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A NEW MERGANSER FROM THE MIOCENE OF VIRGINIA (AVES: ANATIDAE)

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Abstract.—A new species of merganser, *Mergus miscellus*, based on a pelvis with associated tibiotarsi and tarsometarsi from the Middle Miocene Calvert Formation of Virginia, provides the first Tertiary record for the genus and the earliest for the tribe Mergini. The species combines a specialized morphology of the tarsometatarsus, such as seen in Recent *Mergus* (*sensu stricto*) with a more primitive morphology of the pelvis similar to Recent *Mergellus*. Certain characters of the fossil support the presumed relationship between mergansers and goldeneyes (*Bucephala*). A fragmentary ulna representing an indeterminate genus and species of sheldrake (Tadornini) from the Calvert Formation in Maryland is also reported.

In recent years there has been a remarkable increase in the number of specimens of fossil birds known from Tertiary marine deposits of the eastern United States. Although there are several species of ducks represented among the thousands of seabird fossils from the early Pliocene Yorktown Formation in North Carolina (Olson and Wetmore, in press; Alvarez, in prep.), of almost 150 undescribed fossil bird specimens now in the National Museum of Natural History from earlier (Middle and Upper Miocene) deposits in Maryland and Virginia (Calvert, Choptank, St. Marys, and as yet unnamed beds) there are as yet but two specimens referable to the Anatidae. These consist of a pelvis associated with right and left tibiotarsi and tarsometatarsi (USNM 237150) belonging to a diving duck of the tribe Mergini, and the proximal end of a left ulna (USNM 25926), tentatively referred to the Tadornini (sheldrakes). Both specimens are from the Middle Miocene Calvert Formation, and were deposited in an offshore marine environment. Descriptive osteological terminology follows Howard (1929).

Order ANSERIFORMES
Family Anatidae
Subfamily Anatinae
Tribe Mergini

That the associated elements of USNM 237150 are those of a diving duck is shown by features of the tarsometatarsus, particularly the lateral compression of the shaft and trochleae and the elevation and lateral rotation of the inner trochlea. Only the tribes Aythyini, Somateriini, Mergini, and Oxyurini need therefore be considered further.

Comparisons at the tribal level.—The fossil differs from the Aythyini

(pochards) in that the shaft of the tarsometatarsus is more slender and the inner trochlea more rotated; the distal third of the tibiotarsus is stouter; the proximal margin of the outer cnemial crest of the tibiotarsus is at a diagonal to the long axis of the shaft instead of nearly perpendicular; and the anterior margin of the inner cnemial crest is longer.

From the Somateriini (eiders) the fossil differs in the more compressed trochleae and much less medially expanded internal cotyla of the tarsometatarsus, and in having the postacetabular portion of the pelvis longer than the preacetabular portion, whereas these are of about equal length in eiders.

The Oxyurini (stiff-tailed ducks) are very different, with the tarsometatarsus much shorter and stouter, the trochleae less compressed, the tibiotarsus with its distal end bent farther medially, the prominence for the groove of M. peroneus profundus better developed, and the pelvis much narrower and more heavily ossified.

The fossil agrees with the Mergini (sea ducks) and differs from the other tribes of diving ducks in the very slender, laterally compressed shaft and more posteriorly directed inner trochlea of the tarsometatarsus, and in having the outer cnemial crest of the tibiotarsus relatively narrower and more posteriorly oriented.

Comparisons within the tribe Mergini.—Compared to the fossil, the tarsometatarsus in *Melanitta* has the trochleae much broader and more widely separated, the inner trochlea more anteriorly and medially directed, the external surface of the outer trochlea swollen anterior to the excavation on its lateral surface, the anterior opening of the distal foramen relatively wider, the posterior metatarsal groove narrower and less sharply defined, the distal expansion of the shaft greater to accommodate the wider trochleae, the anterolateral margin of the shaft more concave in lateral view, and the lateral surface of the shaft more curved in anterior view. In the tibiotarsus of *Melanitta*, the distal end is more expanded, the distal tendinal opening is larger, the external condyle in lateral view is less rounded, and the fibular crest is longer. The pelvis of *Melanitta* is narrower and longer, particularly anterior to the acetabulum, and the acetabulum is much larger in relation to the antitrochanter.

In the tarsometatarsus of *Histrionicus*, the tubercle for M. tibialis anticus is more swollen, the curvature of the lateral surface of the shaft is more pronounced in anterior view, the outer trochlea is more elevated in posterior view, the outer extensor groove is broader, the inner trochlea is more anteriorly directed, and the shaft is stouter and much flatter anteriorly. The proximal margin of the outer cnemial crest of the tibiotarsus of *Histrionicus* is nearly perpendicular to the shaft, as in *Aythya*, and the distal tendinal opening is much larger than in the fossil. The preacetabular portion of the pelvis is much shorter and broader in *Histrionicus* than in the fossil.

