CLASSIFICATION AND SYSTEMATIC POSITION OF THE EIDERS

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This paper deals with part of the results of research (Humphrey, MS) on the Mergini, a tribe proposed by Delacour and Mayr in 1945 to include the Old-squaw, Harlequin, and Labrador ducks, and the mergansers, golden-eyes, scoters, and eiders. I shall deal here solely with the relationships and systematic position of the eiders, which my evidence indicates do not belong in the Mergini. Delacour and Mayr's conclusions regarding the close relationship of the golden-eyes and mergansers will be discussed elsewhere.

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The eiders, because of their lobed hallux and their habit of diving, have long been grouped with other ducks having those attributes. Hence, in most classifications, the eiders, pochards, scoters, steamer ducks, golden-eyes, and others have been placed together. In 1945, Delacour and Mayr erected the Tribe Aythyini exclusively for the pochards and put the eiders, along with the scoters, golden-eyes, mergansers, Old-squaw, Harlequin Duck, and Labrador Duck, in the Tribe Mergini. They state (*op. cit.*: 32) that "in spite of the wide difference between the extreme forms of the tribe (*Mergus* and *Somateria*), the sea ducks [Mergini] form one of the most closely knit subdivisions of the anatine subfamily."

It is clear from Delacour and Mayr's classification that ducks having the diving habit (and the lobed hallux) are not necessarily closely related. Nonetheless, the classical separation of "diving ducks" from "dabbling ducks" remains essentially unaltered in theirs and in most other recent classifications of the waterfowl.

Although the food habits and locomotor adaptations (including many correlated structural modifications) of the eiders are most like those of the scoters, those two groups of species have little else in common. In fact, the eiders as a group appear to share more characters with the "dabbling ducks" (Anatini) than with any other waterfowl.

Trachea.—Various authors, notably the Heinroths (1928) and Delacour and Mayr (1945), have commented on the value of the trachea as a source of evidence for the classification of ducks. A close examination of this structure in the Mergini suggests a taxonomic arrangement different from that proposed by Delacour and Mayr.

The tracheal bulla of each of the species of eiders has an inflated left chamber which is bulbous in form and lacks membrane-covered fenestrae (see figs. 1*a*, 1*b*, 1*c*, and 1*d*). The tracheas of the eiders lack mid-tracheal swellings and are (except for *Polysticta*) of uniform diameter (see fig. 1*a*). If I depended on tracheal characters alone, I would unhesitatingly place the eiders in Delacour and Mayr's Tribe Anatini. The tracheas and tracheal bullas of males of most members (the tracheas of several species are unknown) of the genus *Anas* (*sensu latu*) are very similar to those of the eiders, differing from them only in minor variations of shape.

The tracheas and tracheal bullas of members of the Tribe Mergini other than the eiders may be described as follows:

