis of this element. The one coracoid trend that occurs in most species assigned to the perching ducks is the thickening of the head. The enlarged ventrolateral portion, upon which the coraco-humeral groove terminates, gives the head an over-all robust appearance. The genera assigned to the tribe by Delacour (1959) fall into four groups. The largest group contains *Cairina*, *Aix*, *Dendronessa*, *Pteronetta*, and *Amazonetta*. Another contains *Chenonetta*, *Nettapus*, and *Cheniscus*. The other two, very different from each other, consist of one genus each, *Sarkidiornis* and *Plectropterus*. The unifying features of the first of these units are associated with the coracoidal head: (1) The anterior end is rather pointed. (2) The ventral prominence is deflected medially. (3) The furcular facet is incised by a conspicuous groove.

Cairina seems the most specialized of the group, and can be distinguished from the others as follows: (1) The groove in the furcular facet is very deep, notching the edge of the facet. (2) Pneumatic foramina are prominent and often large. (3) The depth of the shaft is 13.8 to 14.6 percent of the length. The maximum for the other genera in the group is 12.8 percent.

Aix and *Dendronessa* have frequently been classified as dabbling ducks, but their coracoids show a strong resemblance to that of *Cairina*. The critical features are those listed above associated with its head. An additional criterion is the less-curved median edge of the shaft in these three genera.

Dendronessa cannot be separated from *Aix*, but the two together differ from the other three genera in the group as follows: (1) The depth (12.0 to 12.7 percent of the length) is greater than in *Amazonetta* (11.8 percent) but less than in *Pteronetta* (12.1 percent) and *Cairina*. (2) The groove in the furcular facet is generally deeper than in *Amazonetta* and *Pteronetta*, but not nearly as pronounced as in *Cairina*.

Pteronetta is very different from *Cairina* and similar to *Anas* in the form of the coracoid: (1) The head is wider and less pointed. (2) The groove in the furcular facet is wide and shallow. The ventrolateral portion of the head is enlarged, however, and shows its affinities to the perching ducks. The coracoid of *Amazonetta* is intermediate between those of certain dabbling ducks, namely *Anas discors* and *A. cyanoptera*, and of perching ducks such as *Aix* and *Dendronessa*, but the head seems more pointed than in *Anas*.

The second group, formed by *Chenonetta*, *Nettapus*, and *Cheniscus* agrees in most characters with the preceding group, but lacks the groove in the furcular facet. No coracoidal features distinguish *Cheniscus* from *Nettapus*, but both differ from *Chenonetta* as follows: (1) The depth is 10.7 to 12.9 percent of the length, whereas in *Chenonetta* it is 13.0 to 13.4 percent. (2) The ventral prominence of the head is directed medially. In *Chenonetta* the prominence is directed ventrally.

In *Sarkidiornis* and *Plectropterus* the depression in the triosseal canal is extremely deep. *Sarkidiornis* differs from *Plectropterus* in having the triosseal canal only 16.7 percent of the length, and the ventromedial lip of the sternal facet very short, the shortest of any waterfowl seen.

The *Plectropterus* coracoid differs markedly from those of other perching ducks: (1) The triosseal canal is 19.7 to 21.0 percent of the

length. The range for other perching ducks is 13.4 to 18.5. (2) The coracoidal head is wide and not pointed in medial view. (3) The ventrolateral portion of the coracoidal head is not enlarged, and (4) the neck is prominent.

TRIBE AYTHYINI (POCHARDS). Their coracoids show the pochards form a distinct tribe readily separable from the others, both diving and nondiving. Those of certain genera indicate the derivation of the tribe was from the dabblers. The unique features of the tribe are associated with the head: (1) Its ventral portion is reduced. In medial view, the coracoidal head meets the ventromedial edge of the shaft by a straight or gently curved line. (2) The bicipital attachment is a thin groove instead of an elliptical facet. (3) The furcular facet extends farther posteriad along the shaft. As mentioned in the section on the dabbling ducks, *Rhodonessa* agrees entirely with all these pochard characteristics.

Aythya has the most specialized coracoid of the pochards, whereas *Metopiana* and *Netta* are intermediate between *Aythya* and the dabblers in most features. As the following characteristics indicate, *Rhodonessa* also seems to be one of the less specialized pochards. (1) The relative width of the triosseal canal, given as a percentage of the length, is as follows: *Aythya* 11.6-14.7; *Metopiana* 13.8-15.0; *Netta* 14.6-15.1; *Rhodonessa* 14.8; Dabbling Ducks 14.3-17.9 percent. (2) The angle between the axis of the head and the plane of the dorsal surface has the following variation in degrees: *Aythya* 72-75; *Metopiana* 70-72; *Netta* 69-71; *Rhodonessa* 72.5; Dabbling Ducks 61-71 degrees. (3) The angle between the sternal facet and the internal edge of the element measures: *Aythya* 86.5-91; *Metopiana* 85-87; *Netta* 87-88; *Rhodonessa* 86; Dabbling Ducks 82-86 degrees.

Aythya is best distinguished from *Metopiana* and *Netta* by the depth of the element relative to its length. In *Aythya* the range is from 10.9 to 12.6 percent; *Metopiana* (12.6 to 13.8), *Netta* (13.3 to 13.4), and also *Rhodonessa* (13.5) are relatively deeper.

Metopiana and *Netta* can also be separated by coracoidal features: (1) The width is 10.0 to 10.6 percent of the length in *Metopiana*, 11.9 to 12.3 percent in *Netta*. (2) The sternal facet is 38.1 to 40.4 percent of the length in *Metopiana*, 44.5 to 44.6 in *Netta*. The relatively short length of the sternal facet in *Metopiana* is correlative to the presence of a ventral manubrial spine on the sternum. (3) The ventromedial edge of the head is straighter and more prominent in *Netta*.

TRIBE SOMATERIINI (EIDERS). The eiders are considered an offshoot of the dabbling ducks by Delacour (1956), and Humphrey (1958a), but the coracoid has striking similarities with that of the scoters: (1) The procoracoid flares dorsally and has the base enlarged in both groups. (2) The triosseal canal is wide, 17.1 to 19.9 percent of the length in eiders, 15.3 to 18.7 percent in scoters. (3) The sternal facet is 43.3 to 47.1 percent of the length in eiders, 42.9 to 49.9 percent in scoters. (4) The head has a large ventral prominence in both groups.

The characters that separate the coracoid of eiders from those of scoters and the other sea ducks are less obvious. (1) The sternal facet has the ventromedial lip essentially flush with the shaft. In scoters the lip departs abruptly from the shaft. (2) The sternal facet, at the internal distal angle, is elongated and pointed. In the scoters this region is relatively blunt. (3) The angle between the axis of the head and the plane of the dorsal surface is 70 to 81 degrees. In scoters the range is 77 to 87 degrees. (4) The ventromedial edge of the shaft is a sharp ridge and the surface from the ridge through the triosseal canal is almost flat (a slight depression in many specimens). In scoters the ridge is wider and it then curves abruptly toward the canal that normally houses a rather deep depression. (5) The ventral prominence of the head is situated farther posteriorly than the brachial tuberosity. In scoters the ventral prominence extends no farther back along the shaft than the tuberosity, and frequently it is more anterior than the latter.

The one available specimen of *Lampronetta* shows no qualitative features of the coracoid useful in distinguishing it from *Somateria*. *Polysticta* is distinct from *Somateria* and *Lampronetta*, and certain of its coracoidal features indicate an affinity to *Histrionicus* and *Clangula*: (1) The axis of the head is 81 degrees from the plane of the dorsal surface. The range for other eiders is 70 to 79 degrees. (2) The furcular facet is rounded. In other eiders the facet is flat and usually has a depression ventral to the brachial tuberosity. The furcular portion of the head in *Histrionicus* is similarly rounded.

TRIBE MERGINI (SEA DUCKS). The sea ducks exhibit considerable variation in the conformation of the coracoid, as in their other bony elements. Somewhat useful in defining the tribe is the procoracoid, which tends to flare dorsally with its base extending farther back on the shaft. The eiders share this feature. The tribe may be divided into two distinct groups on the basis of the element. One group contains *Bucephala* and the merganser genera *Lophodytes*, *Mergellus*, and

Mergus; the other contains *Clangula*, *Histrionicus* and the scoters, *Melanitta*, and *Oidemia*.

The following characters of the coracoid distinguish these two groups: (1) In *Bucephala* and the mergansers the sternal facet varies from 33.2 to 39.7 (42.2 in 1 of 35 specimens) percent of the length. In the others the range is 42.1 to 49.9 (39.6 in 1 of 17 specimens). (2) In *Bucephala* and mergansers the sterno-coracoidal process is less produced laterally and forms an angle of less than 45 degrees with the shaft. In the others the process is produced farther laterad to form an angle of more than 45 degrees with the shaft. (3) In *Bucephala* and mergansers the triosseal canal varies from 11.1 to 15.4 percent of the length of the bone. The range for the other four genera is 15.3 to 18.7. (4) In *Bucephala* and mergansers the angle between the axis of the head and the plane of the dorsal surface varies from 69 to 74 degrees, whereas in the others the range is 72 to 87 degrees. (5) In *Bucephala* and mergansers the furcular facet is frequently interrupted by a median depression. In the others the facet is usually distinct throughout its length. *Histrionicus* is an exception. (6) In *Bucephala* and mergansers the ventromedial edge of the shaft remains a sharp ridge to its termination at the furcular facet. In the others the anterior end broadens and underlies much of the furcular facet. *Histrionicus* is intermediate in this respect also. (7) The size of the ventral prominence of the head presents a sequence in which the mergansers, and particularly *Lophodytes*, have the smallest protuberance, *Bucephala* is intermediate, whereas *Histrionicus*, *Clangula*, and the scoters have the largest. The most natural break again seems to fall in the accustomed place, between *Bucephala* and mergansers and the other sea ducks.

The mergansers are distinct from *Bucephala* and the other sea ducks in only one inconstant feature of the coracoid, namely that the ventral lip of the sternal facet in posterior view is prominent as a broad curve to the internal distal angle. In other sea ducks the lip shows a distinct concavity as it approaches the angle; beyond the angle the lip is no longer prominent. Of 10 specimens of *Bucephala*, 2 could not be identified by this character, and 1 specimen of *Melanitta* is aberrant.

The length of the sternal facet relative to the length of the coracoid is useful in separating *Bucephala* (37.2 to 42.1) from *Mergus* (33.2 to 37.2, one 39.7). However, when *Mergellus* (37.2) and *Lophodytes* (34.8 to 38.6) are considered the character becomes less definitive.

Paleontologists have no difficulty in separating *Lophodytes* from *Mergus* on the basis of size. Qualitatively the coracoids of the two genera are very similar, but they show consistent differences in the configuration of the glenoid facet: In *Mergus* the ventral rim of the glenoid facet is rather angular with the anteroventral leg somewhat rounded, the posterior leg essentially straight. In *Lophodytes* the anteroventral portion of the rim is broadly rounded, the posterior part concave. The glenoid facet of *Mergellus*, while not as rounded at the anterior end as in *Lophodytes*, shows its greatest resemblance to that of this genus.

The four available specimens of *Mergus merganser* have deeper triosseal depressions than the 17 of *M. serrator*.

The fossil duck *Bucephala ossivalis* Brodkorb (1955) from the Bone Valley formation, usually referred to the lower Pliocene, is known from the anterior half of a coracoid. The bone is very similar to that of *B. clangula* and *B. albeola*, particularly in the shape of the furcular facet and ventral prominence of the head. Perhaps the similarity of certain features to those of the mergansers *Mergellus* and *Mergus* is of phylogenetic significance. These features are the shallower head (i.e., less pronounced ventrolateral prominence), more curved coraco-humeral groove, and the general appearance of the glenoid facet.

In the second group of sea ducks *Clangula* has the most distinct coracoid: (1) The depth through the scapular facet varies from 12.3 to 13.1 percent of length. The range obtained for *Histrionicus* and the scoters is 13.2 to 14.3 percent. (2) The axis of the head has a smaller angle to the plane of the dorsal surface (71 to 79 degrees); in the scoters the range is 77 to 87 degrees, and in *Histrionicus* 78 degrees was recorded. (3) The sternal facet varies from 39.6 to 43.4 percent of the length, whereas in the others it ranges from 42.9 to 49.9. (4) The furcular facet has a triangular appearance, the smallest angle being at the ventral prominence. In the other three genera the facet presents a more ovoid shape.

Histrionicus is characterized by the following features: (1) The depression in the triosseal canal is very deep in the one available specimen. (2) The ventromedial edge of the shaft is thin. In *Oidemia*, where the triosseal depression is usually deep, the edge is relatively wide, and constitutes about half of the shaft depth, measured between the procoracoid and the head. (3) The head has a less protruding ventral prominence, but the rounded furcular facet appears more triangular than in the scoters. (4) The median portion of the ventral

lip of the sternal facet is inconspicuous, extending only a short distance up the shaft.

Three features in *Oidemia* aid in its separation from *Melanitta*: (1) The sternal facet varies from 46.6 to 49.9 percent of length. *Melanitta* varies from 42.9 to 44.9 percent. (2) The depression in the triosseal canal is deep. Although variable, it is not as deep as in *Melanitta*. (3) The ventral prominence of the head is smaller and results in an almost circular furcular facet. In *Melanitta*, because of the large ventral prominence of the head, the furcular facet is ovoid in shape.

TRIBE OXYURINI (STIFF-TAILED DUCKS). The stiff-tailed ducks have a fairly distinctive coracoid: (1) The ventral portion of the head extends far down the shaft. (2) The brachial tuberosity is reduced. (3) The sterno-coracoidal process is prominent. (4) The sternal facet, in posterior view, is strongly arched throughout its length.

Heteronetta, the least specialized genus, has coracoidal features that indicate a close affinity to the other members of the tribe, but it may be distinguished as follows: (1) The depth through the scapular facet is 11.8 percent of the length. *Nomonyx* and *Oxyura* range from 9.6 to 11.5 percent. (2) The axis of the head is 67 degrees from the plane of the dorsal surface. In other members of the tribe the range is from 72 to 78 degrees. (3) The angle between the sternal facet and the internal edge of the shaft is 84.5 degrees. In other stiff-tails the range is from 86 to 96 degrees. In these three criteria *Heteronetta* is intermediate between more specialized stiff-tailed ducks and the dabbling ducks.

Nomonyx can be separated from other members of the tribe as follows: (1) The triosseal canal is narrow. The distance between the undercut of the brachial tuberosity and the procoracoid constitutes only 10.9 to 11.1 percent of the length. In others the range is from 12.0 to 16.6 percent. (2) The width of the shaft varies from 8.4 to 8.7 percent of the length. A range of 9.1 to 11.1 was obtained for other stiff-tails. (3) The depth through the scapular facet, 10.8 to 11.5 percent, is intermediate between *Heteronetta* (11.8) and *Oxyura* (9.6 to 11.0). (4) The brachial tuberosity is reduced. *Nomonyx* is closest to *Oxyura*, but the numerous characters outlined above speak for its distinctness.

Oxyura is characterized as follows: (1) The relative depth is 9.6 to 11.0 percent. (2) The relative width is 9.1 to 10.7. (3) The angle

between the axis of the head and the plane of the dorsal surface is 72 to 75 degrees. (4) The angle between the sternal facet and the internal edge of the shaft is 87 to 96 degrees. (5) The triosseal canal has a relative width from 12.0 to 15.2 percent. This last feature best distinguishes *Oxyura* from *Nomonyx*, which has a narrow triosseal canal.

Biziura has a unique coracoid, with the ventral portion of the head larger and more ventrally directed than in any other anatid. In medial view the entire area above the glenoid facet appears bent ventrally, which makes the ventral portion of the head even more distinct. The following features aid in characterizing the genus: (1) The depth through the scapular facet is 12.2 percent of the length; a maximum of 11.8 was obtained for the other genera. (2) The width of the shaft is 11.1 percent of the length; a maximum of 10.7 was obtained for the others. (3) The axis of the head is closer to perpendicular to the plane of the dorsal surface (78 degrees) than in other genera (whose maximum is 75 degrees). (4) The triosseal canal is 16.6 percent of the length; 15.2 is the largest in the other stiff-tailed ducks.

Downs (1954) has studied the coracoid of several species of North American ducks. He concludes that the degree of angulation of the head is related to the method of taking flight. Those forms capable of steep ascent (dabbling and perching ducks) have lesser angulation between the axis of the head and the plane of the dorsal surface, whereas those which take off at a low incline (diving ducks) have greater angulation. The data obtained from the present series of ducks support Downs's theory. A range from 61 to 75 degrees was obtained from examples of the dabbling and perching ducks. The range for the species assigned to the four tribes of diving ducks was 69 to 87 degrees, except for *Heteronetta* (67 degrees).

The correlation between structure and function may have wider application. The pied goose, whistling ducks, swans, and geese have considerable angulation between the axis of the head and the plane of the dorsal surface (79 to 93 degrees), and apparently they take flight at a relatively low angle.

Scapula

The scapula has a few features of taxonomic importance. Howard (1946) comments on the marked variability in the structural details of the element in swans. Since only qualitative features are considered, only a few genera and generic units can be characterized.

ANSERANATINAE

As with other elements, there are greater qualitative differences between the scapula of *Anseranas* and those of other waterfowl than exist between those of any other members of the group: (1) The acromion is short, barely extending beyond the coracoidal articulation. In other waterfowl the acromion is long and pointed. (2) The triosseal ridge (a dorsally situated prominence of the acromion) is a knoblike protuberance that extends over the anterior edge of the acromion. (3) The blade is narrow and convex ventrally and the apex is pointed. (4) A pneumatic fossa on the dorsal surface between the glenoid facet and the acromion occurs in other waterfowl only in true geese, *Coscoroba*, and *Cereopsis*.

ANSERINAE

The subfamily Anserinae cannot be characterized adequately by features of the scapula.

TRIBE DENDROCYGINI (WHISTLING DUCKS). The scapula of whistling ducks cannot be separated consistently from those of most of the Anatinae. The one feature that seems fairly characteristic of *Dendrocygna* is a narrow, pointed apex. The blade is also frequently narrow, although in some specimens it is wide. That *Anseranas* also has a pointed apex and a narrow blade may be of phylogenetic significance.

TRIBE ANSERINI (SWANS AND GEESE). The occurrence of the pneumatic fossa near the anterior end of the dorsal surface of the scapula is of taxonomic significance within the swan and goose tribe. Swans lack the fossa, whereas in *Coscoroba* and true geese it is present.

Three scapular features that aid in separating *Olor* from *Cygnus* are listed by Howard (1946): (1) The muscular attachment on the ventral surface of the acromion forms a short crest slightly back from the internal border distally. In *Cygnus* the attachment follows the internal edge more closely. This character made possible the separation of all but 4 or 5 of the 36 available swan specimens. (2) The acromion is shorter and broader in *Olor*. This feature, which is best understood by comparing the angle between the acromion and the shaft, is somewhat useful in distinguishing the two genera. In *Cygnus*, and particularly in *C. melancoriphus*, the angle is more acute between the acromion and the shaft; and, therefore, the acromion appears longer and more slender. (3) The shaft is thinner in *Olor*. This property does not seem applicable to my series of swans. *Chenopsis* resembles *Cygnus* in all of the features discussed above.

The scapula of *Coscoroba* differs from those of geese in the following ways: (1) The pneumatic fossa is shallower. (2) The acromion and its triosseal ridge are smaller. (3) The blade is wider.

Generic criteria are not present on the scapulae of geese. The only comment Miller (1937) made for the five genera of true geese he studied was that the scapula of *Nesochen* is proportionately smaller and weaker. My one *Nesochen* agrees with these generalizations.

ANATINAE

It is not possible to separate any of the closely related tribes of Anatinae on the basis of the scapula, though some features aid in distinguishing certain tribes or tribal groups. These features are discussed below under the classification of Delacour (1954, 1956, 1959).

TRIBE TADORNINI (SHELDRAKES). *Cereopsis* differs from the sheldrakes and resembles the true geese in that the scapula possesses a pneumatic fossa. The genus can be separated from the true geese by the following additional scapular features: (1) The acromion is directed more mediad, and consequently the surface posterior to the acromion, including the genoid facet, is broad. (2) The anterior edge, between the coracoidal articulation and the acromion, is thicker. (3) A protuberance is present on the dorsomedial edge of the neck. *Cereopsis*, true geese, and most other waterfowl possess a dorsal protuberance that lies in the middle of the shaft; but true geese lack the more anterior and median prominence found in *Cereopsis*. (4) The glenoid facet lies almost in the plane of the anterior portion of the shaft. In true geese the anterior portion of the facet is typically inclined lateroventrally.

The remaining genera of sheldrakes have no outstanding qualitative features to separate them from related groups of Anatinae, or from each other.

TRIBE ANATINI (DABBING DUCKS). A few minor differences between the scapulae of dabbling ducks and of diving ducks of the pochard, eider, and sea duck tribes are detectable when large series of the element are studied: (1) The acromion is shorter with the ventral surface flat in dabblers. In diving ducks of the tribes listed above the acromion is longer, and in ventral view it usually reveals a knoblike process. As a result, the anterior edge of the bone between the acromion and the glenoid facet is concave; in dabblers the edge is straighter. (2) The proximal portion of the scapula is not rotated. In the divers, in-

cluding the stiff-tailed ducks, the rotation is such that the internal edge and the acromion appears depressed. (3) The blade is usually broadest near the midpoint. In pochards, and particularly *Aythya*, the blade is narrow and tapers near its apex. In the other diving tribes the blade is wide throughout.