In *Clangula*, the tarsometatarsus is relatively shorter with the proximal

and distal ends more expanded, the outline of the medial edge of the middle trochlea is rounder in medial view, the outer extensor groove is deeper, the tubercle for M. tibialis anticus is more swollen, and the anterolateral margin of the shaft is more concave in lateral view. The external condyle of the tibiotarsus of *Clangula* projects farther medially from the shaft and the pelvis is markedly broader and shallower than in the fossil.

The tarsometatarsus of *Bucephala* differs from that of the fossil in having the trochleae wider both individually and collectively, the shaft wider in anterior view and more deeply excavated proximally, the shaft not as deep in either lateral or medial views, the inner trochlea more anteriorly directed, and the outer extensor groove broader. The tibiotarsus of *Bucephala* differs from that of the fossil in having the inner cnemial crest extending farther proximally and being much more pointed at its proximal apex, with the proximal margin of the outer cnemial crest ascending much more vertically and being less rounded; the outer crest is smaller and less laterally expanded. Also, the anterior intercondylar fossa in distal view is broader in the fossil than in *Bucephala*. The pelvis of *Bucephala* is broader posteriorly, and narrower and much shorter anterior to the acetabulum than in the fossil.

The tarsometatarsus of *Lophodytes* differs from that of the fossil in being much shorter and relatively stouter, and in having the outer trochlea more elevated in posterior view, the anterior face of the shaft not as deeply excavated beneath the hypotarsus, and the anteromedial edge of the middle trochlea rounder in outline. The tibiotarsus of *Lophodytes* is much shorter, the inner cnemial crest is more pointed at its proximal apex, and the proximal margin of the outer cnemial crest forms a straight rather than a gently curving line. The fossil pelvis differs from *Lophodytes* in having the preacetabular portion relatively longer and the pectineal processes shorter.

The fossil tarsometatarsus differs from that of *Mergellus* in its much larger size and more slender proportions and in having the inner trochlea more compressed and posteriorly directed. The inner cnemial crest of the tibiotarsus of *Mergellus* is more pointed at its proximal apex, the internal ligamental attachment extends farther distally, and the outer cnemial crest is more anteriorly directed. The fossil pelvis is similar in proportions to that of *Mergellus*, but differs in having the ilioischiatic fenestrae relatively longer.

Shared and apparently derived characters which argue strongly for inclusion of the fossil form in the modern genus *Mergus* (*sensu stricto*) are the long slender proportions of the tarsometatarsus, the greater posterior rotation of the inner trochlea, the greatly elongate posterior articulating surface of the inner trochlea, the marked depth and narrowness of the middle and outer trochleae in posterior view, and the narrowness of the

anterior opening of the distal foramen, which lies at an oblique angle to the shaft. The fossil tibiotarsus also shows a greater similarity to *Mergus* than to any of the other genera of Mergini. The fossil elements are referable to the genus *Mergus*, but they present sufficient differences from the living species of the genus to warrant recognition as a new species.

Mergus miscellus, new species
(Figs. 1, 2, 3a, b)

Holotype.—Pelvis with associated right and left tibiotarsi and right and left tarsometatarsi in varying states of imperfection. Vertebrate paleontological collections of the National Museum of Natural History, USNM 237150.

Locality and horizon.—Stratford Cliffs, 2 m above beach, 100 m west of east end of set of cliffs immediately east of Little Meadow Swamp, Westmoreland County, Virginia (.85 miles ESE of Maryland–Virginia boundary monument 25; 1.55 miles NNW of Stratford Plantation boundary marker A). Basal part of Zone 13, Calvert Formation, Middle Miocene. Collected by Robert Weems in the summer of 1966.

Measurements.—Left tarsometatarsus: length from intercotylar prominence to most distal point of middle trochlea, 43.6 mm; width through cotylae, 8.4; width of shaft at midpoint of overall length, 3.9; external depth at same point, 4.3; breadth through trochleae, 8.3; breadth through middle and outer trochleae combined, 7.2; depth of inner trochlea, 5.6; width of inner trochlea, 3.0; width of middle trochlea, 3.9; width of outer trochlea, 3.0. Right tibiotarsus: length from external articular surface to most distal point of external condyle, 77.7; greatest width through proximal articular surfaces, 8.5; width of shaft at distal end of fibular crest, 5.1; internal depth at same point, 3.6; width through condyles, 8.8. Pelvis: length of synsacrum, 76.9; width across antitrochanters, 29.2; diameter of acetabulum, 5.4; distance from midline of acetabulum to anteriormost and posteriormost portions of synsacrum, respectively, 32.3, 46.9.

Etymology.—L. *miscellus*, mixed, in allusion to the combination of primitive and derived characters shown by the species.