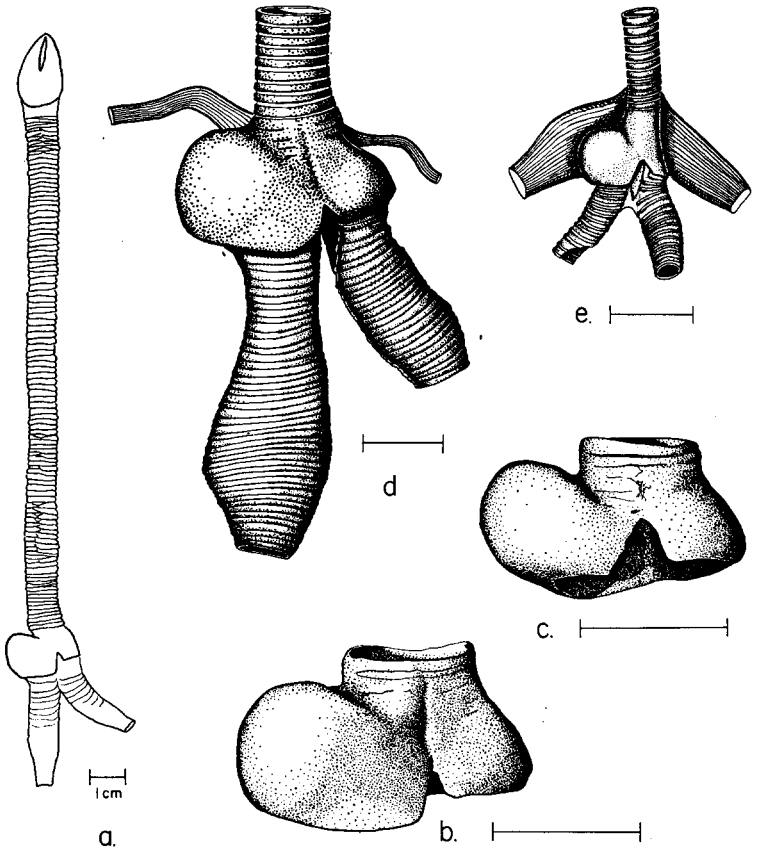

Fig. 1. Dorsal views of trachea and tracheal bullas of male eiders. *a,* trachea of *Somateria spectabilis*; *b,* tracheal bulla of *S. spectabilis*; *c,* tracheal bulla of *S. fischeri*; *d,* tracheal bulla and bronchi of *S. mollissima v. nigra* (note slender sternotrachealis muscles and enlarged left bronchus); *e,* tracheal bulla and bronchi of *Polysticta stelleri* (note enlarged sternotrachealis muscles and bronchi of equal size).

1. *Melanitta nigra.*—Males lack a tracheal bulla and have instead a small, fused (or partially fused), bilaterally symmetrical structure at the lower end of the trachea. This structure is similar to the structure at the lower end of the trachea of females. The tracheal tube is of uniform diameter. For figures see Yarrell (1845:321), Miller (1926:2), and Pycraft (1910:403).

2. *Melanitta fusca* and *M. perspicillata.*—The tracheal bulla of males of these two species is bilaterally symmetrical. The right and left chambers are enlarged and their lateral margins are dorso-ventrally compressed. Neither chamber has a bulbous appearance. The tracheal tube of each of these two species has a prominent mid-tracheal swelling in addition to an odd swelling in the laryngeal region. For figures see Miller (1926: 2) who illustrated the tracheas of *M. perspicillata* and *M. fusca*; also for figures of tracheas of *M. fusca* see Yarrell (1845:315–316), Latham and Romsey (1798: table 15, figs. 3–7), and Pycraft (1910:403).

3. *Clangula, Bucephala, Mergus* (including *Mergellus* and *Lophodytes*).—The tracheal bulla in males of species in these three genera is asymmetrical and consists of

two irregular inflations, at least one of which has one or two membrane-covered fenestrae. There is considerable interspecific variation in the superficial appearance of this type of tracheal bulla, although the basic structures are present in all the species having it. The right chamber may be only slightly inflated or it may be greatly inflated. The amount of fusion of the right chamber is also variable; in some the basic ring structure is easily discernible, while in others fusion is so complete that no rings can be traced at all. The left chamber is also variable. It always has at least one membrane-covered fenestra and fusion is generally so complete that ring outlines are indiscernible. The tracheal tubes of males of the several species of *Clangula, Bucephala* (except *B. albeola*), and *Mergus* have swellings, some of which are highly specialized bulbous structures and others merely slight increases in the diameter of the tube.