Three genera among the dabblers have scapular features that enable them to be distinguished from other members of the tribe: In *Hymenolaimus* the acromion is almost parallel with the trend of the blade, whereas in other dabbling ducks it is more flaring; the blade is of uniform width and has a blunt apex. In *Merganetta* the triosseal ridge is reduced, and the anterior edge of the element is thick and forms almost a straight line; the blade is narrow but rather thick. In *Rhodonessa* the blade is narrow and the proximal portion is rotated as in the pochards, but the ventral surface of the acromion is flat instead of knoblike. Thus another element can be added in which *Rhodonessa* shows affinities with the pochards.

TRIBE CAIRININI (PERCHING DUCKS). In the perching ducks the shape of the blade and the acromion of the scapula is, generally speaking, more like that of the dabblers than the divers. *Plectropterus* differs from other members of the tribe as follows: (1) The muscular line of the dorsal surface extends from the prominence at the posterior end of the neck to the internal edge. In other perching ducks the ridge curves anterolaterally and meets the glenoid facet. (2) The acromion is shorter and thicker.

The *Cairina* scapula is typified by the following characteristics: (1) A wide depression is present on the dorsal surface between the glenoid facet and the triosseal ridge. The depression may contain small pneumatic foramina. (2) The blade is thick and rounded.

The *Pteronetta* scapula lacks the dorsal depression and thick blade of *Cairina*, and is similar to that of *Aix*, *Dendronessa*, *Amazonetta*, *Cheniscus*, and *Nettapus*, none of which is separable from the other. *Chenonetta* possesses a wide, rounded acromion. In *Sarkidiornis* the acromion appears to flare more than in other perchers.

TRIBE AYTHYINI (POCHARDS). The pochard scapulae are characterized as follows: (1) The acromion is longer and with a knoblike ventral surface. (2) The proximal portion of the element is rotated so that the internal edge and acromion appear depressed. (3) The blade is relatively thin throughout. *Metopiana* usually has the blade tapering as in the dabblers, but the anterior end is rotated, and the ventral surface of the acromion is knoblike as in *Aythya*. *Netta* has the acromion

shorter than in other pochards, but it is still knoblike; the blade is narrow and the anterior end is internally depressed.

TRIBE SOMATERINI (EIDERS). The eiders have the anterior end of the scapula rotated as in other divers, and the blade uniform in width and rather wide as in the sea ducks. *Lampronetta* appears indistinguishable from *Somateria* in scapular characters. The *Polysticta* scapular acromion follows the trend of the shaft more closely, which makes it appear longer, and has a larger concave edge between it and the glenoid facet.

TRIBE MERGINI (SEA DUCKS). The scapulae of sea ducks can frequently be separated from those of other waterfowl except the eiders: (1) The anterior end is rotated as previously described. (2) The blade is uniform in width and rather wide with a blunt apex. Often the blade bends abruptly near the posterior end. This should not be confused with the tapering found in approximately the same place in the dabblers. The various members of the tribe cannot be distinguished by qualitative features of the scapula.

TRIBE OXYURINI (STIFF-TAILED DUCKS). The four available genera of stiff-tails form a rather distinct group as evidenced by the following scapular features: (1) The acromion is directed more anteriorly than in other ducks. (2) The blade is very uniform in width, fairly narrow, and often thick. (3) The glenoid facet is laterally compressed.

From the scapula, *Nomonyx* seems the least specialized of the stiff-tails. The glenoid facet is only slightly compressed and affords the best means of separating the genus from other members of the tribe. The thin, anteriorly directed acromion and narrow but thick shaft serve to separate *Nomonyx* from *Aythya*, which it resembles in other scapular features.

Heteronetta is also not as extreme in specialization of the scapula as are *Oxyura*, and *Biziura*, but it is closer to these genera than to *Nomonyx*. In *Heteronetta* the glenoid facet is more compressed medially than in *Nomonyx*, and the acromion is shorter than in *Oxyura* and *Biziura*. In *Oxyura* the internal edge of the acromion forms essentially a straight line with the internal edge of the blade, the glenoid facet is greatly compressed, and the blade is wider than in *Nomonyx* and *Heteronetta*. The *Biziura* scapula is quite similar to that of *Oxyura*, but can be separated by its thicker anterior end and more prominent triosseal ridge; also the blade curves to form a shallow, elongate concavity along the anterointernal edge.

Furculum

Considerable individual variation and a lack of articulating surfaces make the furculum a poor element taxonomically. As with all the elements studied, however, some features are worthy of mention.

ANSERANATINAE

Even an element as poor taxonomically as the furculum shows *Anseranas* to be unique among the waterfowl: (1) The furcular process is large and truncate. (2) Pneumatic foramina are present in the crotch formed at the point of fusion of the two clavicles. (3) The clavicles are compressed, and relatively straight in lateral view. (4) The appearance in anterior view is **V**-shaped instead of **U**-shaped. (5) The coracoidal tuberosity is small or lacking. The distinctive nature of the furcular process and shape of the furculum in anterior aspect were noted by Miller (1919).

ANSERINAE

The Anserinae cannot be distinguished as a unit by features of the furculum.

TRIBE DENDROCYGNINI (WHISTLING DUCKS). The furculum of whistling ducks is nonpneumatic, with a small coracoidal tuberosity and rather deeply curved clavicles. In most cases it is indistinguishable from those of the Anatinae.

TRIBE ANSERINI (SWANS AND GEESE). Most genera in the swan and goose tribe have the furculum pneumatic, with the foramina occurring along the lateral surface of the clavicles. The clavicles tend to be more compressed, and the coracoidal tuberosity smaller than in the Anatinae.

The furcula of swans and geese can be separated in most cases. Swans and *Coscoroba* have the following features: (1) An extended depression occurs along the lateral surface of the clavicles. It is lacking in some *Cygnus melanoriphus*. (2) Pneumatic foramina, one to several, frequently large, are located in the depression.

Coscoroba differs from true swans in a number of ways: (1) The symphysis is narrow and a furcular process is present. (2) The depression on the lateral surface of the clavicles is restricted to the area between the coracoidal and scapular tuberosities. (3) The ridge for the attachment of the interclavicular membrane crosses the lateral

surfaces of the clavicles directly from the coracoidal tuberosity. In true swans the ridge runs a considerable distance along the anterolateral surface before crossing over to the posteromedial side. (4) The pneumatic foramina are small and scattered throughout the depression.

The following features separate *Olor* from *Cygnus* and *Chenopsis*: (1) The symphyseal area is extended posterodorsally to allow space for passage of the trachea ventrally into the sternal carina. In other waterfowl, with the possible exception of *Anseranas*, the trachea remains dorsal to the furcular symphysis. In *Cygnus* and *Chenopsis* the symphyseal area is broad and smooth. (2) The clavicular depression is longer, deeper, and with several large pneumatic foramina. In *Cygnus olor* and *Chenopsis* the depression is less well developed, and in *Cygnus melancoriphus* it is virtually absent. The pneumatic foramina, although typically large, usually number one or two, and in *Cygnus melancoriphus* they are minute or absent. (3) The clavicles are thinner and more pointed. In *Cygnus* and *Chenopsis* they are much thicker and have rather blunt scapular tuberosities.

Geese have no extended depression on the lateral surface of the clavicle, and pneumatic foramina are either absent or, if present, restricted to the area between the coracoidal and scapular tuberosities.

Within the geese, the occurrence of pneumatic foramina in the furculum is of taxonomic significance. *Branta* and *Neochen* lack the foramina, whereas they appear in *Anser*, *Cygnopsis*, *Eulabeia*, and *Philacte*, and in *Chen*, except for 1 of 9 specimens of *C. rossii*. No other criteria were noted for the geese, although Miller (1937) mentions that in *Nesochen* the furculum is smaller and the processes weaker than in the North American genera.

ANATINAE

Within the diverse subfamily Anatinae only a few genera or generic groupings are recognizable from the furculum.

TRIBE TADORNINI (SHELDRAKES). In its furculum *Cereopsis* resembles the geese more than the sheldrakes. Two features easily distinguish it from the latter group: (1) Pneumatic foramina are present in the slight depression along the lateral surface between the coracoidal and scapular tuberosities. (2) The clavicles are compressed and appear straighter in lateral view.

The typical sheldrakes appear intermediate between the Anserinae and the remaining duck tribes in furcular characters. Sheldrakes have

the coracoidal tuberosity poorly developed as in the geese, and the clavicles are only slightly compressed as is typical of ducks. Separation of the sheldrake genera from each other is not possible by qualitative features of the furculum.

TRIBE ANATINI (DABBING DUCKS). In dabbling ducks the furcular process and coracoidal tuberosity are typically large, and the clavicles are rather round in cross section. Exceptions are *Rhodonessa*, *Hymenolaimus*, and *Merganetta*, in which the furcular process is essentially lacking. In the latter two genera the clavicles are weak, and the element is broadly U-shaped.

TRIBE CAIRININI (PERCHING DUCKS). *Plectropterus* does not fit in well with the other genera of perching ducks; its furculum differs in having the coracoidal tuberosity reduced and the clavicles compressed. Both of these are characteristics of the sheldrakes. *Cairina* frequently possesses a small pneumatic foramen in one or both clavicles below the scapular tuberosity, but is otherwise typical of the tribe.

TRIBES AYTHYINI, SOMATERINI, AND MERGINI (POCHARDS, EIDERS, AND SEA DUCKS). Members of these three tribes have the furcular process small or absent, except in the pochard *Metopiana* where it is rather prominent. In *Metopiana* and in those individuals of the other species where a trace of the furcular process occurs, it is typically notched. The feature correlates with an expansion posteroventrally of the double sterno-furcular ligament (see Appendix) with a consequent reduction in the single median ligamentous membrane. *Mergus* shows greater curvature throughout the length of the clavicles in lateral view, but otherwise it is not markedly different from other sea ducks.

TRIBE OXYURINI (STIFF-TAILED DUCKS). The furculum of the stiff-tailed ducks is somewhat characteristic in that the element is thin and rather weak. *Heteronetta*, which Delacour (1959) places only provisionally in the tribe, agrees in the reduction of the element. The least reduced furculum occurs in *Nomonyx*. Typical of all divers, members of this tribe lack a prominent furcular process.

Femur

The leg seems more susceptible to adaptive modifications than the wing. The femur in ducks that dive, for example, shows great uniformity even though other taxonomic criteria indicate many of the genera are only distantly related.

ANSERANATINAE

The long, slender femur of *Anseranas* has several unique properties: (1) The posterior intermuscular line swings from above the internal condyle to the external edge of the shaft, and thence continues to the obturator ridge. In other waterfowl the line is confined to the medial side of the shaft and fails to meet the obturator ridge. (2) The internal condyle is elongate and equal or subequal in distal extent to the external condyle. In other anatids the internal condyle is flattened and does not extend as far distally. (3) The rotular groove is narrow. (4) The element is less contorted so that the head is directed more posteriad than in other waterfowl. (5) The anterior surface of the shaft is convex at a point $2/3$ the distance from the proximal end.

ANSERINAE

One property of the femur tends to link the whistling ducks, swans, and geese, and separate them as a group from the Anatinae. The external condyle has the anterior ridge elevated from the trend of the shaft. In other waterfowl the anterior surface in this region tends to form a straight or posterior-curving line.

TRIBE DENDROCYGNINI (WHISTLING DUCKS). The femur of whistling ducks superficially resembles that of the nondiving Anatinae. The femur of *Dendrocygna* has a shaft convexity similar to that described for *Anseranas*. In other waterfowl the shaft is curved in a similar direction at this point, but the curve continues onto the condyles instead of straightening out distally.

TRIBE ANSERINI (SWANS AND GEES). Swans and geese have the straightest femur of all waterfowl. In lateral view the long axis of the shaft is virtually a straight line. The bone also tapers markedly from the wide trochanteric end to the thinnest point, which lies immediately proximal to the condyles. *Cygnus melancoriphus* shows some curvature. Swans and geese are very similar in the form of the femur. One consistent criterion for separating the two is that the external and fibular condyles flare laterally in swans; in geese they are directed more posteriorly.

Coscoroba can be separated from other swans by characteristics of the femur: (1) The head is shorter and the neck is less distinct. (2) The trochanter, particularly at its anterior tip, extends proximally. The proximal extent of the trochanter is obviously greater than that of the head.

Within the swans no feature of the femur is strong enough to separate *Cygnus*, *Chenopsis*, or *Olor* completely, but the form of the neck as seen in proximal view is helpful. *Cygnus* and *Chenopsis* tend to show a depression on the anterior surface between the trochanter and the head. In *Olor* a low ridge extends from the trochanter toward the head. Thus the neck appears more constricted in *Cygnus* and *Chenopsis* than in *Olor*.

The shape of the femur is of little use in defining the genera of true geese. Miller (1937) lists the following features that aid in the separation of *Chen* and *Branta*: (1) In *Branta* the medial crest bordering the popliteal area is less deflected medially, and hence it is straighter and more in line with the shaft. (2) In *Chen* the rotular groove is narrower, and thus appears deeper. (3) In *Chen* the outer surfaces of the condyles converge toward one another anteriorly, whereas in *Branta* they are more nearly parallel. (4) In *Chen* the internal condyle is narrower. In my series the first of these four features is the most useful, but all are highly fallible and are further obscured by the extreme similarity of the skeleton of *Anser* to that of *Chen*, as noted by Miller (1937) and Howard (1946).

Nesochen differs from other geese, as noted by Miller (1937), in the following ways: (1) The rotular groove is extremely broad. (2) The neck is short and directed more posteriad, less mediad. Miller also states that the femur of *Philacte* has the popliteal depression narrowed by inflation of the lateral margin.

To the features listed above one more can be added. In *Branta* and *Nesochen* the trochanter is extended slightly more proximad at its anterior tip, and the posterior rim straightens instead of curving toward the head. *Chen*, *Anser*, and *Cygnopsis*, in which the trochanter has its most proximal extent in the middle and the posterior rim curves toward the head, are usually separable by this feature. *Eulabeia*, and to a lesser extent *Philacte*, resemble the latter group most in this respect.

ANATINAE

The Anatinae show no significant elevation of the anterior edge of the external condyle from the shaft as do the Anserinae. On femoral characteristics the seven tribes of Anatinae are divisible into two groups; one contains the nondiving tribes, the sheldrakes, dabbling ducks, and perching ducks; the other the diving tribes, the pochards,

eiders, sea ducks, and stiff-tailed ducks. The distinguishing features are as follows: (1) The shaft is less curved in lateral and anterior views in the nondivers. (2) The anterior ridge of the trochanter is larger in the nondivers, and the shaft in lateral view curves anteriorly as it passes proximally to the anterior trochanteric prominence. (3) The popliteal fossa is shallow in the nondivers. (4) The outer surfaces of the condyles are nearer parallel, whereas in divers they diverge posteriorly. These differences cause the femur, when it is placed anterior surface down on a plane, to have the head elevated from the plane in the nondiving tribes, whereas it lies on the plane in the diving tribes. *Merganetta* of the dabblers and *Metopiana* of the pochards are exceptions. *Heteronetta* appears intermediate because the head is slightly elevated from the plane. In *Tachyeres*, although the head is distinctly elevated, there are other features that cause it to resemble the diving assemblage.

TRIBE TADORNI (SHELDRAKES). The following femoral characteristics while not diagnostic, aid in separating the sheldrakes from the other nondiving ducks: (1) The head is directed more proximally, less laterally. (2) The trochanter in lateral view extends more anteriorly, and in proximal view it curves more medially. In dabblers and perchers the posterior portion of the trochanter tends to form an angle, whereas in the sheldrakes it is a smooth curve.

Significant differences in the femur were not found among the sheldrakes, except for the aberrant genera *Cereopsis* and *Tachyeres*. *Cereopsis* resembles the Anserinae in that the anterior ridge of the external condyle is elevated from the shaft. The following additional features serve to distinguish the genus: (1) The external and fibular condyles and the fibular groove are directed medially at the distal end. Thus the fibular condyle extends farther distally than the point of its junction with the external condyle. The opposite is the case in all other waterfowl. (2) The shaft in anterior view is straighter, as described for the true geese.

The femur of *Tachyeres* is unique. (1) A deep pit occurs on the posterior surface medial to the obturator ridge and distal to the iliac facet. (2) A depression is present in the rotular groove. The shaft of the femur in *Tachyeres* is deeply curved and the popliteal fossa is deep—adaptions for diving. Its femur also has a prominent anterior ridge, and the condyles have the outer surface less divergent posteriorly—features of the nondiving ducks.

TRIBES ANATINI AND CAIRININI (DABBING AND PERCHING DUCKS). The numerous genera of dabbling and perching ducks, with but few exceptions, cannot be distinguished on the basis of femoral characteristics. *Hymenolaimus* and *Merganetta*, two diving members of the dabbling-duck tribe, have the popliteal fossa deep. *Hymenolaimus*, the least specialized of the two, possesses the following additional features: (1) The head is larger, and (2) the rotular groove is wider.

Merganetta resembles the divers more than the other dabblers in the features listed to separate the two groups. It can be separated from the diving tribes in the following ways: (1) The internal condyle has the posterior end directed more mediad, a feature shared with the pochards. (2) The trochanter in proximal view has its anterior portion reduced more than in pochards. (3) The posterior intermuscular line forms a more prominent ridge to the base of the head.

Although *Rhodonessa* is very similar to typical dabblers in the shape of the femur, it is linked with the pochards by the first three characteristics to be listed later for *Metopiana*. *Plectropterus* is similar to the sheldrakes in the femoral features listed for that tribe.

TRIBE AYTHYINI (POCHARDS). The femur of pochards is readily told from those of other diving ducks: (1) The trochanter in proximal view extends farther anteriorly. (2) The head in proximal view is smaller. (3) The medial side of the internal condyle is less flared laterally.

Metopiana, as indicated by other taxonomic criteria, is a pochard. The form of the femur indicates it is poorly specialized for diving. On criteria used to differentiate the femora of diving and nondiving ducks *Metopiana* resembles the nondivers, but it may be separated from nondivers as follows: (1) In lateral view the anterior edge of the condyles are more deflected. (2) The external and fibular condyles are produced distally. (3) The internal condyle is enlarged and flares medially to leave a distinct depression on the medial side of the shaft. (4) The posterior surface of the shaft possesses a raised ridge to the external condyle, and the portion of the shaft lateral to the ridge is depressed. (5) The head is directed more proximad, less laterad. *Metopiana*, of course, is separable from other pochards by the features used to separate the nondivers from the divers.

Netta, although closer to *Aythya* than is *Metopiana* in the form of the femur, also appears less specialized for diving than *Aythya*. The popliteal fossa is shallower and narrower, and the anterior portion of the trochanter is produced farther anteriorly.

TRIBES SOMATERIINI AND MERGINI (EIDERS AND SEA DUCKS). The femora of the remaining diving ducks, the eiders, sea ducks and stiff-tailed ducks, are very similar. A combination of the following features separates the more similar eiders and sea ducks from the stiff-tails: (1) The anterior ridge of the internal condyle is approximately equal in size to that of the external condyle. In stiff-tails the ridge of the external condyle is larger. (2) The fibular condyle is less flared laterally. (3) The pit for the tibialis anticus is more prominent than in the stiff-tails.

TRIBE SOMATERIINI (EIDERS). The following features of the femur tend to separate the eiders from the sea ducks: (1) The shaft in lateral view is straighter. Although varying with the genera, in sea ducks where the posterior curvature of the shaft is greater, when the anterior surface of the femur is placed on a plane the internal condyle is elevated from the plane (*Mergus* is an exception). In eiders the internal condyle typically touches the plane. (2) The anterior ridge of the internal condyle curves farther mediad as it extends distally. This feature is poorly developed in *Polysticta*. (3) The scar extending up the lateral surface of the shaft from the fibular condyle is shorter.

Lampronetta cannot be distinguished from *Somateria* by femoral characteristics, but *Polysticta* has several distinguishing features: (1) The anterior portion of the trochanter possesses a more prominent medially directed protuberance. (2) The fibular groove is narrower. (3) The ligamental attachment, on the medial surface of the internal condyle, is a more prominent projection. (4) The anterior ridge of the internal condyle is straighter, not flared as far mediad.

TRIBE MERGINI (SEA DUCKS). The two groups of genera of sea ducks established on the basis of other elements still hold with the femur, but the differences are less apparent: (1) In *Bucephala* and the mergansers the trochanter has more of the anterior edge inflected, and thus the notch between it and the head is narrower. In the other sea ducks more of the trochanter slopes away from the head as it passes anteriorly, only the tip is inflected, and the notch is correspondingly wider. (2) In *Bucephala* and the mergansers the fibular condyle, particularly in anterior view, appears to flare more from the shaft. This feature is especially good for separating *Clangula* and *Histrionicus* from *Bucephala*, but it is poor for the scoters.

Generic characters are distinct within the *Bucephala* and merganser group. In *Bucephala* (1) the shaft has much greater posterior

curvature, and (2) it is thinner. The least width, given as a percentage of the total length, varies from 7.1 to 8.0 percent. *Mergellus* (7.5) also has a thin shaft, but *Lophodytes* (8.3 to 9.2) and *Mergus* (7.9, 8.3 to 9.8) are much stouter.

In other femoral features *Mergellus* and *Lophodytes* are intermediate between *Bucephala* and *Mergus*. (1) The shaft is straighter, without the abrupt bend found in *Bucephala*. (2) The shaft is narrow, without the marked lateral compression found in *Mergus*. The least depth of the shaft, given as a percentage of the total length in *Mergellus* and *Lophodytes* (9.5 to 10.7), overlaps *Bucephala* (8.0 to 9.9), but is narrower than *Mergus* (11.0 to 12.6). *Mergellus* differs from *Lophodytes* in that the shaft is thinner and narrower. (1) The shaft width is 7.5 percent of the total length compared with a range from 8.3 to 9.2 percent on *Lophodytes*. (2) The shaft depth is 9.5 percent compared with a range from 9.8 to 10.7 percent in *Lophodytes*. The characteristics that distinguish the straight, stout, compressed femur of *Mergus* from those of the other three genera are all mentioned above.

The remaining four sea duck genera, *Melanitta*, *Oidemia*, *Histrionicus*, and *Clangula*, are very similar in the form of the femur. The shape of the shaft, however, divides them into two groups. *Melanitta* and *Oidemia* femora in lateral view show a most distinct posterior curvature at the point $\frac{2}{3}$ the distance down the shaft. In *Histrionicus* and *Clangula* the shaft is much straighter. When femora of the four genera are placed anterior surfaces down on a plane, the condyles almost touch the plane in *Histrionicus* and *Clangula*, whereas in *Melanitta* and *Oidemia* the condylar region is elevated more than 2 mm.

Only the relative shaft widths separate the remaining two pairs of these genera; in *Oidemia* this varies from 8.2 to 8.5 percent of the total length, whereas in *Melanitta* it ranges from 7.2 to 8.0 percent. In *Histrionicus* it measures 8.6 percent; in *Clangula* 7.8 to 8.2 percent.

TRIBE OXYURINI (STIFF-TAILED DUCKS). Although other elements of the stiff-tailed ducks are distinctive, only minor differences in the femur separate them from the eiders and sea ducks.

Heteronetta, the least specialized of the four available genera of stiff-tailed ducks, has the following femoral properties: (1) The anterior portion of the trochanter is enlarged. (2) The condyles have the outer surfaces more nearly parallel. (3) The shaft is thin (6.9 percent of the total length); in the other three genera the range is 8.1 to 10.1 percent. (4) The head is small. (5) The ridge extending up

the posterior surface of the shaft from the external condyle is reduced.

Nomonyx is also little specialized: (1) The anterior portion of the trochanter is larger than in *Oxyura* and *Biziura*, but smaller than in *Heteronetta*. (2) The internal condyle has the posterior portion directed more mediad. (3) The ridge extending up the posterior surface of the shaft from the internal condyle is reduced. (4) The shaft in lateral view is straighter, and lacks the distinct posterior flexure. In characteristics of the femur, *Nomonyx* looks less like *Oxyura* than does *Biziura*.

Biziura and *Oxyura* are highly specialized, but in different ways. (1) In *Biziura* the shaft is thicker, 10.1 percent of the total length; in *Oxyura* the range is 8.1 to 8.5 percent. (2) In *Biziura* the trochanter extends proximally well beyond the head, and its distomedial surface is swollen. (3) The posterior intermuscular line is indistinct, but the lobe near the midpoint is more prominent in *Biziura*.

Tibiotarsus

The tibiotarsus is a useful taxonomic element for certain waterfowl, but shows no distinguishing characteristics for others.

ANSERANATINAE

A few features, none of them striking, isolate the tibiotarsus of the primitive pied goose, *Anseranas*: (1) The rim of the internal condyle in medial view is more gently sloping and less extended posteriorly, and lacks the notch present in other waterfowl. (2) The posterior portion of the rim of the external condyle is gently sloping. (3) The posterior ends of the rims of both condyles are elevated from the shaft more than in other waterfowl. (4) The ligamental attachment is small. (5) The inner cnemial crest is almost straight, with little lateral deflection.

ANSERINAE

It is impractical to attempt to define the whistling ducks, swans, and geese as a unit with so poor a taxonomic element as the tibiotarsus.

TRIBE DENDROCYGNINI (WHISTLING DUCKS). A combination of the following features usually identifies *Dendrocygna*: (1) The condyles are almost parallel; in other waterfowl they diverge more as they extend anteriorly. (2) The external ligamental prominence is smaller. (3) The external condyle is little produced anteriorly, and thus appears circular in outline; in other waterfowl the outline is elliptical. (4) The fibular crest is wide towards the distal end.

TRIBE ANSERINI (SWANS AND GEESE). In swans and geese the lateral tip of the outer cnemial crest lacks the distally directed hook characteristic of other waterfowl. The two groups within the tribe can be separated rather easily. In the swans and *Coscoroba* the intermuscular line flares medially to reach the region of the ligamental attachment. In geese the line is straight and fails to reach the ligamental attachment. This feature possibly is correlated with the more terrestrial nature of the geese.

In *Branta* and *Nesochen* the inner cnemial crest is straighter, whereas in the other goose genera it is deflected towards the lateral side. A longer fibular crest, detected by Miller (1937), is useful for distinguishing *Nesochen* from the other geese.

ANATINAE

The Anatinae as a unit cannot be defined conveniently by characteristics of the tibiotarsus. Study of the element for the genera within the group indicates three primary sections: (1) sheldrakes; (2) dabbling ducks, perching ducks, and pochards; (3) eiders, sea ducks, and stiff-tailed ducks.

TRIBE TADORINI (SHELDRAKES). The sheldrakes have the proximal portion of the intermuscular line straight and removed from the anteromedial edge proximally, as in the true geese. In this way they differ from the other Anatinae. Their terrestrial habitat is suggested as a reason for this feature. *Tachyeres* is an exception; it resembles the dabblers.

The most obvious break in the characteristics of the tibiotarsi of the sheldrakes places *Cereopsis*, *Chloephaga*, and *Neochen* in one group, and *Alopochen*, *Tadorna*, and *Casarca* in another. The differences pertain to the distal condylar region: (1) The condyles are in line with the shaft in the first group, displaced medially in the other. (2) In the first group the internal condyle is essentially equal in anterior extent to the external condyle, in the second the internal condyle extends farther anteriorly.

The *Cereopsis* tibiotarsus has the hooked outer cnemial crest typical of the sheldrakes. It is intermediate between those of the sheldrakes and the true geese in the position of the intermuscular line. Perhaps of greatest significance are several unique features: (1) A pronounced ridge extends from the outer cnemial crest onto the anterior surface of the shaft, whose surface is convex; in other sheldrakes the anterior surface is virtually flat. (2) The inner cnemial crest has little lateral flexure of the proximal tip. (3) The external articular surface

has a much more prominent lobe, and the depression immediately anterior to it is much deeper. (4) The shelf medial to the external articular surface extends farther out over the posterior portion of the shaft. (5) The supratendinal bridge tapers toward the medial side, and its medial abutment is recessed from the medial ridge of the shaft. (6) The tubercle for the oblique ligament, situated lateral to the supratendinal bridge, is enlarged (Wetmore, 1943).

Chloëphaga and *Neochen* resemble the other sheldrakes and differ from *Cereopsis* in lacking the pronounced ridge on the anterior surface of the tibiotarsus. *Chloëphaga* and *Neochen* may be separated by the relative width of the shaft. The width, which was taken with the caliper legs parallel to the condyles, is reduced to a percentage of the length, which was taken with the exclusion of the cnemial crests. *Chloëphaga* varies from 4.9 to 5.2 percent; *Neochen* is 4.6 percent.

Alopochen forms a link between *Chloëphaga* and *Neochen* and *Tadorna* and *Casarca*. *Alopochen* differs from *Chloëphaga* and *Neochen* in that the internal condyle has its posterodistal rim curving gently to the shaft. In *Chloëphaga* and *Neochen* the rim extends farther posteriorly and then curves abruptly to the shaft. *Alopochen* differs from *Tadorna* and *Casarca* as follows: (1) The internal condyle has the anterior protuberance almost parallel to that of the external condyle. In *Tadorna* and *Casarca* the internal condyle flares medially. (2) The shaft possesses less medial curvature.

Tachyeres is distinguishable from other sheldrakes in that (1) the intermuscular line follows the anteromedial edge as in ducks other than sheldrakes; and (2) the condyles show greater medial deflection, with the external condyle extending farther distally and the internal condyle extending farther anteriorly, as in the section containing the dabbling ducks. In *Tachyeres* the internal articular surface extends farther posterolaterally than in other members of the dabbling-duck section. Correspondingly the articular surface is supported by a raised ridge on the shaft.

TRIBES ANATINI, CAIRININI, AND AYTHYINI (DABBLING DUCKS, PERCHING DUCKS, AND POCHARDS). In dabblers, perchers, and pochards the condyles of the tibiotarsus are displaced medially so that the external condyle obviously extends farther distad than the internal condyle. In addition the internal condyle tends to extend farther anteriorly than the external condyle. *Merganetta* is not well defined by these features.

TRIBE ANATINI (DABBLING DUCKS). *Chaulelasmus*, *Spatula*, and *Mareca* are not separable from *Anas* by qualitative features of the tibiotarsus, nor is *Callonetta*. The other genera available in my series, *Malaco-*

rhynchus, *Rhodonessa*, *Hymenolaimus*, and *Merganetta*, are distinctive. *Malacorhynchus* is most similar to the typical dabblers. My single specimen, which has the cnemial crests eroded away is distinguished by the enlargement of the ligamental attachment.

Rhodonessa has the following properties of the tibiotarsus: (1) The condyles are more in line with the shaft. (2) The internal condyle extends farther anteriorly, resembling *Netta*. (3) The inner cnemial crest is directed more proximad, less anteriorly, as in pochards. *Hymenolaimus* has the outer cnemial crest extending farther proximad, with the external edge directed more anteriorly, less laterad, and the shaft with a more distinct curvature, the medial side being concave. *Merganetta* has the greatest number of distinctive features: (1) The inner cnemial crest is directed more proximad, less anteriorly. (2) The outer cnemial crest has the laterodistal end directed more anteriorly, less laterad. (3) The condyles are almost equal in distal extent.

TRIBE CAIRININI (PERCHING DUCKS). Diagnostic features of a qualitative nature are not well developed in the tibiotarsus of perching ducks. Apparent differences between certain genera usually break down in series. *Plectropterus* is the most distinct genus assigned to the tribe; the external condyle is almost in line with the external edge of the shaft, a feature typical of the sheldrakes. *Cairina* has the condyles displaced farther medially than in most other perchers, and the shaft is robust, 5.9 to 6.7 percent of the length; the maximum in other genera is 5.7 percent in *Pteronetta*.

TRIBE AYTHYINI (POCHARDS). The posterior intercondylar sulcus tends to be wider in pochards than in dabbling and perching ducks, but no additional features of the tibiotarsus are diagnostic of the tribe. Within the tribe, *Metopiana* has the following distinguishing characteristics: (1) The outer cnemial crest is broader and directed farther laterad. (2) The shaft is more robust; the width varies from 5.6 to 6.0 percent of the length. In addition to these features, the shaft is markedly bowed, the medial surface being concave, but my three specimens are all from captive birds, in which bowing of certain elements including the tibiotarsus often occurs.

Netta and *Aythya* show closer resemblance to each other in the tibiotarsus than either does to *Metopiana*. In both genera the outer cnemial crest is narrower and directed more anteriorly, and the shaft is thinner, the width being usually less than 5.0 percent of the length. *Netta* can be distinguished from *Aythya* as follows: (1) The outer cnemial crest lacks the prominent terminal apex and its medial portion

is less deeply concave. (2) The inner cnemial crest is shorter. (3) The condyles are more in line with the shaft, less deflected medially.

TRIBES SOMATERIINI, MERGINI, AND OXYURINI (EIDERS, SEA DUCKS, AND STIFF-TAILED DUCKS). Three duck tribes, the eiders, sea ducks, and stiff-tailed ducks, compose a group in which the condyles of the tibiotarsus are typically equal in distal and anterior extent. *Heteronetta* and *Nomonyx* are exceptions and show certain resemblances to the nondivers.

TRIBES SOMATERIINI AND MERGINI (EIDERS AND SEA DUCKS). Eiders and sea ducks are similar and differ from the stiff-tailed ducks as follows: (1) The internal condyle is less extended anteromedially. (2) The external ligamental prominence is small and does not extend as far laterad from the external condyle.

TRIBE SOMATERIINI (EIDERS). The eiders differ from the sea ducks and also from the stiff-tailed ducks in the shape and direction of the outer cnemial crest, which is wider and directed more laterad, less anteriorly. *Polysticta* can be distinguished from *Somateria* and *Lampronetta* by one qualitative feature of the tibiotarsus; in *Polysticta* the condyles lie more nearly in line with the shaft. *Lampronetta* shows no significant differences from *Somateria*, as has been the case with other elements; in both the internal condyle is deflected farther medially.

TRIBE MERGINI (SEA DUCKS). The narrower, more posteriorly directed outer cnemial crest separates sea-duck tibiotarsi from those of the similar eiders. The usual break in the sea-duck genera is evident from the tibiotarsus. In *Bucephala*, *Lophodytes*, *Mergellus*, and *Mergus* the proximal edge of the outer cnemial crest is virtually a straight diagonal line. In *Melanitta*, *Oidemia*, *Histrionicus*, and *Clangula* the proximal rim of the outer cnemial crest is distinctly bent towards the inner cnemial crest as it nears the juncture of the two.

Bucephala and the mergansers are very similar in the appearance of the tibiotarsus. They differ slightly in additional details of the cnemial crests. In *Bucephala* the inner cnemial crest appears narrower in medial view and it extends proximally as a prominent peak. When the element is placed with the posterior surface, including both condyles, lying on a plane, the external articular surface extends farther laterad than the outer cnemial crest. In *Mergus* the inner cnemial crest is wider, and at its juncture with the outer crest it bends anteriorly. In the same view, in *Mergus* the outer cnemial crest usually extends farther laterad than the external articular surface. *Lophodytes* and *Mer-*

gellus are closer to *Mergus* in the width of the inner cnemial crest and in the lateral extent of the outer cnemial crest, but they are more like *Bucephala* in that the peak is directed farther proximad. *Lophodytes* generally has a wider shaft (5.2 to 5.8 percent of the length) than *Bucephala* (4.8 to 5.4), whereas *Mergellus* is thinner (5.0) than *Lophodytes*.

Clangula and *Histrionicus* differ slightly from the scoters in that the enlarged external ligamental prominence protrudes beyond the rim of the external condyle. In *Histrionicus*, but not in *Clangula*, the anteroproximal portion of the external condyle is thicker, and in lateral view it appears more circular, less elliptical. No significant differences were noted between the tibiotarsi of *Melanitta* and *Oidemia*.

TRIBE OXYURINI (STIFF-TAILED DUCKS). The stiff-tailed ducks are separable from the eiders and sea ducks by the following properties of the tibiotarsus: (1) The internal condyle overhangs the anteromedial edge of the shaft to a greater extent than in the other two tribes. (2) The external ligamental prominence is enlarged so that it extends well lateral of the condyle.

Heteronetta is the least specialized of the four genera available. Its tibiotarsus appears intermediate between those of the other stiff-tails and those of the nondivers: (1) The condyles are displaced farther medially than in nondiving ducks, but not to the extent found in other divers. (2) The external condyle extends farther distad than the internal condyle as in the nondivers. (3) The amount of anterior overhang of the internal condyle is greater than in the nondivers, but less than in other stiff-tails. (4) The outer cnemial crest is directed more laterad, less anteriorly. In this respect *Heteronetta* resembles nondiving ducks, and not stiff-tails. (5) The shaft is thinner (4.1 percent of length) than in other stiff-tails (5.0 to 6.4 percent).

Nomonyx appears less specialized for diving than either *Oxyura* or *Biziura*. Its tibiotarsus has the following characteristics: (1) The external condyle extends farther distad as in the nondivers and *Heteronetta*. (2) The external ligamental prominence is obscure in anterior view. (3) The direction of the outer cnemial crest is intermediate between *Heteronetta* and the other stiff-tails. (4) The inner cnemial crest lacks the long ridge found in the more specialized genera of the tribe. (5) The shaft width (5.4 percent of length) is similar to that of *Oxyura* (5.0 to 5.4), thicker than *Heteronetta* (4.1), and thinner than *Biziura* (6.4).

Oxyura and *Biziura* share the following features of the tibiotarsus: (1) The distal extent of the two condyles is equal or subequal. (2) The

external ligamental prominence is obvious in anterior view. (3) The outer cnemial crest is directed more anteriorly than in the two less specialized stiff-tails. (4) The inner cnemial crest possesses a ridge that extends distally beyond the proximal end of the fibular crest.

Although the tibiotarsi of *Biziura* and *Oxyura* are quite similar, at least three good qualitative characters separate them. (1) In *Biziura* the shaft is thicker, 6.4 percent of the length, as opposed to a maximum of 5.4 percent in the other genera. (2) In *Biziura* the shaft is virtually straight in lateral view. In *Oxyura* and *Nomonyx* a distinct curvature makes the posterior side concave. (3) In *Biziura* the proximal edge of the outer cnemial crest is virtually a straight line; in *Oxyura* it is deeply concave.

Tarsometatarsus

The tarsometatarsus is the best taxonomic element of the leg. The many articulating surfaces partly account for its usefulness. As with other leg bones, adaptive modifications frequently obscure the more basic features.

ANSERANATINAE

Anseranas has many distinctive tarsometatarsal features: (1) The median calcaneal ridge of the hypotarsus is greatly enlarged. In all other waterfowl the median ridge is the largest of the four, but it is not proportionately as large as in *Anseranas*. (2) The facet for metatarsal I is deep and prominent, possibly as a reflection of a stronger hind toe useful for perching; other waterfowl show virtually no evidence of this facet. (3) The shaft in lateral view is thin. In other waterfowl the shaft is thicker, especially distally. (4) The wing of the trochlea for digit II is greatly enlarged. (5) The trochlea for digit II lacks a pronounced median groove. (6) The external rim of the groove of the trochlea for digit IV is extended posteriorly.

ANSERINAE

One feature of the tarsometatarsus indicates a close relationship between the whistling ducks and the swans and geese. The trochlea for digit II has a prominent lobe on the anterior side at the point of the most proximal extent of the articulating surface.

TRIBE DENDROCYGNINI (WHISTLING DUCKS.) The following distinguishing characteristics of the tarsometatarsus of *Dendrocygna* seem most important: (1) The anteromedial edge is sharply ridged. (2) The internal cotyla is deeply cupped by a proximal extension of the internal edge. (3) The shaft is rather uniform in width. (4) The trochlea for

digit II lacks a prominent median groove, and the internal edge has a pit that extends distally to bisect the articular surface. *Anseranas* is the only other anatid without a groove in the second trochlea.

TRIBE ANSERINI (SWANS AND GEESE). The tarsometatarsi of swans and geese show a marked resemblance to those of sheldrakes. From waterfowl other than sheldrakes, the swans and geese can be separated by the following tarsometatarsal features: (1) The trochlea for digits II and IV, and particularly II, are spread. (2) The shaft is narrow in anterior view, and the external edge has a prominent curve. In other waterfowl the external margin is usually a straighter line onto the trochlea for digit IV.

The following additional features aid in separating swans and geese from sheldrakes: (1) The trochlea for digit II in internal view is directed more posteriorly and proximally. (2) The distal foramen in posterior view appears more nearly perpendicular to the shaft. True swans differ slightly from geese in that the groove in the trochlea for digit IV continues anteroproximally to the most proximal part of the trochlea. In geese the groove is interrupted by a swelling. *Coscoroba* has a swelling, but this is smaller than in geese.

Individual differences and the size differences permit the separation of many swan specimens, but consistent criteria of a qualitative nature are nonexistent. Howard (1946) remarks that in the swans generic distinctions are less apparent in the tarsometatarsus than in some of the other elements, and my observations agree. Even *Coscoroba* cannot be satisfactorily characterized from this element. In geese, as opposed to other waterfowl, the trochlea for digit IV has a prominent swelling at the proximal end of the anterior surface of the trochlear groove.

The present series of goose tarsometatarsi supports the statement made by Miller (1937) that no one feature serves to differentiate *Branta*, *Anser*, or *Chen*. It is even difficult to identify tarsometatarsi of these three genera by a combination of characters, although Miller feels this can be done. With *Eulabeia* and *Cynopsis* included the task is even more difficult. The characters for *Branta*, *Anser*, and *Chen*, according to Miller, are as follows: *Branta* shows an inflation of the lateral margin just distal to the head, which is less pronounced in *Anser* and usually is lacking in *Chen*. In *Branta* the trochlea for digit II joins the shaft of the bone at a more abrupt angle and is shorter than in *Anser* and markedly shorter than in *Chen*. *Branta nigricans* is not typical of the genus in this respect.

In *Anser* the median side of the hypotarsus makes a less acute angle with the remainder of the medial surface; the tendinal groove of the anterior surface is more prominent, and the entire bone is slightly more stocky than in *Branta* or *Chen*. The tarsometatarsus of *Anser* averages wider (7.9 to 9.0 percent of total length) than in *Branta* (6.3 to 8.0) and *Chen* (6.6 to 7.9), but it is difficult to substantiate any of the other characters listed above. Furthermore, no characters were found for *Eula-beia* or *Cygnopsis* other than that they are both robust with widths 7.9 and 9.1 to 10.8 percent of the total length, respectively. The extremely wide tarsometarsi in the available specimens of *Cygnopsis* are possibly a reflection of the many centuries of domestication of certain strains of the species.

The tarsometatarsus of *Nesochen* is distinctive. The outer margin of the shaft is straighter than in any other goose, and the shaft is wide (8.0 percent of total length). In addition, the trochleae are directly in line with the shaft. Miller states that this latter feature is to be associated with running habits.