For figures of the trachea of *C. hyemalis* see Yarrell (1845:361–362), Montagu (1831:515), Sabine (1819: table 30, figs. 3 and 4), and Ruppell (1933:477). There is no readily available published figure of the trachea of *B. albeola* although a trachea of a male of that species is figured by Humphrey (MS). There are many figures of the trachea of *B. clangula* and *B. islandica*; the tracheas of both species are figured by Taverner (1919:58), Gilpin (1878:398–399), and Kortright (1942:261). The trachea of *M. albellus* was figured by Harrison (1943: pl. 7, fig. 1), Yarrell (1843:281), and Latham and Romsey (1798: table 16, figs. 3 and 4). Beard (1951:300) illustrated the trachea of *M. cucullatus*. For figures of the trachea of *M. merganser* see Eyton (1836: 76), Yarrell (1827: table 15; 1845:399), and Pycraft (1910:403). The trachea of *M. serrator* has been figured by Yarrell (1845:394), Latham and Romsey (1798: table 16, figs. 1 and 2), and Newton (1861:420). The tracheas of *M. australis, M. squamatus,* and *M. octosetaceus* are figured by Humphrey (MS).

The eiders (characterized by tracheas which lack swellings and which have bullas which are inflated to the left, bulbous in form, and lacking membrane-covered fenestrae) cannot be easily placed with *Clangula, Melanitta, Bucephala,* and *Mergus* on the basis of the structures of the trachea and the tracheal bulla.

The tracheal bullas of *Somateria mollissima* (fig. 1*d*), *S. spectabilis* (fig. 1*b*), and *Lampronetta* (formerly *Arctonetta,* see Parkes, 1955:85–86) *fischeri* (fig. 1*c*) are practically identical in form; they differ from one another only in size. *Somateria mollissima v. nigra* (fig. 1*d*) has the largest tracheal bulla and *Lampronetta fischeri* the smallest; the tracheal bulla of *Somateria spectabilis* is intermediate in size. The tracheal bullas of other races of *Somateria mollissima* are smaller than that of *S. m. v. nigra* but they are slightly larger than that of *Somateria spectabilis*. The left chamber of the tracheal bulla of each of the above three species is expanded mostly laterally; it is expanded slightly in an anterior direction; medially and ventrally the left chamber bulges in a ventral direction. The pessulus is a thin, vertical bar of bone; it is located anteriorly, close to the tracheal aperture of the bulla.

The tracheal bulla of *Polysticta stelleri* (fig. 1*e*) is smaller than those of *Somateria* and *Lampronetta* and differs from them as follows:

1. The left chamber is proportionately less expanded.

2. The left chamber has a prominent ventral protuberance at the posterior ventral margin of the bulla between the bronchial apertures.

3. The pessulus is wide (antero-posteriorly) in *Polysticta*; it is very narrow in *Somateria* and *Lampronetta*.

4. The shape of the left chamber in *Polysticta* differs from that of *Somateria* and *Lampronetta*.

The tracheas of all the eiders except *Polysticta* are of uniform diameter. The trachea of *Polysticta* gradually increases in diameter for the anterior quarter of its length.

The bronchi of all the eiders except *Polysticta* are enlarged, the left one more so than the right. The bronchi of *Polysticta* are not enlarged and are of equal size (figs. 1*d* and 1*e*). The bronchi of all the eiders are very close to one another anteriorly. Males of *Polysticta* are unique among the eiders in having very much enlarged sternotrachealis muscles (compare figs. 1*d* and 1*e*).

Plumage patterns.—On the basis of the plumage patterns of adult and immature females and downy young, Delacour and Mayr's Tribe Mergini can be divided into two groups: (1) the eiders, and (2) the scoters, Old-squaw, golden-eyes, Harlequin, and mergansers.

The eiders are at once distinguished from the other members of the Mergini by the barred, somewhat *Anas*-like pattern of the females. Females of the rest of the Mergini are either more or less uniform sooty brown with various head markings (*Melanitta, Histrionicus*) or they are contrasting, that is, having a brown head with or without markings, and a gray back contrasting with the light, unmarked belly (*Bucephala, Mergus, Clangula*).