Miller found the tarsometatarsus of *Philacte* markedly different from those of *Anser*, *Chen*, *Branta*, and *Nesochen*. The plantar surface, just proximal to the trochlea, is stated to be much flatter and broader and the trochlea for digit II more sharply deflected medially. The one specimen in the present series, unfortunately poorly preserved, does not have these features.

ANATINAE

Although the Anatinae are easily distinguished from *Anseranas* and *Dendrocygna* through the presence of a prominent groove in the trochlea for digit II of the tarsometatarsus, it is difficult to separate them from the swans and geese with this element. Only two features, both weak, can be listed: (1) The trochlea for digit II in internal view is slightly more in line with the other two instead of being deflected more posteroproximad. (2) The distal foramen in posterior view is more oblique, less nearly perpendicular to the shaft.

The shape and position of the trochlea for digit II divides the Anatinae into two groups, the nondiving sheldrakes, dabbling ducks, and perching ducks, and the diving pochards, eiders, sea ducks, and stiff-tailed ducks. In the nondivers the trochlea for digit II is shorter (length measured parallel to the shaft), and it extends farther distad. The median ridge of this trochlea extends distally beyond the level of proximal extent of the facet of the trochlea for digit III, as seen in ventral view. In the divers the distal end of the median ridge of the trochlea for digit II fails to reach the level of the proximal end of the facet

for digit III. Six of the 43 available genera do not fit the system, namely: *Tachyeres* of the sheldrakes, *Merganetta* of the dabblers, *Metopiana* of the pochards, *Polysticta* of the eiders, and *Heteronetta* and *Nomonyx* of the stiff-tails. These forms are discussed under the tribes to which they are assigned by Delacour (1954, 1956, 1959). Obviously a correlation between function and structure is involved here, but several of the tribes can be characterized as units on structures of more deep-seated phylogenetic significance.

TRIBE TADORNINI (SHELDRAKES). The sheldrakes resemble the geese in the form of the tarsometatarsus and can be separated from other Anatinae because the trochleae for digits II and IV, and particularly the former, are spread, and the shaft is narrow in anterior view, with the external edge displaying a prominent curve out onto the trochlea for digit IV. Sheldrakes differ from the swans and geese by the characters listed under that tribe.

Within the sheldrake tribe the features of the tarsometatarsus are most useful taxonomically. The relative distal extent of the trochlea for digit II separates the tribe into two groups: In *Cereopsis*, *Chloëphaga*, and *Neochen* the trochlea for digit II lies farther distad; it extends beyond the base of the external intertrochlear notch. In *Alopochen*, *Tadorna*, *Casarca*, and *Tachyeres* the trochlea for digit II lies more proximad; it does not extend beyond the base of the external intertrochlear notch. *Cereopsis* and *Tachyeres*, the two genera that from other elements seem more closely related to other tribes, are the most widely separated, and *Neochen* is nearest to being intermediate between the two groups.

Cereopsis differs from all other sheldrakes as follows: (1) The intercotylar prominence in anterior view is large and essentially symmetrical in outline. In other sheldrakes the prominence is skewed on the external side, to make the internal cotyla appear deeper. (2) The trochlea for digit II in anterior view has the groove extending farther proximad, and (3) it has a more prominent proximomedial swelling.

Neochen differs from *Chloëphaga* in that the shaft and trochlea are thinner in anterior view; the shaft measures 6.7 percent of the total length. Seven specimens of *Chloëphaga* range from 7.2 to 7.9 percent.

The tarsometatarsi of *Tadorna*, *Casarca*, and *Alopochen* are all rather similar in form. No useful features were found for separating *Casarca* from *Tadorna*, but some allow for separating *Alopochen* from the others. In *Alopochen*: (1) The shaft is thinner, its width ranging from 6.8 to 7.6 percent of the total length in 3 specimens; in 9 specimens of *Tadorna* and *Casarca* the range is from 7.8 to 8.2 percent. (2)

The trochlea for digit II extends farther ventrad and has the proximal edge sloping gently to the shaft; in *Tadorna* and *Casarca* the trochlea is situated more mediad, and the proximal edge drops off abruptly to the shaft.

Tachyeres is easily separated from other sheldrakes: (1) The trochlea for digit II is longer and lies more proximad; the distal tip does not extend beyond the proximal extent of the trochlea for digit III. (2) The shaft is robust, 10.8 percent of the length; the thickest shaft recorded for the other sheldrake specimens measures 8.2 percent (*Tadorna*). (3) The lobe on the anterior side at the point of the most proximal extent of trochlea for digit II is small. A prominent lobe in this position is typical of sheldrakes.

TRIBE ANATINI (DABBING DUCKS). The dabbling and perching ducks cannot be separated by tarsometatarsal features. Differences between the genera are discussed within the arrangement of Delacour (1956, 1959), although some intertribal comparisons are made.

Chaulelasmus and *Spatula* are indistinguishable from *Anas*, but the *Mareca* tarsometatarsus is distinct: (1) Its shaft is more robust at the proximal end just below the cotylar area. (2) Its anterolateral edge is less prominent. In anterior view the shaft appears to taper more because of these two features. (3) In *Mareca* the trochleae are usually smaller.

Malacorhynchus differs slightly from the typical dabblers in that the trochleae are spread more laterally. *Callonetta* has a thicker and more elevated proximal portion of the anteromedial ridge in the one available specimen. Whether or not this feature would remain valid in a series remains questionable. *Hymenolaimus*, although not differing markedly from typical dabblers can be distinguished as follows: (1) The cotylae form almost a right angle with the anterior surface. In other dabblers and in the perchers the angle is smaller. (2) In distal view the posterior rims of the trochleae converge. (3) The trochlea for digit II in posterior view flares more medially.

The tarsometatarsus of *Merganetta* is the most distinct found in the dabbling ducks. The median ridge of the trochlea for digit II does not quite reach the level of the proximal end of the facet for digit III, and thus it resembles that of the divers. But the trochlea for digit II is shorter, and the shaft of the bone is thinner (7.3 to 8.0 percent of total length) than is typical of the divers. It is even thinner than in all the other members of the dabbling ducks (8.3 to 11.0 percent). An additional character isolates *Merganetta* among the dabblers: the antero-medial edge of the shaft is much lower than the anteroexternal edge.

The tarsometatarsi of *Cairina* and *Pteronetta* can be distinguished from those of other perching ducks and from the dabbling ducks by the shape of the middle groove of the hypotarsus. In these two genera it is shallower than the grooves on either side, and the floor of the groove does not reach the shaft. *Cairina* is unique because of its robust shaft with a width/length ratio of 12.5 to 12.6 percent. The middle groove of the hypotarsus is by far the shallowest in this form. *Pteronetta* has a slimmer shaft, 10.9 percent of the total length, and the groove, though shallow, is deeper than in *Cairina*.

Two perchers, *Amazonetta* (7.9 percent of total length); and *Plectropterus* (7.7 to 7.8 percent) have thin shafts. Other than in *Merganetta* the next thinnest shaft recorded in either the perchers or the dabblers measures 8.0 percent. The fact that the shaft in *Amazonetta* is relatively much thinner than in typical dabblers (minimum 8.3 percent) speaks for its recognition as a genus apart from *Anas*.

Qualitative features of the trochlea separate the large tarsometatarsus of *Plectropterus* from the small one of *Amazonetta*. In *Plectropterus* the trochleae are directed medially and, the trochlea for digit II extends farther posteriorly. *Sarkidiornis* is unique in that it has a massive outer trochlea; the lateral edge of the shaft swings out as a ridge to meet the trochlea.

Chenonetta has a tarsometatarsus similar in form to that of *Aix* and *Dendronessa*, but it is considerably longer and proportionately slimmer. The width varies from 8.0 to 8.9 percent of the total length in two specimens. *Dendronessa* (5 specimens) varies from 9.3 to 10.2 percent, and *Aix* (11 specimens) from 9.7 to 11.3 percent.

Size separates the four remaining genera into two groups, the larger *Aix* and *Dendronessa* and the smaller *Nettapus* and *Cheniscus*. None of these is separable on qualitative features of the tarsometatarsus.

TRIBE AYTHYINI (POCHARDS). The tarsometatarsus of pochards is generally thicker than in eiders (width 9.5 to 12.0 and 8.5 to 9.8 percent of length, respectively), and the external edge is almost straight instead of flaring sharply to meet the outer edge of the spread trochleae, as in eiders. It differs from that of stiff-tailed ducks in that the inner calcaneal ridge is proportionately smaller, and the shaft in medial view curves up to meet the trochleae. The greatest similarity is to that of the sea ducks, from which it can be distinguished as follows: (1) The shaft is wide proximally and with little lateral compression. (2) The trochlea for digit III in posterior view forms a slight angle with the shaft, so that the groove is directed laterally as it passes proximally.

(3) The trochlea for digit II has a smaller gap between its medial ridge and the proximal end of the facet of the trochlea for digit III.

Within the tribe, *Metopiana* and *Netta* differ from *Aythya* in that the trochlea for digit II in medial view is curved in outline. In *Aythya* the posteroproximal tip is extended proximally, and thus a distinct angle interrupts the curved outline. The median ridge of the trochlea for digit II surpasses the level of the proximal extent of the facet for digit III in *Metopiana* and indicates the genus is less specialized for diving than either *Netta* or *Aythya*.

TRIBE SOMATERIINI (EIDERS). The eiders can be separated from other waterfowl quite easily by features of the tarsometatarsus. The shaft is thinner (8.5 to 9.8 percent of total length) than in most other divers. The large trochleae are spread, and the external edge of the shaft curves markedly in order to reach the spread trochlea for digit IV. In other diving ducks the external edge of the shaft is virtually a straight line.

The tarsometatarsus of the one available specimen of *Polysticta* does not show a space between the levels of the medial rim of the trochlea for digit II and the posterior extent of the facet for digit III, because the facet tapers gradually to a point; this may not be typical of the genus. The trochlea for digit II is long, as is typical of divers. The other two eider genera, *Somateria* and *Lampronetta*, possess no qualitative features to separate them.

TRIBE MERGINI (SEA DUCKS). The external edge of the tarsometatarsus of sea ducks shows very little curvature, in distinction to that of the eiders. The inner calcaneal ridge is not so enlarged as in the stiff-tailed ducks, and the shaft in medial view curves up to meet the trochleae. The following several tarsometatarsal features in combination should separate the sea ducks from the pochards: (1) The shaft is laterally compressed and frequently the narrowest width is through a prominent groove that lies near the proximal end on the median side. (2) The trochlea for digit III in posterior view is essentially parallel with the shaft. (3) The gap between the described parts of the trochleae for digits II and III is wider.

One feature suggests separation of the sea-duck genera into the two usual groups: In *Bucephala* and the mergansers the external edge of the outer trochlea in anterior view is straight or inflected; in *Histrionicus*, *Clangula*, and the scoters the external edge is concave and continuous with the arc of the shaft.

Bucephala can be separated from the mergansers by the size and direction of the distal foramen. In posterior view particularly, the dis-

tal foramen is larger and more perpendicular to the shaft. In the mergansers the smaller foramen lies at a more oblique angle to the axis of the shaft. In addition the shaft of *Bucephala* tends to show greater curvature, and the anterolateral edge is more elevated.

The three merganser genera are distinguishable by the relative width of the shaft. In the larger *Mergus* the width varies from 7.7 to 9.1 percent of the total length; *Mergellus* is intermediate with a figure of 9.8 percent; whereas *Lophodytes* is quite stout, ranging from 10.6 to 11.7 percent. No good qualitative features separate the tarsometatarsae of *Histrionicus*, *Clangula*, and the scoters, *Melanitta* and *Oidemia*. The one available specimen of *Histrionicus* has a lower intercotylar prominence, a smaller distal foramen, and a less elevated anteromedial edge to the shaft; perhaps some of these are valid features.

TRIBE OXYURINI (STIFF-TAILED DUCKS). The tarsometatarsus of stiff-tailed ducks can be recognized without great difficulty: (1) The inner calcaneal ridge is enlarged more than in other Anatinae. (2) In median view the anterior surface of the shaft is essentially at the same level as the trochleae; in other divers the shaft curves anteriorly to the elevated trochleae. (3) The raised anterolateral edge of the shaft is virtually straight out onto the trochlea for digit IV. (4) The trochlea for digit IV in distal view has the inner ridge higher and the outer ridge anteroproximally reduced. (5) The intercotylar prominence has a deeper anteroexternal notch. (6) The shaft is wide, 10.8 to 16.3 percent of the total length.

The tarsometatarsi of *Heteronetta* and *Nomonyx* have no space between the levels of the median rim of the trochlea for digit II and the proximal extent of the facet for digit III. Features 1, 3, 5, and 6 above, however, are present in these two less specialized genera. The narrower width (10.8 percent of the length) of the shaft and the lack of a space between the levels of the named parts of the trochleae for digit II and III identify the tarsometatarsus of *Heteronetta*.

Nomonyx (12.6) and *Oxyura* (11.6 to 12.8) are similar in the relative width of the shaft, but *Nomonyx* has no space between the levels of the named parts of the trochleae for digits II and III. *Biziura* is very similar in the form of the tarsometatarsus, but the shaft is much stockier with the width 16.3 percent of the total length.

Pelvis

The pelvis is of little use for classifying the waterfowl. This element displays remarkable similarity throughout the family, and those differences that appear are in the nature of individual variation.

One ratio proved somewhat useful, the least width through the acetabula divided by the length of the element. The length was measured from the most anterior point on the centrum of the first vertebra to the posterior end of the ilium or ischium.

ANSERANATINAE

Anseranas, as noted by Miller (1919), has the most distinct pelvis of all the waterfowl: (1) The posterior iliac crest is broad, and sharply angled at a ridge running posteriad from the antitrochanter, with the larger portion lying in the horizontal plane. (2) The posterior edge of the ilium is much shorter than the ischium. (3) The width through the acetabula is 28.0 to 31.5 percent of the length, greater than in any of the superficially similar Anserinae, in which the range is from 15.7 to 26.9 percent.

ANSERINAE

The Anserinae as a unit cannot be characterized by the structure of the pelvis.

TRIBE DENDROCYGNINI (WHISTLING DUCKS). One feature of the pelvis in *Dendrocygna* and *Anseranas* is found nowhere else in the waterfowl. The ilium is distinctly shorter than the ischium, with the posterior border of the former lying considerably anterior to the posterodorsal corner of the latter. In other waterfowl the posterior edges of the two bones form an oblique line, usually with a notch where the two bones fuse.

TRIBE ANSERINI (SWANS AND GEESE). The relative width through the acetabula separates the true swans from the geese. The range for 36 swan specimens is 15.7 to 19.4 percent of the length; for 34 goose specimens the range is 19.8 to 26.9 percent. *Coscoroba* (23.0) falls with the geese, but between the averages for the swans (17.56) and the geese (24.19). The relatively greater width of the goose pelvis may be related to the more terrestrial habits of these birds.

ANATINAE

The pelvis is too poor an element taxonomically to allow for characterizing the diverse subfamily of ducks.

Among the genera assigned to the sheldrakes *Cereopsis* has the relative width through the acetabula (21.8 to 22.5 percent) below the range for the other, more typical, members of the tribe (22.9 to 32.9), and within the range of true geese. *Chloëphaga*, *Neochen*, and *Alopo-*

chen (22.9 to 28.3 percent) have relatively wider pelves than *Tadorna* and *Casarca* (28.9 to 32.9 percent).

Within the remaining Anatinae the pelves are usually narrower in the diving species than in the nondivers. For example, the average relative width through the acetabula for 82 specimens of nondivers, *Anas*, *Chaulelasmus*, *Mareca*, and *Spatula*, is 31.92 percent; in 67 specimens of the diving *Aythya* the average is 24.46 percent. *Rhodonessa* (27.7) and *Metopiana* (27.66) are intermediate in the width of the pelvis; *Rhodonessa* seldom dives and *Metopiana* dives less efficiently than *Aythya* according to Delacour (1956, 1959).

Hymenolaimus, although a diving species, has a rather wide pelvis (29.6 percent), whereas in the torrent duck, *Merganetta*, it is very narrow (22.7 to 23.6 percent).

Although the eiders are considered by Delacour (1959) to be closely allied to the dabblers, the pelvis is narrow. Seven specimens of *Somateria* and one of *Lampronetta* average 24.53 percent. This average lies outside the range of all dabbling ducks except *Merganetta*, but within the wide range recorded for the sea ducks. *Polysticta* has a relative width of 27.0 percent, beyond the range obtained for the large eiders (22.5 to 26.1 percent), and near the figures for *Histrionicus* (28.5 percent) and *Clangula* (24.4 to 26.8 percent).

The relative width through the acetabula is not useful for separating sea ducks from other Anatinae, nor does it support the intratribal groups (*Bucephala* and the mergansers, versus *Histrionicus*, *Clangula* and the scoters) that, from other evidence, seem natural. Within the first of these groups, *Bucephala* (26.4 to 29.9) and *Lophodytes* (22.8 to 30.0) have wide pelves in contrast with the narrow pelves of *Mergus* (16.2 to 20.7) and *Mergellus* (21.6). In the other group the wide pelves of *Histrionicus* (28.5) and *Clangula* (24.4 to 26.8) contrast with the narrow pelves of *Melanitta* (19.3 to 23.5) and *Oidemia* (15.4, 18.6 to 20.8).

On the basis of pelvic structure, as with several other structural elements discussed above, the stiff-tailed ducks are the most distinct group within the Anatinae. The pelvis is very narrow (14.7 to 21.1 percent) and overlaps that of only a few genera from other tribes. *Nomonyx* (19.5 to 20.4 percent) falls within the range of *Oxyura* (17.4 to 21.1), but it averages significantly broader, 19.91 compared with 18.96 percent, respectively. *Biziura* has the narrowest pelvis of any species of waterfowl (14.7 percent).

Vertebral Column

Verheyen (1955) bases his classification of the waterfowl primarily on the number of vertebrae in the various regions of the column. Although the present study is concerned mainly with qualitative features of the appendicular skeleton, counts of vertebrae in addition to those of Verheyen are presented in table 1. It is interesting that many of the changes suggested by the present study are supported by these data.

The four regions in the column—cervical, thoracic, sacral, and caudal—are defined as in Verheyen.

TABLE 1. VERTEBRAL COUNTS IN WATERFOWL

Species	Cerv.	Thor.	Sacr.	Caud.	Total	Auth.*
ANSERINATINAE						
<i>Anseranas semipalmata</i>	20	5	16	6	47	(V1)
	19	5	17	6	47	(W1+)
ANSERINAE						
Whistling Ducks						
<i>Dendrocygna eytoni</i>	18	5	15	7	45	(V1)
<i>arcuata</i>	18	5	15	7	45	(V1)
<i>bicolor</i>	17	5	15-16	7-8	44-46	(V4)
<i>arborea</i>	17	5	15-16	7-8	44-45	(V3)
	17	5	15-16	7	44-45	(W2)
<i>javanica</i>	17	5	15	8	45	(V1)
	17	5	15	7	44	(W2)
<i>viduata</i>	17	5	15-16	7-8	44-46	(V8)
	17	5	14	8	44	(W1)
<i>autumnalis</i>	17	5	16	6-7	44-45	(V2)
	17	5	15	7	44	(W2)
Swans						
<i>Coscoroba coscoroba</i>	21	5	18-19	6-7	51-52	(V5)
<i>Chenopsis atratus</i>	25	4-5	20-22	8-10	59-61	(V8)
<i>Cygnus olor</i>	24-25	5-6	20-21	9	59-60	(V7)
<i>melancoriphus</i>	22-24	5-6	18-20	8-9	55-57	(V9)
<i>Olor cygnus</i>	24	5	20	7-8	56-57	(V2)
	24	5	21	9	59	(W2)
<i>buccinator</i>	23	5	21	8	57	(W1)
<i>columbianus</i>	23	5	20	9	57	(V1)
	22-23	5	19-20	7-8	54-56	(W5)

Continued

* Counts by Verheyen (1955) are indicated by a V followed by the number of specimens examined. Additional counts are indicated by a W.

TABLE 1 (continued)

Species	Cerv.	Thor.	Sacr.	Caud.	Total	Auth.
Geese						
<i>Cygnopsis cygnoid</i>	19	5	18	7	49	(V1)
	19	5	17-19	7	48-50	(W2)
<i>Anser anser</i>	18	5	17	7	47	(V1)
	19	5	17	8	49	(W1)
<i>albifrons</i>	19	5	19	6-7	49-50	(V2)
	19	5	18	7	49	(W1)
<i>erythropus</i>	19	5	18	6-7	48-49	(V3)
<i>fabilis</i>	20	5	19	7	51	(V1)
	20	5	19	?	?	(W1)
<i>brachyrhynchus</i>	19	5	18	8	50	(V2)
<i>Chen caerulescens</i>	19	5	18-19	6-7	48-50	(V3)
	18	5	19	7	49	(W1)
<i>hyperborea</i>	19	5	19	6	49	(W1)
<i>rossi</i>	19	5	17	7	48	(V1)
	19	5	17-18	7-8	48-50	(W4)
<i>Philacte canagica</i>	19	5	18	7	49	(V1)
	19	5	17	7	48	(W1)
<i>Eulabeia indiana</i>	19	5	19	7	50	(V1)
	19	5	18	7	49	(W1)
<i>Nesochen sandwicensis</i>	19	5	19	7	50	(V1)
	20	5	19	7	51	(W1)
<i>Branta canadensis</i>	20	5	18	7-8	50-51	(V1?)
	19-20	5	19-20	6-8	50-52	(W4)
<i>leucopsis</i>	19	5	17	7-8	48-49	(V2)
<i>ruficollis</i>	19	5	17	7-8	48-49	(V4)
	19	5	17	8	49	(W1)
<i>bernicla</i>	20	5	18	7-8	50-51	(V3)
	20	5	18	8	51	(W3)
ANATINAE						
Sheldrakes						
<i>Cereopsis n.hollandiae</i>	19-20	5	16-17	7	48	(V2)
	19	4	18-19	6-7	48	(W2)
<i>Chloëphaga melanoptera</i>	16	5	17-18	7-8	46	(W4)
<i>poliocephala</i>	17	5	17	6	45	(V1)
<i>picta</i>	16	5	17	6-7	44-45	(V6)
<i>hybrida</i>	16	5	16	6	43	(V1)
<i>Neochen jubata</i>	17	4	17	7	45	(V1)
	16	4-5	17	7	45	(W1+)
<i>Alopochen aegyptiaca</i>	16	5	17-18	7-8	45-46	(V5)
	16	5	18	7	46	(W1)

Continued

TABLE 1 (continued)

Species	Cerv.	Thor.	Sacr.	Caud.	Total	Auth.
<i>Casarca tadornoides</i>	17	5	18	7	47	(V1)
	17	5	18	8	48	(W1)
<i>variegata</i>	16-17	5	17-18	7	45-47	(V5)
	16-17	5	17	7-8	46	(W2)
<i>cana</i>	16	5	18	7	46	(V3)
	16-17	5	18	8	47-48	(W2)
<i>ferruginea</i>	16	5	17	7	45	(V3)
<i>radjah</i>	16	5	16	7	44	(V1)
<i>Tadorna tadorna</i>	17	5	17	7	46	(V6)
<i>Tachyeres pteneres</i>	16	5	17	8	46	(V1)
	16	5	17	9	47	(W1)
Dabbling Ducks						
<i>Anas platyrhynchos</i>	16	5	16-17	7-8	45-46	(V4)
<i>fulvigula</i>	16	5	17	7	45	(V1)
	16	5	16-18	7-8	44-46	(W6)
<i>rubripes</i>	16	5	16-17	7-9	45-47	(W5)
<i>poecilorhyncha</i>	16	5	16	8	45	(V2)
	16	5	16	8	45	(W1)
<i>superciliosa</i>	16	5	17	7	45	(V1)
<i>luzonica</i>	16	5	16	?	?	(W1)
<i>melleri</i>	16	5	16	8	45	(W1)
<i>undulata</i>	16	5	16	7-8	44-45	(V2)
	16	5	16	8	45	(W1)
<i>castanea</i>	16	5	16	7	44	(W2)
<i>flavirostris</i>	16	5	15-16	7-8	43-45	(V3)
<i>crecca</i>	16	5	16	7	44	(V9)
	16	5	15	7-8	43-44	(W2)
<i>formosa</i>	16	5	16	7	44	(W1)
<i>falcata</i>	16	5	17	7	45	(W1)
<i>Chaulelasmus streperus</i>	16	5	17	7	45	(V1)
	16	5	17	7-8	45-46	(W4)
<i>Mareca penelope</i>	16	5	17	7	45	(V5)
	16	5	16-17	7-8	44-46	(W10)
<i>americana</i>	16	5	18	7	46	(V1)
	16	5	17	7	45	(W3)
<i>sibilatrix</i>	16	5	17-18	8	46-47	(V3)
	16	5	17	7	45	(W1)
<i>Anas bahamensis</i>	16	5	16	7-8	44-45	(V2)
	16	5	15-16	7-8	43-45	(W2)
<i>spinicauda</i>	16	5	16	8	45	(V1)
<i>acuta</i>	17-18	5	17	7	46-47	(V2)
	17-19	5-6	16-17	7-8	44-48	(W12)

Continued

TABLE 1 (continued)

Species	Cerv.	Thor.	Sacr.	Caud.	Total	Auth.
<i>Anas erythrorhynchos</i>	16	5	16	7	44	(V1)
<i>angustirostris</i>	16	5	16	7	44	(V1)
<i>versicolor</i>	16	5	15-16	8	44-45	(V3)
<i>querquedula</i>	16	5	16	7	44-45	(V4)
<i>discors</i>	16	5	16	7	44	(V1)
	16	5-6	15-17	7	44-45	(W5)
<i>cynoptera</i>	16	5	16	8	45	(V3)
	16	5	15-16	7-8	43-45	(W3)
<i>Spatula platalea</i>	16	5	17	7	45	(V1)
	16	5	16	8	45	(W1)
<i>clypeata</i>	16	5	16	7	44	(V4)
	16	5	16-17	7	44-45	(W2)
<i>Callonetta leucophrys</i>	16	5	15	8	44	(V1)
	16	5	15	8	44	(W1)
<i>Malacorhynchus</i>						
<i>membranaceus</i>	16	5	15	7	43	(V1)
	?	?	15	7	?	(W1)
<i>Hymenolaimus</i>						
<i>malacorhynchus</i>	16	5	17	7	45	(V1)
	16	5	16	7	44	(W1)
<i>Merganetta armata</i>	16	5	16	7	44	(V1)
	16	5	16	8	45	(W1+)
<i>Stictonetta naevosa</i>	18	5	17	7	47	(V1)
<i>Rhodonessa</i>						
<i>caryophyllacea</i>	17	5	16	8	45	(V1)
	17	5	17	?	?	(W1)
Pochards						
<i>Netta rufina</i>	17	5	17	7	46	(V2)
	17	5	17	8	47	(W2)
<i>Metopiana peposaca</i>	17	5	17	7-8	46-47	(V2)
	17	5-6	16-17	7-8	46-47	(W3)
<i>Aythya valisineria</i>	17	5	17	7	46	(W3)
<i>ferina</i>	17	5	17	8	47	(V5)
	17	5	16	8	46	(W1)
<i>americana</i>	17	5	17	7	46	(V1)
	17	5	17-18	7-9	46-48	(W4)
<i>nyroca</i>	17	5	17	7-8	46-47	(V3)
	17	5	16	8	46	(W1)
<i>collaris</i>	17	5	17	8	47	(V1)
	17	5	16-17	7-8	45-47	(W7)
<i>fuligula</i>	17	5	17-18	7-8	46-48	(V4)
	17	5	17	8	47	(W1)

Continued

TABLE 1 (continued)

Species	Cerv.	Thor.	Sacr.	Caud.	Total	Auth.
<i>Aythya affinis</i>	17	5	18	7	47	(V1)
	17	5-6	17-18	7-8	46-47	(W8)
<i>marila</i>	17	5	18	7-8	47-48	(V9)
	17	5	17-18	7-8	47-48	(W6)
Perching Ducks						
<i>Amazonetta brasiliensis</i>	16	5	15-16	7	43-44	(V2)
	16	5	16	7	44	(W1)
<i>Chenonetta jubata</i>	16	5	17	7	45	(V1)
	16	5	16-17	7	44-45	(W2)
<i>Aix sponsa</i>	16	5	16	7	44	(V2)
	16	5	16	7	44	(W3)
<i>Dendronessa galericulata</i>	16	5	17	7	45	(V3)
	16	5	16	7	44	(W2)
<i>Nettapus auritus</i>	16	5	15	7	43	(V1)
	16	5	15	7	43	(W1)
<i>Cheniscus pulchellus</i>	16	5	15	7	43	(V1)
	16	5	15	7	43	(W1)
<i>coromandelinus</i>	16	5	15	7	43	(V1)
	16	5	14	7-9	42-44	(W4)
<i>Sarkidiornis melanotos</i>	16	5	16	7	44	(V2)
	16	5	16	7	44	(W1)
<i>Cairina moschata</i>	16	5	16	7-8	44-45	(V3)
	16	5	16-17	7-8	45	(W4)
<i>Pteronetta hartlaubi</i>	16	5	16	8	45	(V1)
	16	5	16	8	45	(W1)
<i>Plectropterus gambensis</i>	17	5	17	7	46	(V2)
	17	4	17	7	45	(W2)
Eiders						
<i>Somateria mollissima</i>	16	5	17	7-8	45-46	(V4)
	16	5	17	8-9	46-47	(W5)
<i>spectabilis</i>	16	5	16	7	44	(V1)
	16	5	17	8	46	(W3)
<i>Lampronetta fischeri</i>	16	5	16	9	46	(W1)
<i>Polysticta stelleri</i>	16	5	16	8	45	(W1)
Sea Ducks						
<i>Melanitta fusca</i>	16	5	16-17	7-9	44-46	(V?)
	16	5-6	16-17	7-9	45-47	(W5)
<i>perspicillata</i>	16	5	17	8	46	(W1)
<i>Oidemia nigra</i>	16	5	16-17	7-9	44-46	(V?)
	16	5	16-17	7-9	45-46	(W4)
<i>Histrionicus histrionicus</i>	16	5	17	8	45	(V2)
	16	5	16	8	45	(W1)

Continued

TABLE 1 (continued)

Species	Cerv.	Thor.	Sacr.	Caud.	Total	Auth.
<i>Clangula hyemalis</i>	16	5	16	8	?44	(V1)
	16	5	15-16	8-9	44-45	(W5)
<i>Bucephala islandica</i>	16	5	17	8	?45	(V1)
<i>clangula</i>	16	5	16	8	45	(V4)
	16	5	16	7	44	(W1)
<i>albeola</i>	16	5	15	8	44	(V1)
	16	5	15-16	7-9	44-45	(W7)
<i>Mergellus albellus</i>	16	5	16	8	45	(V4)
	16	5	16	8	45	(W1)
<i>Lophodytes cucullatus</i>	16	5	17	8	46	(V1)
	16	5	16-17	7-8	45-46	(W4)
<i>Mergus serrator</i>	16	5	17	8	46	(V1)
	16	5-6	17-18	7-8	45-47	(W7)
<i>merganser</i>	16	5	17	8	46	(V1)
	16	5	17-18	8	46-47	(W4)
Stiff-tailed Ducks						
<i>Nomonyx dominica</i>	16	5	15	7	43	(V1)
	16	5	15	?	?	(W1)
<i>Oxyura jamaicensis</i>	16	5	16	9	46	(V1)
	16	5-6	15-17	8-9	44-46	(W4)
<i>vittata</i>	16	5	15	9	45	(V1)
	16	5	15	9	45	(W1)
<i>Biziura lobata</i>	16	6	16	7+	45+	(W1)
<i>Heteronetta atricapilla</i>	16	5	16	8	45	(V1)
	16	5	15	9	45	(W1)

The cervical region begins with the axis and terminates with the most posterior vertebra anterior to the synsacrum lacking a complete rib, (one composed of both vertebral and sternal parts and an uncinat process). Usually the last cervical and occasionally the last two cervicals have incomplete ribs composed of the vertebral portion and a rudimentary uncinat process.

The thoracic region begins with the first vertebra supporting a complete rib and terminates with the last free vertebra anterior to the synsacrum.

The sacral region is composed of the vertebrae that are fused to form the synsacrum. Older specimens tend to show greater fusion at the posterior end of the synsacrum. The fusion accounts for much of the variation in this region and in the caudal region.

The caudal region begins with the first free vertebra posterior to the synsacrum and terminates with the pygostyle. Although the pygostyle is composed of several fused vertebrae, it is counted as one element. Older specimens tend to have more vertebrae fused into the pygostyle to give additional variation in this region.

The vertebrae of large series of a few species were counted to make certain that the methods in the present study were comparable to those of Verheyen. When this was established, counts were generally made to bring the sample up to at least five individuals.

DISCUSSION AND CONCLUSIONS

Study of the postcranial skeleton indicates that the current classification of the waterfowl needs reevaluating. Osteological characters of the taxa as here recognized are summarized below, and the proposed classification and hypothetical relationships are presented in table 2 and figure 5 respectively.

Family Anseranatidae

Anseranas, the pied goose, has been variously regarded as belonging to a separate family (Stejneger, 1885; Miller, 1919; Verheyen, 1955), to a monotypic subfamily (Salvadori, 1895; Boetticher, 1943; Mayr and Amadon, 1951; Delacour, 1954), to a subfamily that otherwise includes only *Plectropterus* (Peters, 1931), to the perching duck tribe of the Anatinae (Delacour and Mayr, 1945), and tentatively to the sheldrakes (Newton, 1896: 837).

The details of the postcranial skeleton show conclusively that *Anseranas semipalmata* is an isolated and primitive species. The genus is highly distinct from all other waterfowl genera. Its osteological differences, summarized below, are far greater than those listed for the widely recognized nonpasserine family Falconidae (Brodkorb, 1960). *Anseranas* should be separated from the other waterfowl as a distinct family, the Anseranatidae, characterized as follows:

Humerus with (1) prominent medially situated capital shaft ridge, and correspondingly restricted proximal and lateral extent of external head of triceps. Carpometacarpus with (2) no notch in external rim of carpal trochlea; (3) metacarpal II distally curved upwards; (4) metacarpal III decidedly curved throughout its length; (5) facet for digit III protruding distally. Sternum with (6) costal margin long; (7) basin deep, perforated by numerous foramina, and crossed by transverse ridges, its posterior end trilobed. Coracoid with (8) coracoidal foramen opening into the shaft; (9) sterno-coracoidal process promi-

TABLE 2. PROPOSED CLASSIFICATION OF THE ANSERIFORMES

	Subörder Anhimae	
	Family Anhimidae	
<i>Anhima</i>		<i>Chauna</i>
	Subörder Anseres	
	Family Anseranatidae	
	<i>Anseranas</i>	
	Family Anatidae	
	Subfamily Anserinae	
Tribe Dendrocygnini		Tribe Anserini
<i>Dendrocygna</i>		<i>Anser</i>
<i>Stictonetta</i> *		<i>Branta</i>
		<i>Nesochen</i>
Tribe Cygnini		Tribe Cereopsini
<i>Coscoroba</i>		<i>Cereopsis</i>
<i>Cygnus</i>		
<i>Olor</i>		
	Subfamily Anatinae	
Tribe Tadornini		Tribe Merganettini
<i>Plectropterus</i>		<i>Merganetta</i>
<i>Chloëphaga</i>		
<i>Cyanochen</i> *		Tribe Aythyini
<i>Neochen</i>		<i>Rhodonessa</i>
<i>Alopochen</i>		<i>Metopiana</i>
<i>Tadorna</i>		<i>Netta</i>
<i>Lophonetta</i> *		<i>Aythya</i>
Tribe Anatini		Tribe Mergini
<i>Sarkidiornis</i>		<i>Melanitta</i>
<i>Pteronetta</i>		<i>Somateria</i>
<i>Asarcornis</i> *		<i>Polysticta</i>
<i>Cairina</i>		<i>Camptorhynchus</i> *
<i>Nettapus</i>		<i>Histrionicus</i>
<i>Aix</i>		<i>Clangula</i>
<i>Chenonetta</i>		<i>Bucephala</i>
<i>Amazonetta</i>		<i>Mergellus</i>
<i>Callonetta</i>		<i>Lophodytes</i>
<i>Anas</i>		<i>Mergus</i>
<i>Salvadorina</i> *		
<i>Malacorhynchus</i>		Tribe Oxyurini
<i>Hymenolaimus</i>		<i>Heteronetta</i>
<i>Tachyeres</i>		<i>Nomonyx</i>
		<i>Oxyura</i>
		<i>Thalassornis</i> *
		<i>Biziura</i>

* Not examined.

nent and knoblike; (10) head wide; (11) neck broad. Scapula with (12) acromion short; (13) triosseal ridge a knob extending over anterior edge. Furculum with (14) furcular process truncate; (15) pneumatic foramina in crotch; (16) over-all appearance V-shaped. Femur with (17) posterior intermuscular line displaced laterally; (18) internal condyle elongated distally; (19) head directed posteriad. Tibiotarsus with (20) inner cnemial crest straight. Tarsometatarsus with (21) median calcaneal ridge greatly enlarged; (22) facet for metatarsal I deep and prominent; (23) wing of trochlea for digit II greatly enlarged. Pelvis with (24) postacetabular ilium broadened horizontally; (25) posterior border of ilium shorter than that of ischium.

To these osteological characters can be added cranial features recorded by other authors: Palatines narrow (Miller, 1919); prevomer without a posteroventral angle; lacrimal bone with short, descending process, not reaching halfway to jugal bar; occiput sloping upward and forward (McDowell, in Delacour, 1954).

In males the trachea is long (approximately 150 cm.) and convoluted, situated outside the pectoral muscle on the left side, under the skin and attached to both by cellular tissue (Gadow, 1891: 723; Delacour, 1954).

Other morphological traits typical of *Anseranas* are the following: bill long and strong, deep at base; nostrils small, situated in middle and close together; lamellae much reduced; rostral nail large, strong, curved, pointed, and overhanging; lower mandible with a corresponding convex mental tip; forehead and lores naked; wings long; the 1st primary equaling the 7th, the 2nd to 5th longest; no wing spur; tail long and square, of 12 rectrices; legs long, a large portion of the tibia naked; tarsus reticulate; toes long and slender, nails long, curved, and sharp; hallux long and on a level with anterior toes (Delacour, 1954); webbing much reduced, extending only half length of toes (Gadow, 1893:154).

The electrophoretic pattern of the egg-white proteins of *Anseranas* is readily separable from those of 30 of Peters' genera of waterfowl, although it has some characteristics in common with these birds' patterns (Sibley, 1960). Unlike all other waterfowl, the wing molt is gradual, and adults never lack the power of flight. Furthermore the species exudes a strong, musky smell similar to that of certain parrots (Delacour, 1954). The general behavior according to Johnsgard (1960b) is also at variance with all other waterfowl.

Some of the characters of *Anseranas*, particularly those of the humerus, carpometacarpus, sternum, coracoid, skull, and external morphology, show similarities to the Anhimidae. These characters indicate affinities between the Anhimidae and the Anatidae, with the Anseranatidae forming the connecting link. Therefore, placing the families Anhimidae and Anatidae in the same order (Wetmore, 1960) better reflects their relationships than segregating them in two orders as Stresemann (1959) suggests.

Family Anatidae

With the genus *Anseranas* given separate familial rank, the remaining waterfowl, comprising the family Anatidae, can be defined osteologically by the following features.

Humerus with (1) capital shaft ridge lying farther laterad, and consequently depression for external head of triceps more extensive laterally and especially proximally. Carpometacarpus with (2) notch in external rim of carpal trochlea; (3) metacarpal II straight distally; (4) metacarpal III nearly straight throughout; (5) facet for digit III not protruding distally. Sternum with (6) costal margin short; (7) basin shallow with foramina restricted or absent, and no transverse ridges. Coracoid with (8) coracoidal foramen lacking; (9) sterno-coracoidal process compressed; (10) head narrow; (11) neck constricted. Scapula with (12) acromion long; (13) triosseal ridge elongate and not extending over anterior edge. Furculum with (14) furcular process rounded; (15) no pneumatic foramina in crotch; (16) over-all appearance U-shaped. Femur with (17) posterior intermuscular line lying along medial edge; (18) internal condyle short; (19) head directed laterad. Tibiotarsus with (20) inner cnemial crest deflected laterally. Tarsometatarsus with (21) median calcaneal ridge small; (22) facet for metatarsal I obscure; (23) wing of trochlea for digit II lacking. Pelvis with (24) postacetabular ilium greatly compressed horizontally; (25) posterior border of ilium forming a continuous oblique line with the ischium, except in whistling ducks.

The trachea fails to make a loop under the skin.

The adult sequence of molts includes a flightless stage.

The egg-white profiles of 30 of Peters' genera, distributed through the 9 tribes of Delacour, are very similar (Sibley, 1960).

Osteological features indicate two main branches of evolution within the family Anatidae. These branches constitute the subfamilies Anserinae and Anatinae. With two exceptions, *Cereopsis* and possibly

Stictonetta, the division supports the subfamilies as established by Delacour (1954, 1956, 1959).

SUBFAMILY ANSERINAE

The subfamily Anserinae includes the whistling ducks (*Dendrocygna* and probably *Stictonetta*), the swans (*Cygnus*, *Chenopsis*, and *Coscoroba* of Peters, 1931), and the true geese (*Anser*, *Cygnopsis*, *Chen*, *Philacte*, *Eulabeia*, *Branta*, and *Nesochen* of Peters). The postcranial osteology indicates that *Cereopsis* should also be included. The most important postcranial skeletal features of the subfamily are:

Humerus with (1) prominent capital shaft ridge directed towards head; (2) capital groove short; (3) depression of external head of triceps restricted; (4) area of pectoral attachment on external tuberosity elevated and somewhat circular. Carpometacarpus with (5) metacarpal II flat dorsally; (6) extensor attachment confined to tip of short but high process of metacarpal I. Sternum with (7) basin relatively deep; (8) posterior surface of dorsal sulcal lip extended posteriorly. Coracoid with (9) angle between axis of head and plane of dorsal surface relatively large; (10) angle between sternal facet and shaft relatively small; (11) ventral lip of sternal facet wide and prominent. Femur with (12) anterior edge of external condyle elevated from trend of shaft. Tarsometatarsus with (13) prominent lobe on anterior surface of trochlea for digit II. (14) Cervical vertebrae 17 to 25.

Delacour (1954) lists the following morphological and behavioral features: neck long; posture and body shape gooselike; tarsus reticulate; plumage, voice, and structure of syrinx very similar for both sexes; speculum absent; plumage nonmetallic; displays simple and not sexually dimorphic; pairing for life; male assisting in care of young, and in some species in incubation; chief food vegetable.

The subfamily Anserinae is composed of four definable units, all of which are about equally distinct in osteology. These constitute the tribes Dendrocygnini, the whistling ducks; Cygnini, the swans; Anserini, the geese; and Cereopsini, the Cape Barren goose.