The patterns of the downy young of the various species of Mergini fall into two main groups—the eiders in one and the rest of the species in the other. Downy eiders are brown and, except for *Polysticta,* all of them are quite pale. None of them has the bold pattern characteritstic of the golden-eyes, mergansers, scoters, Harlequin, and Old-squaw. All of the downy Mergini except the eiders are either slaty-brown or almost black. The face pattern of the downy eiders consists of a faint, pale superciliary and a fine, dark line through the eye; the other downy Mergini have a light cheek-patch, usually white but entirely or in part reddish-brown in most of the mergansers, contrasting with the dark crown. This cheek-patch is clearly apparent in *Melanitta nigra* and *M. perspicillata,* both of which lack the contrasting body markings of the mergansers, golden-eyes, and others.

Except for the head, the plumage patterns of downy young eiders are practically identical. All have light under parts and darker upper parts. The under parts vary from pale tan to pale grayish brown. Dorsally, the plumage varies from light brown to dark reddish brown and is unrelieved by any light markings. All except *Polysticta stelleri* have a prominent, pale superciliary; *Polysticta* has a narrow, light brown superciliary which does not extend anteriorly to the base of the bill.

Food habits.—I have observed adult Spectacled and Pacific eiders on the nesting grounds in Igiak Bay, Alaska, tipping up for plant food; my few observations lead me to suspect that eiders may take large percentages of plant foods while on the breeding grounds. Eiders take predominantly animal foods when away from the breeding grounds. Unfortunately, there are too few data from adult birds taken on the breeding grounds to describe their feeding habits in that season.

Cottam (1939:93, 104, 113) has described the stomach contents of downy young eiders as follows: *Polysticta stelleri* about 40 per cent plant food, *Somateria mollissima v. nigra* about 70 per cent plant food, and *Lampronetta fischeri* about 45 per cent plant food. The diets of downy young of the scoters, Old-squaw, golden-eyes, and Bufflehead contained no more than 25 per cent plant material (Cottam, *op. cit.*).

The winter (or marine) diets of the eiders (except *Polysticta*) are very similar to those of the scoters (see Phillips, 1926; Madsen, 1954; Cottam, 1939). The winter diet of *Polysticta* seems to be roughly similar to that of *Clangula.*

Diving habits.—Very little is known of the eiders' method of underwater locomotion. There is general agreement that the eiders use their half-spread wings in diving; no one, however, has determined whether or not they use their feet underwater. Bent (1925:89) states that "in diving the wings are partially opened and used to a limited

extent in swimming under water, but the wings are not wholly spread; progress seems to be made mainly by the use of the feet, and there is nothing like the full subaqueous flight practiced by some of the Alcidae." Phillips (*op. cit.*:91) says "there is no question but that Eiders use their wings under water, whether or not they are wounded . . . The Eider uses its wings just as does the Harlequin, held close to the sides and beaten with short jerks, not extended as in aerial flight." My own observations, and those of Frank McKinney (*in litt.*), are in agreement with Phillips' remarks.

When feeding in shallow water on the breeding grounds, eiders tip up like dabbling ducks. I have observed this behavior many times in *Somateria mollissima v. nigra* and *Lampronetta fischeri*; it is probably also a habit of *Somateria spectabilis* and *Polysticta stelleri*.

Genera.—Delacour and Mayr (1945:33) place the four species of eiders in the genus *Somateria* on the ground that differences in plumage patterns and bill shape do not constitute valid generic criteria. I agree with those authors that *Lampronetta* should be placed in *Somateria* for the following reasons:

1. The structure of the trachea and tracheal bulla of *Lampronetta* is practically indistinguishable from that of *Somateria* (see figs. 1*b*, 1*c*, and 1*d*).

2. The plumage pattern of downy young *Lampronetta* differs from that of *Somateria* only in a slight modification of the pattern around the eye.

3. The differences between the plumage patterns of adult male *Lampronetta* and *Somateria* are principally ones of distribution of black on the ventral parts and of pattern on the head; in most other particulars the plumage patterns are very similar.