TRIBE DENDROCYGNINI (WHISTLING DUCKS). The whistling ducks of the genus *Dendrocygna* have a superficial resemblance to certain true ducks of the subfamily Anatinae, but the many trenchant characters, osteological and otherwise, previously listed for the subfamily Anserinae, indicate their true affinities are with the swans and geese. Summarized below are the most important postcranial skeletal features of the tribe.

Humerus with (1) space between external condyle and facet for anterior articular ligament reduced. Carpometacarpus with (2) metacarpal II distinctly incurved; (3) external rim of carpal trochlea only slightly notched; (4) a prominent neck between carpal trochlea and metacarpal III. Sternum with (5) costal margin long; (6) basin deep; (7) dorsal and ventral manubrial spines lacking. Coracoid with (8) shaft thin; (9) pneumatic foramina minute; (10) ventral surface housing a unique depression. Furculum with (11) pneumatic foramina lacking. Femur with (12) anterior convexity on shaft. Tibiotarsus with (13) external and internal condyles nearly parallel; (14) external condyle circular in lateral outline. Tarsometatarsus with (15) groove in trochlea for digit II obsolete. Pelvis with (16) posterior border of ilium shorter than that of ischium. (17) Cervical vertebrae 17 to 18.

Several characteristics of the postcranial skeleton are found only in *Dendrocygna* and *Anseranas*, and it seems best to consider the whistling ducks as the nearest living relatives of the pied goose. The features indicating this relationship are: carpometacarpus with external rim of carpal trochlea unnotched or only slightly notched; sternum with costal margin long, basin deep, both manubrial spines lacking; scapula with blade frequently narrow, apex frequently pointed; femur with anterior convexity of shaft; tarsometatarsus without prominent groove in trochlea for digit II; pelvis with posterior border of ilium shorter than that of ischium.

No skeleton of the aberrant freckled duck, *Stictonetta naevosa*, has been available for this study, but the sparse published information indicates the species possesses the important features of the subfamily Anserinae listed by Delacour (1954). The tarsus is reticulate; the structure of the syrinx is similar in both sexes, lacking a true bulla; the plumage is nonmetallic, sexual dimorphism and the speculum are lacking, and the chief food is vegetable (Delacour and Mayr, 1945). Additional support is gained for this thesis from the fact that Verheyen (1955) places *Stictonetta* in a separate group between the whistling ducks and the geese, basing his decision on limb proportions and skull characters.

Within the subfamily Anserinae, *Stictonetta* is most like the whistling ducks and is tentatively transferred to this tribe. The form of the body and bill is ducklike, but the cervical vertebrae number 18, the trachea has a slight swelling in the male, and the wing beat is slow (Delacour, 1956), as in the whistling ducks. Further study may indicate it deserves tribal ranking within the Anserinae.

TRIBE CYGNINI (SWANS). The characteristics of the postcranial skeleton that separate the swans, genera *Cygnus*, *Chenopsis*, and *Coscoroba* of Peters (1931), from both the whistling ducks and the true geese are:

Humerus with (1) space between external condyle and facet for anterior articular ligament wide; (2) distal end narrow (12.2 to 13.9 percent of total length); (3) entepicondyle not distally extended; (4) entepicondylar prominence extended laterally; (5) internal tuberosity short, with tip rounded. Carpometacarpus with (6) metacarpal II relatively straight; (7) external rim of carpal trochlea distinctly notched; (8) neck between carpal trochlea and metacarpal III obsolete; (9) external rim of carpal trochlea sloping sharply downward from process of metacarpal I; (10) pit on internal side below and distal to pisiform process separated from intermetacarpal space by a raised area; (11) process of metacarpal I low; (12) external rim of facet for digit II widely rounded. Sternum with (13) ventral manubrial spine present; (14) intermuscular line distinctly angling over plate and reaching carina anterior to its posterior end; (15) sternal notches shallow; (16) a pit, or even a large excavation, in dorsal portion of carinal margin in some specimens of all species. Coracoid with (17) shaft robust; (18) pneumatic foramina small and extending under entire furcular facet. Scapula with (19) pneumatic fossa absent or reduced. Furculum with (20) extended depression along lateral surface containing one or more pneumatic foramina, frequently large. Femur with (21) shaft straight. Tibiotarsus with (22) external and internal condyles diverging anteriorly; (23) external condyle elongate in lateral outline. Tarsometatarsus with (24) prominent groove in trochlea for digit II. Pelvis with (25) posterior borders of ilium and ischium approximately equal in posterior extent. (26) Cervical vertebrae 21 to 25.

Delacour and Mayr (1945) divide the subfamily Anserinae into only two tribes, uniting the swans and geese under the tribe Anserini. To support this arrangement Delacour (1954) states: "Swans and geese agree so closely in structure, pattern of downy chicks, general behavior, courtship and nesting habits that it is preferable to include them all in the same tribe." Then to a degree he refutes his conclusion by adding "Swans are larger and better adapted to aquatic life; consequently they have shorter legs, larger feet, and longer necks with more vertebrae (twenty-three to twenty-five, against eighteen to nineteen). But the latter feature is not very important as it varies with the species. Certain of their habits, however, are at some variance with those of the geese, and their chromosome number is not the same."

Osteologically swans form no less distinct a tribe than the whistling ducks, although they are distinct in different ways. The most import-

ant of the criteria listed for the tribe is probably the displaced intermuscular line on the sternum. It indicates a significant difference in the supracoracoideus muscle. As table 1 discloses, the number of cervical vertebrae varies at the species level, but the fact that true swans have a minimum of 22, true geese a maximum of 20, and *Coscoroba* lies between with 21, seems significant.

Genera of Swans.—Peters (1931) recognizes two genera of swans, *Chenopsis* for the black swan of Australia, and *Cygnus* for the others. Delacour and Mayr (1945) combine all swans in the genus *Cygnus*. Wetmore (1951) feels that the genus *Olor* is worthy of recognition, and gives osteological evidence to support his view—the presence of the sternal loop of the trachea and the modified furculum in *Olor*, which are lacking in *Cygnus*.

Some additional skeletal differences between *Olor* and *Cygnus* are seemingly not associated with the sternal tracheal loop. These features, many of which are listed by Howard (1946), are summarized below for *Olor*:

Humerus with (1) intermuscular line on capital shaft ridge turning inward about $\frac{1}{4}$ -inch below head; (2) attachment of supraspinatus poorly marked, spreading past median crest, and lacking raised bordering line at edge; (3) ligamental furrow relatively narrow and deep; (4) attachment of anterior articular ligament long, narrow, and smoothly rounded at edges; (5) impression of brachialis anticus short, broad particularly at proximoexternal edge, clearly outlined, usually deeply depressed. Carpometacarpus with (7) cuneiform fossa lacking distinct proximal and medial rims; (8) metacarpal I with only a shallow depression on external surface immediately proximal to facet for digit II. Coracoid with (9) furcular facet undercut for its full extent; (10) procoracoid larger; (11) coracoidal notch absent. Scapula with (12) muscular attachment forming a short crest running from acromion along ventromedial edge of bone. Furculum with (13) clavicular depression long, containing several large foramina. Femur with (14) low ridge extending from trochanter towards head to make neck appear less constricted.

These features seem sufficient to establish *Olor* as a valid unit. The genus contains the species *O. cygnus*, *O. bewickii*, *O. columbianus*, and *O. buccinator*.

Possibly the changes that allow the trachea to pass into the carina are more involved than realized. In Anatidae other than *Olor*, and in most other birds, including cranes of the genus *Grus*, the trachea remains dorsal to the furcular symphysis. In *Olor* the trachea passes

ventral to the furculum to reach the carina. After looping back and leaving the carina at the anterior end, the trachea curves around the furculum and passes posteriorly to the lungs.

Chenopsis is so similar to *Cygnus* in the characteristics of the postcranial skeleton that recognition of the genus does not seem warranted. Behavioral data (Johnsgard, 1960b) support the classification of swans in two genera as here proposed.

Coscoroba, although certainly most closely related to the true swans, is less specialized. The peculiarities of the genus indicate to Delacour and Mayr (1945) an affinity with the whistling ducks. Several osteological features, however, suggest *Coscoroba* to be intermediate between the true swans and the geese. The relative width of the distal end of the humerus is 13.9 percent in *Coscoroba*, intermediate between that of the true swans (12.2 to 13.9) and the geese (14.1 to 15.6). In *Coscoroba* the intermuscular line of the sternal plate extends farther posteriad before reaching the carina than in true swans, although it does not extend as far as in geese or other waterfowl. In *Coscoroba* the posterior lateral processes are intermediate in length between those of true swans and geese. The coracoid in *Coscoroba* has a slight depression in the triosseal canal; in true swans there is none; in geese it is deep. The angle between the head and the plane of the dorsal surface of the coracoid is 83 degrees in *Coscoroba*. The range for true swans is from 83 to 93 degrees, the range for geese from 80 to 85 degrees. In *Coscoroba* the pneumatic fossa of the scapula is shallow; it is deep in geese and absent in swans. In *Coscoroba* the depression along the lateral surface of the furculum is shallower and more restricted than is typical of swans, whereas geese have none. In the tarsometatarsus of *Coscoroba* the groove in the trochlea for digit II is interrupted anteroproximally by a slight swelling, absent in true swans, but large in geese. The width through the acetabula is 23.0 percent of the pelvic length in *Coscoroba*. In swans the range is 15.7 to 19.4 percent, with an average of 17.56. In geese the range is from 19.8 to 26.9 percent with an average of 24.19. In *Coscoroba* the cervical vertebrae number 21; the range for true swans is 22 to 25, and for geese 18 to 20. The total number of vertebrae varies in *Coscoroba* from 51 to 52. The range for true swans is 54 to 61 and for geese 48 to 52.

TRIBE ANSERINI (GEESE). The tribe Anserini is composed of the true geese, the genera *Anser*, *Cygnopsis*, *Chen*, *Philacte*, *Eulabeia*, *Branta*, and *Nesochen* of Peters (1931). The osteological properties of the postcranial skeleton of the Anserini are:

Humerus with (1) space between external condyle and facet for an-

terior articular ligament wide; (2) distal end wide (14.1 to 15.6 percent of total length); (3) entepicondyle distally extended; (4) entepicondylar prominence not extended laterally; (5) internal tuberosity long. Carpo-metacarpus with (6) metacarpal II relatively straight; (7) external rim of carpal trochlea distinctly notched; (8) neck between carpal trochlea and metacarpal III obsolete; (9) external rim of carpal trochlea forming relatively small angle with proximal edge of process of metacarpal I; (10) pit on internal side below and distal to pisiform process confluent with intermetacarpal space; (11) process of metacarpal I high with proximal edge nearly perpendicular to shaft; (12) external rim of facet for digit II almost straight. Sternum with (13) ventral manubrial spine present; (14) intermuscular line extending along plate essentially parallel to carina and curving onto carina at its posterior end; (15) sternal notches deep; (16) no pit in dorsal portion of carinal margin. Coracoid with (17) shaft robust; (18) pneumatic foramina normally restricted to area beneath brachial tuberosity. Scapula with (19) pneumatic fossa prominent. Furculum with (20) no depression on lateral surface, and pneumatic foramina either absent or located in area between coracoidal and scapular tuberosities. Femur with (21) shaft straight. Tibiotarsus with (22) external and internal condyles diverging anteriorly; (23) external condyle elongate in lateral outline. Tarsometatarsus with (24) prominent groove in trochlea for digit II. Pelvis with (25) posterior borders of ilium and ischium approximately equal in posterior extent. (26) Cervical vertebrae 18 to 20.

Genera of Geese.—Three divisions of the true geese can be supported by their postcranial osteology: (1) *Anser*, including *Cygnopsis*, *Chen*, *Philacte*, and *Eulabeia* of Peters' classification, (2) *Branta*, and (3) *Nesochen*. Delacour and Mayr (1945) recognized only two genera, by further combining *Nesochen* in *Branta*. While the osteology supports the views of Delacour (1954) and Humphrey (1958b) that *Nesochen* is an offshoot of *Branta* stock, its skeletal features are as distinct, and in some instances, more distinct than those between *Anser* and *Branta*.

The features that separate *Branta* and *Nesochen* from *Anser*, in the broad sense, are as follows. In *Branta* and *Nesochen* the humerus has the depression for the external head of the triceps distinctly bordered. In *Anser* it is obscure. In *Branta* and *Nesochen* the coracoid has the furcular facet undercut for its full extent. In *Anser* the facet is deeply undercut dorsally, flattened against the shaft in the middle, and only slightly undercut ventrally. In *Branta* and *Nesochen* the furculum lacks pneumatic foramina. In *Anser* prominent pneumatic foramina are almost always present. In *Branta* and *Nesochen* the femur has the

anterior tip of the trochanter extended slightly more proximad, and the posterior rim straighter. In *Anser* the femur has the most proximal extent of the trochanter in the middle, and the posterior rim curves toward the head. In *Branta* and *Nesochen* the tibiotarsus has the inner cnemial crest straighter. In *Anser* the inner cnemial crest is deflected laterally. In *Branta* the sternum has the ventral manubrial spine vertically spatulate. In *Anser* and *Nesochen* the spine is typically peglike.

From these comparisons *Nesochen* seems most closely related to *Branta*, but the following additional characteristics separate the genus from all other geese:

Sternum with (1) width narrow, varying from 37 to 40 percent of basin length (a minimum of 41 percent is recorded for the other genera); (2) carina visibly lower; (3) ventral manubrial spine less developed; (4) dorsal manubrial spine a transverse ridge (it is a buttonlike prominence in other genera); (5) pneumatic foramen very small; (6) intermuscular line less prominent. Coracoid with (7) depression in triosseal canal shallow; (8) coraco-humeral surface more nearly transverse to shaft. Scapula with (9) processes generally smaller and weaker. Femur with (10) rotular groove broad; (11) neck short, directed more posteriad. Tibiotarsus with (12) fibular crest long. Tarsometatarsus with (13) outer margin straighter; (14) trochleae more in line with shaft.

TRIBE CEREOPSINI (CAPE BARREN GOOSE). Structure of its postcranial skeleton assigns *Cereopsis* to the Anserinae instead of the Anatinae, where it is tentatively placed by Delacour and Mayr (1945) and Delacour (1954). The genus agrees with the Anserinae in all fourteen of the characteristics listed as diagnostic for this subfamily.

Features other than those of the postcranial skeleton support the placement of *Cereopsis* in the Anserinae. Most of the characters listed for the subfamily by Delacour (1954) are found in *Cereopsis*. The reticulate tarsus, the absence of a syrinx, and the long neck, composed of 19 or 20 cervical vertebrae, are probably the most important. A conspicuous "triumph ceremony" and the similarity of the sexes in voice and display, in addition to skeletal features listed by Verheyen (1955), has led Johnsgard (1960b) to the same conclusion. Verheyen (1955) places *Cereopsis* in a separate group near the geese, swans, and *Coscoroba*.

Cereopsis is an aberrant genus with no close, living relatives, and it should not be assigned to any of the recognized tribes. The following postcranial characteristics distinguish the monotypic tribe to which it is here assigned:

Humerus with (1) deltoid crest evenly curved throughout its length;

(2) head confluent with shaft on anconal side. Carpometacarpus with (3) proximal edge of process of metacarpal I sloping forward, and distal edge concave, with tip more pointed; (4) distal metacarpal symphysis greatly lengthened. Sternum with (5) concavity beneath dorsal sulcal lip reduced; (6) dorsal manubrial area notched; (7) ventral manubrial spine lacking; (8) xiphisternum curving inward; (9) carinal margin relatively more curved. Coracoid with (10) depression in triosseal canal reduced; (11) head relatively wider and shallower. Scapula with (12) acromion directed more mediad, and consequently surface posterior to acromion, including glenoid facet, broad; (13) anterior edge between acromion and coracoidal articulation thick; (14) dorsomedial edge of neck with extra protuberance; (15) glenoid facet lying in plane of anterior portion of shaft; (16) pneumatic fossa present. Furculum with (17) pneumatic foramina present in slight depression; (18) clavicles compressed. Femur with (19) fibular condyle extending farther distally than point of its junction with external condyle. Tibiotarsus with (20) outer cnemial crest hooked; (21) pronounced ridge extending from outer cnemial crest onto anterior surface of shaft, whose surface is convex; (22) shelf medial to external articular surface extending relatively farther out over posterior portion of the shaft; (23) supratendinal bridge tapering towards medial side, and medial abutment recessed; (24) tubercle for oblique ligament enlarged. Tarsometatarsus with (25) intercotylar prominence symmetrical in outline; (26) trochlea for digit II more nearly in line with the other two.

SUBFAMILY ANATINAE

The subfamily Anatinae as here proposed includes 48 nominal genera listed by Peters (1931), plus two additional ones (*Amazonetta* and possibly *Lophonetta*) recognized by Delacour and Mayr (1945). This arrangement is similar to the subfamily Anatinae of Delacour (1954, 1956, 1959) except that *Stictonetta* and *Cereopsis* are removed to the Anserinae. Skeletons of 8 of the 50 nominal genera (*Cyanochen*, *Pseudotadorna*, *Lophonetta*, *Salvadorina*, *Nesonetta*, *Asarcornis*, *Camptorhynchus*, and *Thalassornis*) were not available. Of these only *Camptorhynchus*, for which a drawing of the pectoral girdle is available (Rowley, 1877), is included in the following discussion.

The principal postcranial osteological features of the subfamily Anatinae as here defined are:

Humerus with (1) prominent capital shaft ridge lacking or directed towards external tuberosity; (2) capital groove extended laterally over anconal surface deeply excavating head; (3) depression of external head of triceps extended laterally; (4) area of pectoral attachment on

external tuberosity depressed distally and elliptical. Carpometacarpus with (5) metacarpal II rounded dorsally; (6) extensor attachment typically extending distally onto distal edge of process of metacarpal I. Sternum with (7) basin flattened; (8) posterior surface of dorsal sulcal lip reduced. Coracoid with (9) angle between axis of head and plane of dorsal surface relatively large; (10) angle between sternal facet and shaft relatively large (11) ventral lip of sternal facet less prominent, sloping sharply toward shaft. Femur with (12) anterior edge of external condyle not significantly elevated from shaft. Tarsometatarsus with (13) lobe on anterior surface of trochlea for digit II obsolete. (14) Cervical vertebrae 16 to 17 (17 to 19 in *Anas acuta*).

The following morphological features are listed as diagnostic of the Anatinae by Delacour (1954): tarsus scutellate in front; plumage and structure of syrinx sexually dimorphic; speculum present. The removal of *Stictonetta* and *Cereopsis* from the Anatinae reduces the exceptions to all these features. It makes the type of tarsal sheath an infallible subfamilial criterion as indicated by table 1 in Delacour and Mayr (1945:44).

Based on osteology, the subfamily Anatinae is divisible into six tribes: the sheldrakes, Tadornini; the pond ducks, Anatini; the torrent duck, Merganettini; the pochards, Aythyini; the sea ducks, Mergini; and the stiff-tailed ducks, Oxyurini. The tribal assignments of the genera available for the present study are:

Tadornini: *Chloephaga*, *Neochen*, *Alopochen*, *Tadorna*, *Casarca*, and *Plectropterus*.

Anatini: *Anas*, *Chaulelasmus*, *Mareca*, *Spatula*, *Malacorhynchus*, *Hymenolaimus*, *Tachyeres*, *Chenonetta*, *Aix*, *Dendronessa*, *Nettapus*, *Cheniscus*, *Sarkidiornis*, *Cairina*, *Pteronetta*, and *Amazonetta*.

Merganettini: *Merganetta*.

Aythyini: *Rhodonessa*, *Metopiana*, *Netta*, *Aythya*.

Mergini: *Somateria*, *Lampronetta*, *Polysticta*, *Melanitta*, *Oidemia*, *Histrionicus*, *Clangula*, *Bucephala*, *Lophodytes*, *Mergellus*, and *Mergus*.

Oxyurini: *Heteronetta*, *Nomonyx*, *Oxyura*, and *Biziura*.

Delacour and Mayr (1945) recognize seven tribes of Anatinae, the additional group being the perching ducks, tribe Cairinini, containing genera herein included in the Anatini. Delacour (1954) also recognizes seven tribes, but they are somewhat different. He removes the eiders from the Mergini as the tribe Somateriini, and includes the torrent ducks in the tribe Anatini.

TRIBE TADORNINI (SHELDRAKES). The sheldrake tribe includes the available genera *Chloephaga*, *Neochen*, *Alopochen*, *Tadorna*, *Casarca*, and

Plectropterus listed by Peters. The characteristics of the postcranial skeleton that define the tribe are:

Humerus with (1) fairly prominent capital shaft ridge directed toward external tuberosity; (2) area of origin of external head of triceps relatively narrow; (3) deltoid crest relatively large and flaring, and in lateral view more rounded, or if an abrupt bend occurs, it lies more posteriad; (4) deltoid crest extending farther distad; (5) head rotated so that external tuberosity is higher. Carpometacarpus with (6) external scapholunar ligamental attachment broad, usually prominent, situated relatively higher and more distad; (7) lobe at distal end of external rim of carpal trochlea relatively large; (8) process of metacarpal I relatively high, short, and with a rugose cap. Sternum with (9) costal margin tapering posteriorly and with six or less costal processes; (10) dorsal sulcal lip rather prominent; (11) pneumatic foramina usual in basin; (12) pneumatic fossa large and bordered laterally by stout bars; (13) prominent posterior extension of sterno-coracoidal process. Coracoid with (14) procoracoid somewhat enlarged; (15) triosseal depression somewhat deep; (16) depression in furcular facet ventral to brachial tuberosity; (17) brachial tuberosity undercut extensively; (18) angle between sternal facet and shaft relatively small. Furculum with (19) coracoidal tuberosity poorly developed; (20) clavicles relatively compressed. Femur with (21) head directed slightly more proximad; (22) trochanter extending slightly more anteriorly. Tibiotarsus with (23) proximal portion of intermuscular line straight, removed from anteromedial edge. Tarsometatarsus with (24) trochleae for digits II and IV, and particularly the former, spread; (25) trochlea for digit II more in line with other two; (26) distal foramen less nearly perpendicular to shaft. (27) Cervical vertebrae 16 to 17.

Genera of Sheldrakes.—The recognition of *Chloëphaga*, *Neochen*, and *Alopochen* as distinct but closely related genera is supported by the details of the postcranial skeleton. All three genera have diagnostic elements, and all three have basic similarities. These details are presented in the body of the paper.

The merging of *Casarca* in the genus *Tadorna* is justified by the absence of any good osteological distinctions between them. This has already been done on other grounds, by Delacour and Mayr (1945), followed by Verheyen (1955).

Plectropterus agrees with the sheldrakes in the many features listed as characteristic of the tribe, and should itself be considered an aberrant sheldrake.

Features in addition to those discussed in this paper support the move. Sheldrakes typically have a spurlike knob at the bend of the wing, and are quarrelsome (Delacour, 1954). *Plectropterus* has the scapholunar enlarged as a spur (Rand, 1954), and is extremely pugnacious (Delacour, 1959). Furthermore, of the 5 genera with which *Plectropterus* has hybridized, 3, *Chloëphaga*, *Alopochen*, and *Tadorna*, are sheldrakes (Johnsgard, 1960a). According to Verheyen (1955), who places *Plectropterus* in a taxon with the genera here included in the Tadornini, there are a number of similarities in the skull. Although Johnsgard (1960b) does not remove *Plectropterus* from the Cairinini, he moves this tribe to a position immediately following the sheldrakes, and considers *Plectropterus* as a relict genus.

TRIBE ANATINI (POND DUCKS). The tribe Anatini as here defined includes the genera *Anas*, *Chaulelasmus*, *Mareca*, *Spatula*, *Malacorhynchus*, *Hymenolaimus*, *Tachyeres*, *Amazonetta*, *Chenonetta*, *Aix*, *Dendronessa*, *Nettapus*, *Cheniscus*, *Sarkidiornis*, *Cairina*, and *Pteronetta* (Peters, 1931; Delacour and Mayr, 1945). The postcranial characteristics of the tribe are:

Humerus with (1) capital shaft ridge obsolete; (2) pneumatic fossa opening, containing bony struts; (3) ectepicondyle typically equal or subequal in height to entepicondyle. Carpometacarpus with (4) noticeable prominence on external rim of carpal trochlea; (5) cuneiform fossa intermediate in depth between that of pochards and sea ducks; (6) external scapholunar ligamental attachment prominent and on a prominent ridge; (7) flexor attachment extending beyond proximal fornx; (8) process of metacarpal I relatively high and straight (in comparison with sea ducks). Sternum with (9) basin shallow (in comparison with sheldrakes); (10) pneumatic foramen elliptical or round (in comparison with sheldrakes); (11) width relatively narrow; (12) posterior lateral processes relatively straight (in comparison with diving tribes, pochards, sea ducks, stiff-tailed ducks). Coracoid with (13) angle between axis of head and plane of dorsal surface relatively small. Scapula (in comparison with the diving tribes) with (14) acromion relatively short; (15) proximal portion less rotated; (16) blade broadest at midpoint. Femur (in comparison with diving tribes) with (17) shaft relatively straight; (18) anterior ridge of trochanter relatively large; (19) outer surface of condyles more nearly parallel. In addition (in comparison with sheldrakes) (20) head directed relatively farther laterad; (21) trochanter forming an angle. Tibiotarsus with (22) intermuscular line following anteromedial edge (in comparison with sheldrakes); (23) external condyle extending farther distad than internal condyle

(in comparison with sea ducks and stiff-tailed ducks); (24) posterior intercondylar sulcus relatively narrow (in comparison with pochards). Tarsometatarsus with (25) distal end of median ridge of digit II reaching level of proximal end of facet for digit III (in comparison with diving tribes); in addition (in comparison with sheldrakes) (26) trochleae approximate; (27) external edge relatively straight. (28) Cervical vertebrae 16, except 17 to 19 in *Anas acuta*.

Delacour and Mayr (1945) recognized an additional tribe, the Cairinini, for some of the genera here included in the tribe Anatini. They give many good criteria, such as general proportions, plumage, voice, and life habits, as characteristics of this group. While the tribe Cairinini probably deserves recognition on these characters, unfortunately I could find only three skeletal features, all quite fallible, to support this action. Perching ducks ("Cairinini") show a trend towards reducing the pneumatic fossa in the humerus to a restricted, circular opening rimmed with heavy bone. In dabbling ducks (Anatini, *sensu stricto*) the fossa tends to be ovaloid through an upward extension into the internal tuberosity. In perching ducks the external scapholunar ligamental attachment on the carpometacarpus tends to be obscure, and the process of metacarpal I is higher, shorter, and straighter. In dabbling ducks the ligamental scar is usually prominent, and the process of metacarpal I lower, longer, and inflected. In perching ducks the ventrolateral portion of the head of the coracoid tends to be more enlarged than in dabbling ducks. These features appear too inconstant to merit tribal recognition. The perching habit characteristic of these genera may not be a reflection of common group ancestry.

Genera of Pond Ducks.—No features of the postcranial skeleton support the recognition of *Chaulelasmus* and *Spatula* as distinct from *Anas*, and they should be merged with that genus, as is done by Delacour and Mayr (1945). *Mareca* differs from *Anas* (*sensu stricto*) to a small degree in the form of the tarsometatarsus and in the robustness of the humeral shaft. There is also a tendency towards fusion of certain of the thoracic vertebrae. These differences seem too weak and inconstant for generic recognition however. This action has already been taken by Delacour and Mayr (1945) on the basis of external morphology.

Malacorhynchus is distinct in several of the postcranial skeletal elements, and is aberrant in having a closed pneumatic fossa in the humerus. The form deserves generic rank. *Hymenolaimus* is distinct from the typical dabbling ducks in most postcranial skeletal elements, as discussed in the body of the paper. Riley (1957) suggests that *Hymenolaimus* may be a sheldrake, and the attachment of the external

scapholunar ligament supports this suggestion. However, in spite of its swift-water environment, it agrees with the typical pond ducks in many important characters.

In the well-marked genus *Tachyeres* the four best taxonomic elements of the skeleton, the humerus, carpometacarpus, coracoid, and sternum, all possess characters that require placing the genus in the Anatini, as discussed in the body of the paper. None of the four elements shows any of the numerous diagnostic features of the Tadornini, where Delacour and Mayr (1945) tentatively place *Tachyeres*. The properties of the femur in particular indicate the genus is not closely related to any of the diving tribes. A possible relationship of *Tachyeres* to *Anas* is suggested by Ripley (1957). Moynihan (1958) feels the genus deserves tribal ranking on the basis of behavior.

The recognition of the genus *Amazonetta* for the species *Anas brasiliensis* of Peters (1931), as proposed by Delacour and Mayr (1945), is substantiated by the species' postcranial osteology: Humerus with (1) shaft strongly sigmoid; (2) deltoid crest markedly flared; (3) head inflected; (4) ectepicondyle slightly elevated above entepicondyle. Carpometacarpus with (5) process of metacarpal I high and straight; (6) distal portion of external rim of carpal trochlea lacking a swelling. Coracoid with (7) head relatively pointed. Tarsometatarsus with shaft thin, 7.9 percent of total length. The minimum recorded for other Anatini, as here defined, is 8.0 percent; the minimum recorded for *Anas*, as here defined, is 8.3 percent.

The recognition of a separate genus for the species *Anas leucophrys*, is necessitated by its skeletal peculiarities: Humerus with (1) shaft sigmoid; (2) ectepicondyle elevated above entepicondyle; (3) entepicondyle distally elongate; (4) deltoid crest more rounded distally from bend. Carpometacarpus with (5) proximal edge of process of metacarpal I sloping sharply proximally; (6) flexor attachment reduced; (7) base of metacarpal III relatively narrow; (8) external rim of carpal trochlea long and narrow. Sternum with (9) ventral manubrial spine relatively thin; (10) costal processes reduced to six. Tarsometatarsus with (11) anteromedial ridge relatively thick and elevated. The name *Callonetta* Delacour (1936) originally proposed as a subgenus of *Anas*, is available and is here elevated to generic rank (see page 13).

The behavior of *Callonetta* suggests to Delacour and Mayr (1945) a relationship with the pochards, but skeletal features, and particularly those of the humerus, strongly oppose this hypothesis. Boetticher (1952) and later Delacour (1956) believe an affinity with the perching ducks more probable. Derscheid (1938), and Verheyen (1955) see such a relationship and go so far as to place the species in the genus *Amazo-*

netta along with *A. brasiliensis*. Although affinity to *Amazonetta* is supported by features of the humerus, other criteria, and in particular those of the carpometacarpus, indicate that the species deserves separate generic ranking as *Callonetta leucophrys*. Johnsgard (1960b) proposes such an arrangement based on behavioral data.

The postcranial skeletons of *Nettapus* and *Cheniscus* show no differences of generic worth, and the merging of *Cheniscus* in the genus *Nettapus*, as proposed by Delacour and Mayr (1945), is valid.

Pteronetta has a number of important differences in the postcranial skeleton, and the species deserves recognition from *Cairina* at the generic level. This opposes the procedure followed by Delacour and Mayr (1945), but agrees with that of Johnsgard (1960b). The most diagnostic skeletal features are: Humerus with (1) depression for external head of triceps relatively broad; (2) deltoid crest distally elongate. Carpometacarpus with (3) process of metacarpal I higher; (4) lowest point of internal rim of carpal trochlea below pisiform process; (5) depression along external edge of base of carpal trochlea lacking. Sternum with (6) basin nonpneumatic except for one anteriorly and centrally located foramen. Coracoid with (7) head relatively wide, rounded; (8) groove in furcular facet wide and shallow. Scapula with (9) dorsal depression lacking; (10) blade relatively thin.

Aix and *Dendroessa* are indistinguishable, by features of the postcranial skeleton, and the latter genus should be synonymized. This action is taken by Delacour and Mayr (1945) on other grounds and agreed with by Verheyen (1955). The details of the postcranial skeleton of *Aix* (*sensu lato*) reveal that the genus is closer to *Cairina* and *Chenonetta* than to *Anas*. This is evident in the humerus, carpometacarpus, coracoid, and sternum. These similarities, which are discussed under the respective elements, support the behavioral evidence of Lorenz (undated) and the serological evidence of Cotter (1957).

Chenonetta and particularly *Sarkidiornis* have many diagnostic skeletal features and are both worthy of generic rank.

TRIBE Merganettini (Torrent Duck). *Merganetta* may well be derived from pond duck stock, as the form of the syrinx and sternum and the presence of a speculum suggests to Niethammer (1952), but the structure of the skeleton, including the sternum, is too much at variance with that of the typical Anatini to consider the genus a member of the same tribe. It shows more basic differences from *Anas* than do *Hymenolaimus*, *Tachyeres*, or even *Metopiana* of the pochards. These differences, the most important of which are summarized below, demand tribal recognition for the genus, which was the original procedure

followed by Delacour and Mayr (1945). Verheyen (1955) places the genus in a separate family, one of 16, but has it immediately following his family Anatidae.

Humerus with (1) ligamental furrow extremely shallow; (2) brachial depression relatively broad; (3) anterior articular ligament relatively low; (4) deltoid crest reduced; (5) bicipital crest joining shaft at relatively wide angle. Carpometacarpus with (6) metacarpals greatly shortened; (7) rims of carpal trochlea enlarged; (8) cuneiform fossa very deep; (9) base of metacarpal III narrow, and restricted laterally; (10) tuberosity of metacarpal II greatly reduced; (11) process of metacarpal I enlarged, curving sharply proximad, and frequently knobbed. Sternum with (12) basin wide; (13) carina greatly reduced; (14) dorsal manubrial area deeply notched. Coracoid with (15) angle between axis of head and plane of dorsal surface relatively large, 72 degrees; (16) head deflected ventrally. Scapula with (17) triosseal ridge reduced; (18) blade narrow and thick. Furculum with (19) clavicles weak, connected in form of broad U. Pelvis with (20) acetabular width very small, 22.7 to 23.6 percent of pelvic length. (21) Cervical vertebrae 16.

TRIBE AYTHYINI (POCHARDS). The pochards, *Metopiana*, *Netta*, and *Aythya*, with the inclusion of *Rhodonessa*, form a closely knit group easily distinguished from the other diving tribes. The postcranial skeletal characteristics that support this view are: Humerus (in comparison with other diving tribes) with (1) impression for brachialis anticus distinct; (2) entepicondyle higher than ectepicondyle; (3) intercotylar furrow and olecranal fossa essentially confluent. In addition (in comparison with pond ducks), (4) shaft relatively thin; (5) facet for anterior articular ligament relatively low. Carpometacarpus with (6) distal portion of external rim of carpal trochlea without swelling; (7) cuneiform fossa shallow; (8) external scapholunar ligamental attachment prominent but small; (9) flexor attachment proximal to proximal fornx; (10) process of metacarpal I high and straight (in comparison with other diving tribes). Sternum (in comparison with pond ducks) with (11) basin relatively wide; (12) ventral manubrial spine lacking (*Metopiana* is an exception). Coracoid with (13) ventral portion of head reduced; (14) bicipital attachment a thin groove; (15) furcular facet extending farther posteriad along shaft. Scapula with (16) blade narrow; (17) proximal portion rotated. Furculum (in comparison with pond ducks) with (18) furcular process reduced. Femur (in comparison with other diving tribes) with (19) trochanter extended farther anteriorly; (20) head smaller; (21) medial side of internal condyle less flared

laterally. Tibiotarsus (in comparison with other diving tribes) with (22) external condyle extending farther distad than internal condyle. Tarsometatarsus (in comparison with other diving tribes) with (23) external edge almost straight; (24) trochlea for digit II forming slight angle with shaft. (25) Cervical vertebrae 17.

Delacour (1959) cites general behavior and color and pattern of the downy young as important evidence of only a distant kinship between the pochards and the other diving ducks. The skeleton supports the distinctness of the pochards from the other diving tribes.

Rhodonessa discloses its affinities to the other pochards by numerous skeletal characteristics. Of particular importance are the form of the coracoid, humerus, and sternum, discussed at length under these respective elements. Unfortunately, the distal limb elements were unavailable. The total of 17 cervical vertebrae is also important as pointed out by Verheyen (1955), who also united the four genera here considered the pochards under one taxon. Therefore, *Rhodonessa* is transferred from the dabbling ducks, where it is placed by Delacour and Mayr (1945), to the pochards.

Metopiana and *Netta* have numerous skeletal differences, and it is a mistake to consider the two as congeners, as Delacour and Mayr believe (1945). Features by which *Metopiana* differs from *Netta* are: Humerus with (1) bicipital crest more prominent; (2) head more robust. Carpometacarpus with (3) tuberosity of metacarpal II and external rim of facet for digit II produced laterad. Sternum with (4) ventral manubrial spine present; (5) basin relatively narrow; (6) pneumatic foramen relatively large; (7) posterior lateral processes longer, thinner, and straighter. Coracoid with (8) shaft relatively narrow; (9) sternal facet relatively short. Scapula with (10) blade tapering. Femur with (11) shaft less curved; (12) anterior edge of trochanter enlarged; (13) popliteal fossa shallow. Tibiotarsus with (14) outer cnemial crest relatively broad; (15) shaft more robust. Tarsometatarsus with (16) median ridge of trochlea for digit II extending beyond level of proximal end of facet for digit III.

The eight available species of the genus *Aythya* are extremely similar in skeletal features. Furthermore, the modifications of *Aythya* indicate it is better adapted for diving than are *Metopiana*, *Netta*, or *Rhodonessa*. *Netta* seems closest to *Aythya* in most respects, but in a few aspects *Metopiana* is closer to *Aythya*. *Rhodonessa* is probably the least specialized member of the tribe.

TRIBE MERCINI (SEA DUCKS). The diverse tribe of sea ducks includes the genera *Somateria*, *Lampronetta*, *Polysticta*, *Melanitta*, *Oidemia*,

Histrionicus, *Clangula*, *Bucephala*, *Mergellus*, *Lophodytes*, and *Mergus*. The principal skeletal characteristics of the tribe are: Humerus with (1) pneumatic fossa closed (two exceptions); (2) internal tuberosity short, deep; (3) facet for anterior articular ligament low; (4) pit for origin of pronator longus extending proximad; (5) pit for origin of pronator brevis situated farther distad; (6) external condyle elevated above entepicondyle; (7) impression for brachialis anticus distinct; (8) intercotylar furrow and olecranal fossa separated by a transverse bar; Carpometacarpus with (9) distal portion of external rim of carpal trochlea possessing a prominent swelling; (10) cuneiform fossa relatively deep; (11) external scapholunar ligamental attachment obscure. Sternum with (12) basin wide; (13) ventral manubrial spine reduced or absent. Coracoid with (14) procoracoid flared dorsally and base enlarged; (15) triosseal canal wide; (16) head with large ventral prominence. Scapula with (17) anterior end rotated; (18) blade uniformly wide. Femur with (19) shaft curved; (20) anterior portion of trochanter reduced; (21) popliteal fossa deep; (22) fibular condyle less flared laterally; (23) pit for tibialis anticus prominent. Tibiotarsus with (24) condyles equal in distal extent; (25) external ligamental prominence small; (26) internal condyle shorter anteromedially. (27) Cervical vertebrae 16.

Genera of Sea Ducks.—Avian taxonomists have long considered the mergansers a separate subfamily of ducks, with features such as the narrow, serrated bill, long neck, and supposedly compressed tarsi listed as diagnostic (Phillips, 1926). The postcranial skeleton clearly shows the mergansers to be close relatives of the genus *Bucephala*, as pointed out by Delacour (1936), and indeed, that *Bucephala* and the mergansers form a more distinct unit than do the mergansers by themselves. The several features that set *Bucephala* and the mergansers apart from the other sea ducks are: Carpometacarpus with (1) process of metacarpal I relatively high, and with extensor attachment relatively short; (2) pollical facet in line with or proximal to internal rim of carpal trochlea, and with only a small lateral lobe. Sternum with (3) both fenestrae and abdominal plate. Coracoid with (4) sternal facet short, 33.2 to 39.7 percent of length; (6) sterno-coracoidal process less produced laterally; (6) triosseal canal narrow, 11.1 to 15.4 percent of length. Femur with (7) anterior edge of trochanter decidedly inflected; (8) fibular condyle widely flaring. Tibiotarsus with (9) proximal edge of outer cnemial crest virtually a straight, diagonal line. Tarsometatarsus with (10) external edge of outer trochlea straight or inflected.

The skeletal anatomy of the mergansers does not allow the merging of either *Mergellus* or *Lophodytes* in the genus *Mergus*, as proposed by Delacour and Mayr (1945) and followed by many recent workers. All three merganser genera are far more distinct osteologically than many recognized genera of waterfowl, and with certain elements *Mergellus* and *Lophodytes* are closer to *Bucephala* than to *Mergus* (*sensu stricto*). Clearly the proposed synonymizing of these two generic names would obscure relationships. Johnsgard (1960b) states that behaviorally *Bucephala* is linked to the mergansers through *Mergellus*, and that *Mergus serrator* and *Mergus merganser* show surprising differences from *Mergellus* and *Lophodytes* in male display patterns. He continues to recognize but one genus, however.

Mergus, the most specialized of the four genera, is characterized by: Humerus with (1) shaft relatively straight; (2) deltoid crest large and sharply angular; (3) pneumatic fossa open. Carpometacarpus with (4) process of metacarpal I low, 17.9 to 22.6 percent of total length. Sternum with (5) carinal overlap long, 25.6 to 35.6 percent of basin length (average 31.59). Coracoid with (6) ventral rim of glenoid facet rather angular with anteroventral leg somewhat rounded, and posterior leg essentially straight. Furculum with (7) clavicles deeply curved. Femur with (8) shaft straight, stout, and compressed, depth 11.0 to 12.6 percent of length. Tibiotarsus with (9) inner cnemial crest relatively wide, and bent anteriorly at its juncture with outer cnemial crest; (10) outer cnemial crest produced laterally beyond external articular surface. Tarsometatarsus with (11) distal foramen relatively small and oblique; (12) shaft narrow, 7.7 to 9.1 percent of total length. Pelvis (13) narrow, acetabular width 16.2 to 20.7 percent of pelvic length.

Lophodytes and *Mergellus* are both less specialized than *Mergus*, but frequently in different ways. The sum total of the differences between these two genera and *Mergus* indicates that *Lophodytes* may be somewhat closer to *Mergus* than is *Mergellus*. The features that characterize *Lophodytes* are: Humerus with (1) shaft sigmoid and width 7.1 to 7.7 percent of total length; (2) deltoid crest large and sharply angular; (3) pneumatic fossa open. Carpometacarpus with (4) process of metacarpal I relatively high, 23.2 to 23.6 percent of total length. Sternum with (5) carinal overlap short, 18.5 to 19.9 percent of basin length (average 19.39). Coracoid with (6) anteroventral portion of rim of glenoid facet broadly rounded, posterior part concave. Furculum with (7) clavicles relatively straight (in comparison with *Mergus*). Femur with (8) shaft depth 9.8 to 10.7 percent of total length; (9) shaft

wide, 8.3 to 9.2 percent of total length. Tibiotarsus with (10) shaft width 5.2 to 5.8 percent of length. Tarsometatarsus with (11) distal foramen relatively small and oblique; (12) shaft wide, 10.6 to 11.7 percent of total length. Pelvis (13) wide, acetabular width 22.9 to 30.0 percent of pelvic length.