4. The plumage patterns of the females are very similar, the major peculiarity of *Lampronetta* being the modified pattern around the eye.

5. The skeletal proportions of *Lampronetta* and *Somateria* are very similar.

6. One adult male specimen of *Lampronetta* (Colorado Museum of Natural History No. 8663) has the black gular "V" characteristic of *Somateria spectabilis* and *Somateria mollissima v. nigra*. This V-shaped throat marking has appeared frequently in races of *Somateria mollissima* other than *v. nigra*. Its occurrence suggests that all the forms in which it appears are closely related.

On the other hand, I consider that *Polysticta* should not be merged with *Somateria* for the following reasons:

1. The structure of the tracheal bulla and the associated sternotrachealis muscles of *Polysticta* differ from those of *Somateria* (see figs. 1*b*, 1*c*, 1*d*, and 1*e*).

2. The plumage patterns of adult *Polysticta* are very different from those of *Somateria*. The presence of a speculum in both sexes of *Polysticta* sets that species apart from the species of *Somateria*.

3. The skeletal proportions of *Polysticta* are strikingly different from those of *Somateria*.

4. The bill of *Polysticta* is entirely different from that of *Somateria*. The differences exhibited by the bill of *Polysticta* are not merely exaggerations or modifications of characteristics present in the bills of *Somateria*. The presence of soft skin along the distal half of the "cutting edge" of the upper mandible, and the absence of a well-defined nail not only distinguish *Polysticta* from *Somateria* structurally but also suggest that the species has a method of feeding quite different from that of *Somateria*.

5. In flight *Polysticta* has none of the attributes of the large eiders. *Polysticta* is not only swifter on the wing than any of the species of *Somateria* but it is also much more maneuverable. The flight of Steller's Eider is comparable in speed and maneuverability to that of the Old-squaw; I have seen both species flying together in a small, loose flock.

Systematic position of the eiders.—The structure of the trachea and tracheal bulla

and the plumage patterns of adult and young eiders lead me to believe that these birds are not closely related to the scoters, golden-eyes, and mergansers. In structure, the trachea and tracheal bulla of the eiders and the dabbling ducks (Anatini) are very similar; likewise, the plumage patterns of the females of both groups have much in common. I believe that the eiders are much more closely related to the dabbling ducks than they are to the scoters, golden-eyes, and mergansers. The diets of downy eiders consist of from 40 to 70 per cent plant food; presumably the adults on the breeding grounds also consume a great deal of plant material. Although much more information is needed on the diets of the eiders on their breeding grounds, my observations suggest that their summer feeding habits resemble those of the dabbling ducks, which depend largely on plant food. Furthermore, the eiders' method of feeding in shallow water on the breeding grounds (tipping up) is very similar to that of the dabbling ducks.

The eiders probably developed from a group of dabbling ducks (Anatini) that invaded the marine coastal habitat. There, the ancestral eiders presumably developed feeding habits in which animal material played an increasingly important role. Development of the diving adaptation enabled these birds to utilize food resources in deeper water. Most dabbling ducks dive occasionally; in diving, they use their half-opened wings as the means of underwater propulsion. The marine coastal nesting distribution of the eiders and their dependence on the wings as an important means of underwater locomotion lead me to think that they underwent the early stage of their adaptive evolution in that environment.

Delacour's (1956:17) suggestion that the eiders be placed in a separate tribe, the Somateriini, next to the Anatini, seems to me the most satisfactory arrangement.

SUMMARY

The tracheal structure, plumage patterns, food habits, and diving habits of the genera in the Tribe Mergini (Delacour and Mayr, 1945) are compared.

It is concluded that the eider genus *Lampronetta* should be placed in the genus *Somateria,* but that *Polysticta* should be maintained as a separate genus.

It is further concluded that the eiders have their closest relationships with the Anatini, and that they should be placed in a separate Tribe Somateriini, next to the Anatini, as proposed by Delacour (1956).

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