Mergellus can be distinguished from the other three genera in this group of sea ducks by: Humerus with (1) deltoid crest angular, but reduced; (2) pneumatic fossa closed; (3) width 6.4 percent of total length. Carpometacarpus with (4) process of metacarpal I relatively high, 22.8 percent of total length. Sternum with (5) carinal overlap short, 18.5 percent of basin length. Coracoid with (6) anteroventral portion of rim of glenoid facet somewhat rounded. Furculum with (7) clavicles relatively straight (in comparison with *Mergus*). Femur with (8) shaft depth 9.5 percent of total length; (9) shaft narrow, 7.5 percent of total length. Tibiotarsus with (10) shaft width 5.0 percent of length. Tarsometatarsus with (11) distal foramen relatively small and oblique; (12) shaft narrow, 9.8 percent of total length. Pelvis (13) narrow, acetabular width 21.6 percent of pelvic length.

Bucephala can be separated from the merganser genera as follows: Humerus with (1) shaft sigmoid; (2) pneumatic fossa closed; (3) deltoid crest relatively small. Carpometacarpus with (4) process of metacarpal I relatively high, 22.5 to 23.9 percent of total length; (5) lobe at distal end of external rim of carpal trochlea relatively large. Sternum with (6) carinal overlap short, 11.4 to 22.0 percent of basin length (average 16.13); (7) pneumatic foramen relatively small. Coracoid with (8) ventral lip of sternal facet usually with distinct concavity near internal distal angle. Furculum with (9) clavicles relatively straight (in comparison with *Mergus*). Femur with (10) shaft strongly curved; (11) shaft depth 8.0 to 9.9 percent of total length. Tibiotarsus with (12) inner cnemial crest narrow, and prominently peaked. Tarsometatarsus with (13) distal foramen relatively large and perpendicular to shaft. Pelvis (14) wide, acetabular width 26.4 to 29.9 percent of pelvic length.

The striking differences between the behavior patterns of the goldeneyes (*Bucephala clangula* and *B. islandica*) and the bufflehead (*Bucephala albeola*), lead M. T. Myres (in Johnsgard, 1960b) to feel that the latter species deserves generic ranking. No strong differences in the postcranial skeleton substantiate this view.

The remaining genera of sea ducks (*Clangula*, *Histrionicus*, *Melanitta*, *Oidemia*, *Somateria*, *Lampronetta*, *Polysticta*) can be separated from *Bucephala* and the mergansers by: Carpometacarpus with (1) process of metacarpal I relatively low, and with extensor attachment relatively

long; (2) pollical facet distal to internal rim of carpal trochlea, and with a large lateral lobe. Sternum with (3) notches. Coracoid with (4) sternal facet long, 42.1 to 49.9 percent of length; (5) sterno-coracoidal process produced laterad; (6) triosseal canal relatively wide, 15.3 to 18.7 percent of length. Femur with (7) anterior edge of trochanter less inflected.

These genera may be divided into two groups, either one of which is much less well-defined osteologically than the group containing *Bucephala* and the mergansers. The features that separate *Clangula*, *Histrionicus*, and the scoters from the eiders are: Carpometacarpus with (1) flexor attachment relatively short, approximately half as long as in eiders; (2) upper surface of metacarpal II straight. Sternum with (3) large abdominal plate or greater curvature throughout length, or small ventral manubrial spine. Coracoid with (4) sternal facet at internal distal angle relatively blunt; (5) ventromedial edge of shaft possessing a wide ridge; (6) triosseal canal possessing a deep depression. Femur with (7) shaft relatively more curved; (8) scar on lateral surface proximal to fibular condyle relatively long. Tibiotarsus with (9) outer cnemial crest relatively narrow, and directed farther anteriorad. Tarsometatarsus with (10) external edge of shaft almost a straight line.

The sea ducks *Clangula* and *Histrionicus* are generally recognized as distinct genera, and it does not seem necessary to summarize their many skeletal characteristics. The study of their postcranial osteology has borne out the conclusion of Delacour and Mayr (1945) that they form a central group among the sea ducks. It appears that evolution has preceeded in one direction from *Clangula* through *Bucephala* to the mergansers, and in another through *Histrionicus* to the scoters.

Whether one genus of scoters should be recognized or two has been a difficult decision to make. Since genera, as well as other taxonomic units, are arbitrary divisions of the continuum of evolution, it is only logical that varying degrees of distinctness will be found among the existing biota. The scoters represent an intermediate stage between the concepts of species and genera, and perhaps should be considered as two subgenera. As most of the differences between them are proportions, and as the species of scoters exhibit trends in some of these proportions, they are treated as a single genus, *Melanitta*, as in Delacour and Mayr (1945). According to Hartert (1923), *Melanitta* Boie, 1822 (apparently published in May), has priority over *Oidemia* Fleming, 1822 (apparently published in June).

The differences between "*Oidemia*" and *Melanitta* (*sensu stricto*) are: In "*Oidemia*" the width through the distal condyles varies from

13.9 to 14.4 percent of the total length of the humerus; the range for *Melanitta (sensu stricto)* is from 14.5 to 15.8 percent. In "*Oidemia*" the width through metacarpal II varies from 6.5 to 7.1 percent of the total length of the carpometacarpus; the range for *Melanitta (sensu stricto)* is from 7.0 to 7.9 percent. In "*Oidemia*" the sternal facet varies from 46.6 to 49.9 percent of the length of the coracoid; the range for *Melanitta (sensu stricto)* is from 42.9 to 44.9 percent. In "*Oidemia*" the depression in the triosseal canal is usually deeper than in *Melanitta (sensu stricto)*, and the furcular facet is circular in outline, instead of ovoid as in *Melanitta (sensu stricto)*. In "*Oidemia*" the width of the shaft of the femur varies from 8.2 to 8.5 percent of the total length of the element; the range in *Melanitta (sensu stricto)* is from 7.2 to 8.0 percent. And finally, in "*Oidemia*" the acetabular width varies from 15.4 to 20.8 percent of the pelvic length; in *Melanitta (sensu stricto)* the range is from 19.3 to 23.5 percent.

A third evolutionary trend is manifest from the *Clangula-Histrionicus* core toward the eiders. Delacour (1956, 1959) and Humphrey (1958a) believe the eiders form a tribe Somateriini, more closely related to the dabbling ducks than to the sea ducks, and give the structure of the tracheal bulla, plumage patterns, food habits, and diving habits as evidence. No feature of the postcranial skeleton supports this view, and the similarity of the skeletons of the eiders to those of other sea ducks is so great that it seems best to include the eiders within the Mergini. Myres (in Johnsgard, 1960b) concludes from behavioral studies that the eiders show no close affinities to *Anas*, a view supported by Johnsgard (1960b).

The characteristics that tend to set the eiders apart from the other two groups of sea ducks are: Humerus with (1) pneumatic fossa closed, but relatively deep. Carpometacarpus with (2) flexor attachment relatively long, approximately twice as long as in other sea ducks; (3) upper surface of metacarpal II arched. Sternum with (4) notches, no significant abdominal plate, and wide posterior lateral processes. Coracoid with (5) sternal facet elongate at internal distal angle; (6) ventromedial edge of shaft a sharp ridge; (7) triosseal canal with essentially no depression. Femur with (8) shaft relatively straight; (9) scar on lateral surface proximal to fibular condyle relatively short. Tibiotarsus with (10) outer cnemial crest relatively wide, and directed farther laterad. Tarsometatarsus with (11) external edge of shaft distinctly curved. This character is the most diagnostic.

No skeletal features support the recognition of the genus *Lampronetta*, and it should be merged in the genus *Somateria*, as Delacour and Mayr (1945) do on other grounds.

Polysticta is synonymized with *Somateria* by Delacour and Mayr (1945), but Humphrey (1958a) revives the genus because of the presence of a speculum and differences in the tracheal bulla, adult plumage patterns, shape of the bill, characteristics of flight, and skeletal proportions which, although not explained, he considers striking. Delacour (1959) now follows Humphrey. The qualitative features of its postcranial skeleton strongly support the recognition of *Polysticta*: Humerus with (1) distal condyles strongly rotated, with external condyle elevated above entepicondyle. Carpometacarpus with (2) notch in external rim of carpal trochlea reduced; (3) lobe at distal end of external rim of carpal trochlea relatively small; (4) cuneiform fossa relatively shallow. Sternum with (5) ventral manubrial spine small but single. Coracoid with (6) angle between axis of head and plane of dorsal surface relatively large, 81 degrees compared to 70 to 79 degrees; (7) furcular facet rounded. Scapula with (8) acromion more in line with shaft, therefore, appearing relatively long, and with larger concavity between it and shaft. Femur with (9) anterior portion of trochanter possessing more prominent, medially directed protuberance; (10) fibular groove relatively narrow; (11) ligamental attachment on medial surface of internal condyle a prominent projection; (12) anterior ridge of internal condyle relatively straight instead of flaring medially. Tibiotarsus with (13) condyles more in line with shaft. Tarsometatarsus with (14) median rim of trochlea for digit II extending beyond level of posterior extent of facet for digit III.

Most of the skeletal features that distinguish *Polysticta* from large eiders also show the genus to be near the central group of sea ducks, *Clangula* and *Histrionicus*. Particularly worthy of note are the rotation of the distal end of the humerus, manubrial spine of the sternum, and angle of the head of the coracoid. Furthermore, *Histrionicus* has a speculum similar to that of *Polysticta*, and according to Humphrey (1958a) the flight behaviors of *Clangula* and *Polysticta* are similar. Thus it appears that the third direction of evolution in the diverse tribe of sea ducks has been from *Histrionicus* and *Clangula* through *Polysticta* to *Somateria*, as originally suggested by Delacour and Mayr (1945). The published figure of the sternum of *Camptorhynchus* (Rowley, 1877) further indicates the derivation of the eiders from a *Histrionicus*-like stock, for it seems intermediate between the sterna of *Histrionicus* and *Polysticta*.

Working largely with behavioral characteristics Johnsgard (1960c) reaches conclusions almost identical to mine on the assignment and arrangement of the genera in this tribe.

mental attachments deeply grooved. Sternum with (7) pneumatic foramen lacking or minute; (8) ventral manubrial spine directed steeply dorsad (except in *Biziura*, where spine is lacking); (9) basin very shallow. Coracoid with (10) ventral portion of head extending far down shaft; (11) brachial tuberosity reduced. Scapula with (12) acromion directed more anteriorly; (13) blade uniform in width, fairly narrow, and often thick; (14) glenoid facet laterally compressed. Furculum with (15) clavicles thin and rather weak. Tarsometatarsus with (16) inner calcaneal ridge enlarged (17) trochlea for digit IV with inner ridge elevated. Pelvis with (18) acetabular width very small. (19) Cervical vertebrae 16.

As *Heteronetta* has all these striking skeletal features of the tribe Oxyurini, no doubt remains about the relationship of the genus. In most elements *Heteronetta* shows a lesser degree of specialization than occurs in other stiff-tails and certain of these suggest an ancient tie with the pond ducks. The details are discussed at length in the body of the paper.

In external morphology, *Nomonyx* is similar to *Oxyura*, with which it is synonymized by Delacour and Mayr (1945); but its skeletal anatomy is very distinctive. The many skeletal features that define the genus *Nomonyx*, most of which show a lesser degree of specialization in comparison with *Oxyura*, are: Humerus with (1) internal tuberosity elongate; (2) depression for external head of triceps less excavated; (3) shaft relatively thick. Carpometacarpus with (4) process of metacarpal I relatively narrow; (5) distal margin of internal rim of carpal trochlea deflected slightly laterally; (6) tuberosity of metacarpal II small; (7) groove in external rim of carpal trochlea shallow. Sternum with (8) basin relatively narrow; (9) ventral manubrial spine long, thin, and peglike; (10) notches relatively deep; (11) xiphisternum relatively narrow. Coracoid with (12) triosseal canal narrow; (13) shaft width reduced; (14) brachial tuberosity relatively small. Scapula with (15) glenoid facet only slightly compressed. Furculum with (16) clavicles more massive (in comparison with the other three genera of stiff-tailed ducks). Femur with (17) shaft relatively straight. Tibiotarsus with (18) external condyle extending relatively farther distad; (19) inner cnemial crest lacking long ridge found in the more specialized *Oxyura* and *Biziura*. Tarsometatarsus with (20) median rim of trochlea for digit II extending beyond level reached by proximal extent of facet for digit III.

The two most specialized of the four available genera, *Oxyura* and *Biziura*, and particularly the *Biziura*, have many unique properties of the skeleton.

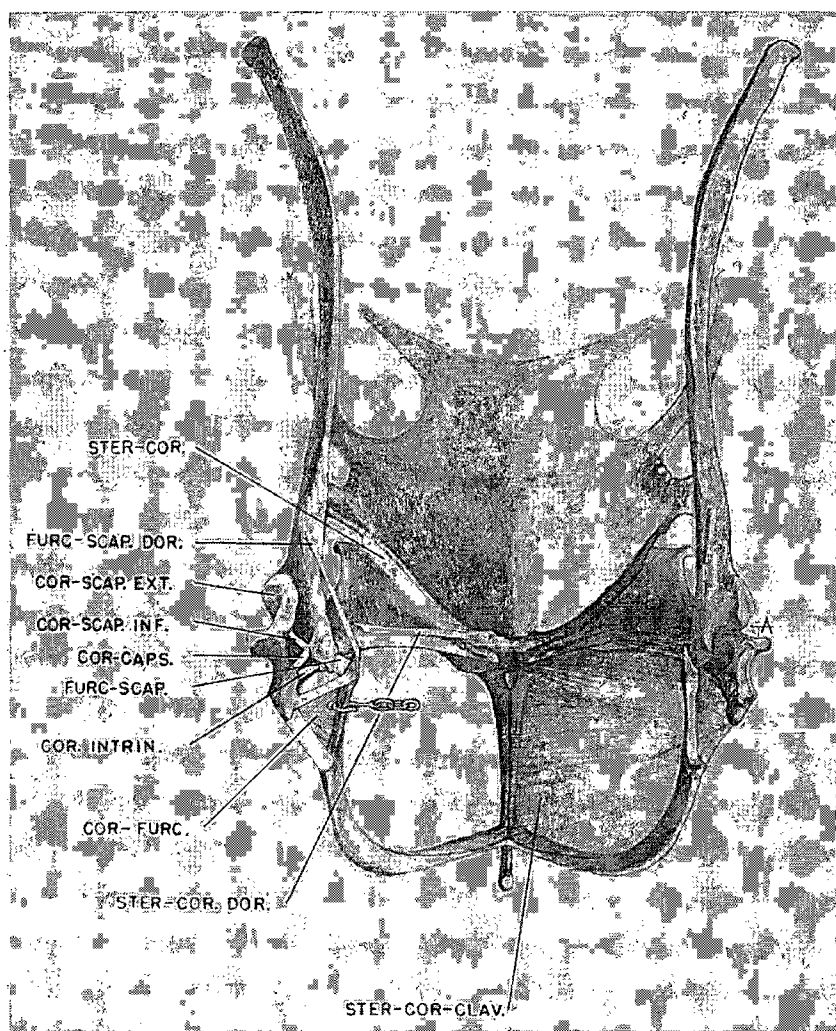


FIGURE 6. LIGAMENTS OF PECTORAL GIRDLE. Anterodorsal view of *Anas penelope*. Ligaments removed from left side. Membrana sterno-coraco-clavicularis removed from right side. Membrana interclavicularis completely removed.

cor-caps.	Ligamentum coraco-capsulare
cor-furc.	Ligamentum coraco-furculare
cor. intrin.	Ligamentum coracoideum intrinsicum
cor-scap. ext.	Ligamentum coracoideo-scapulare externum
cor-scap. inf.	Ligamentum coracoideo-scapulare inferius
furc-scap.	Ligamentum furculo-scapulare
furc-scap. dor.	Ligamentum furculo-scapulare dorsale
ster-cor.	Ligamentum sterno-coracoideum
ster-cor-clav.	Membrana sterno-coraco-clavicularis
ster-cor. dor.	Ligamentum sterno-coracoideum dorsale

APPENDIX: LIGAMENTS OF THE PECTORAL GIRDLE

To understand the functional significance of the various processes on the bones of the pectoral girdle, it was necessary to study the ligaments connecting the three elements to each other and to the sternum. Nowhere in the literature are the ligaments in this area concisely explained, and some appear to be unnamed, (see fig. 6).

MEMBRANA STERNO-CORACO-CLAVICULARIS. Gadow, 1891

Lames latérales and *Lame médiane postérieure ou verticale de l'appareil épisternal* combined. Harting, 1864, see Gadow, 1891.

Ligamentum sterno-furculare. Gadow, 1891 (may be a synonym for only a part of the membrane).

Composed of a single posteroventral sheet and a pair of anterolateral sheets.

The single ligamentous sheet (*Lame médiane postérieure*) extends posteriorly from a line between the anterior tip of the ventral manubrial spine of the sternum and the furcular process of the furculum to the anterior carinal margin of the sternum. In species lacking a prominent spine the extent of the single sheet is reduced.

The sheet becomes double (*Lames latérales*) as it passes from the tip of the ventral manubrial spine onto the lateral ridges on the dorsal surface of the spine and from the furcular process onto the clavicles. Each sheet stretches from the ventral manubrial spine to the coracoid, where it attaches along the internal margin, from the midpoint of the shaft to the procoracoid and brachial tuberosity. From the brachial tuberosity the sheet passes to the lateral ridge on the coracoidal tuberosity of the furculum (an anteriorly directed process near the scapular tuberosity) by means of the anterior portion of *Ligamentum coraco-furculare*. Thence, it soon passes posterolaterally to the medial side, where it reaches the symphysis of the furculum and joins the sheet from the other clavicle. A ligamentous line on the lateral surface of the sheet extends from the intermuscular line of the carina to the triosseal canal, to separate *M. supra-coracoideus* dorsomedially from *M. pectoralis* ventrolaterally.

MEMBRANA INTERCLAVICULARIS

Lame médiane antérieure ou horizontale. Harting, 1864, see Gadow, 1891.

Interclavicular membrane. Humphrey, 1958b.

A membranous sheet stretching between the arms of the furculum, attaching along the medial edge of the bone from the symphysis almost to the tip of the scapular tuberosity of the furculum whence it extends to the short medial ridge of the acromion of the scapula and thence to the axial musculature. It is pierced in the middle by the trachea, and more dorsally by the esophagus. The tracheal bulla, when present, lies posterior to this membrane.

LIGAMENTUM CORACOIDEO-SCAPULARE EXTERNUM. Gadow, 1891

Attaches the glenoid facets of the coracoid and scapula, respectively, and forms a U-shaped groove for the head of the humerus. It is very thick.

LIGAMENTUM CORACOIDEO-SCAPULARE INFERIUS. Gadow, 1891

Extends from the ridge on the dorsal edge of the procoracoid and the rim of the scapular facet of the coracoid to the anterior edge of the scapula. It holds the coracoidal articulation of the scapula in the scapular facet of the coracoid.

LIGAMENTUM CORACO-CAPSULARE. Gadow, 1891

Extends from the brachial tuberosity of the coracoid to the triosseal ridge on the dorsal surface of the acromion of the scapula.

LIGAMENTUM CORACOIDEUM INTRINSICUM

Connects the procoracoid and the brachial tuberosity of the coracoid. This ligament and *L. coraco-capsulare* are very strong and closely parallel each other and *Membrana sterno-coraco-clavicularis*. The two ligaments seal off the medial side of the triosseal canal. In some birds *L. coracoideum intrinsicum* is osseous.

LIGAMENTUM STERNO-CORACOIDEUM. Gadow, 1891

Extends from the most anterior rims of the coracoidal sulcus of the sternum to the most anterior ridges of the sternal facet of the coracoid.

LIGAMENTUM STERNO-CORACOIDEUM DORSALE

Extends from the lateral prominence of the dorsal manubrial area of the sternum to the uppermost scar on the dorsal surface of the coracoid.

LIGAMENTUM CORACO-FURCULARE. Gadow, 1891

Extends from the most anterior portion of the brachial tuberosity of the coracoid to the lateral ridge of the scapular tuberosity of the furculum, and from the ventral portion of the furcular facet of the coracoid to the coracoidal tuberosity of the furculum. The tissue between these two strengthened portions of the ligament is membranous. *Membrana sterno-coraco-clavicularis* attaches to the latter of the two ligamentous portions described as it passes from coracoid to furculum. In geese the portion that extends to the coracoidal tuberosity is considerably broadened; and the coracoidal tuberosity forms a ridge instead of a tubercle.

LIGAMENTUM FURCULO-SCAPULARE. Gadow, 1891

Extends from the posterior surface of the scapular tuberosity of the furculum to the dorsal surface of the acromion of the scapula.

LIGAMENTUM FURCULO-SCAPULARE DORSALE

Extends from the extreme tip of the scapular tuberosity of the furculum to the sometimes obscure ridge lying anteromedial from the dorsal protuberance (a swelling in the middle of the dorsal surface of the neck) of the scapula.

In waterfowl the furculum plainly makes no direct articulation with either of the other elements of the pectoral girdle, but instead is held in close proximity medially by several strong ligaments. The freedom of movement of the furculum can be detected in fresh specimens.

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