Diagnosis.—Comparable in size to Recent *Mergus serrator*. *M. miscellus* differs from Recent species of *Mergus* in having (1) the shaft of the tarsometatarsus relatively deeper, with the anterolateral edge elevated above the anteromedial edge for over half the total length of the bone, (2) the inner trochlea more compressed and posteriorly directed, (3) the wing of the inner trochlea with a distinct projection on its posteroproximal edge, and (4) the external margin of the distal foramen a straight ridge of bone lying nearly parallel to the long axis of the shaft. The tibiotarsus of *M. miscellus* closely resembles that of living species of *Mergus*, the

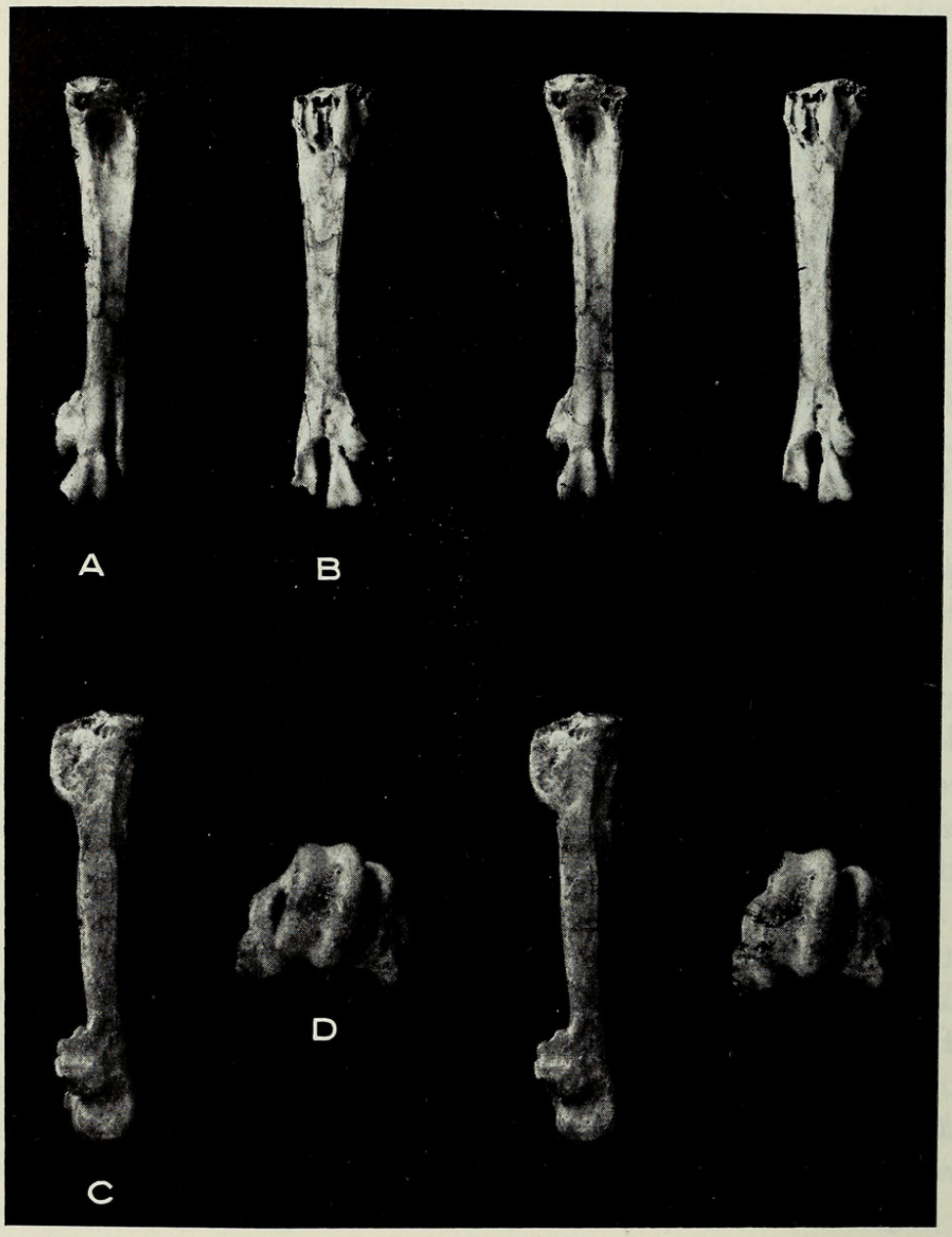

Fig. 1. Right tarsometatarsus of holotype of *Mergus miscellus* (USNM 237150). Stereo pairs: a, anterior view; b, posterior view; c, medial view; d, distal view. a–c, about natural size; d, 2×.

primary differences being the shorter inner cnemial crest and the more curved proximal margin of the outer cnemial crest of the fossil. The ilioischiatic fenestrae of the fossil pelvis are long, as in mergansers and not as in other Mergini. The pelvis of *M. miscellus*, however, is more similar in proportions to that of *Mergellus albellus*, and is not as long and narrow as in the larger, more specialized Recent species of *Mergus*. The combination of highly specialized features of the tarsometatarsus with an apparently primitive pelvic morphology distinguishes *M. miscellus* from any known mergansers of the genera *Mergus*, *Mergellus*, and *Lophodytes*.

Description.—Tarsometatarsus with medial and lateral surfaces of shaft

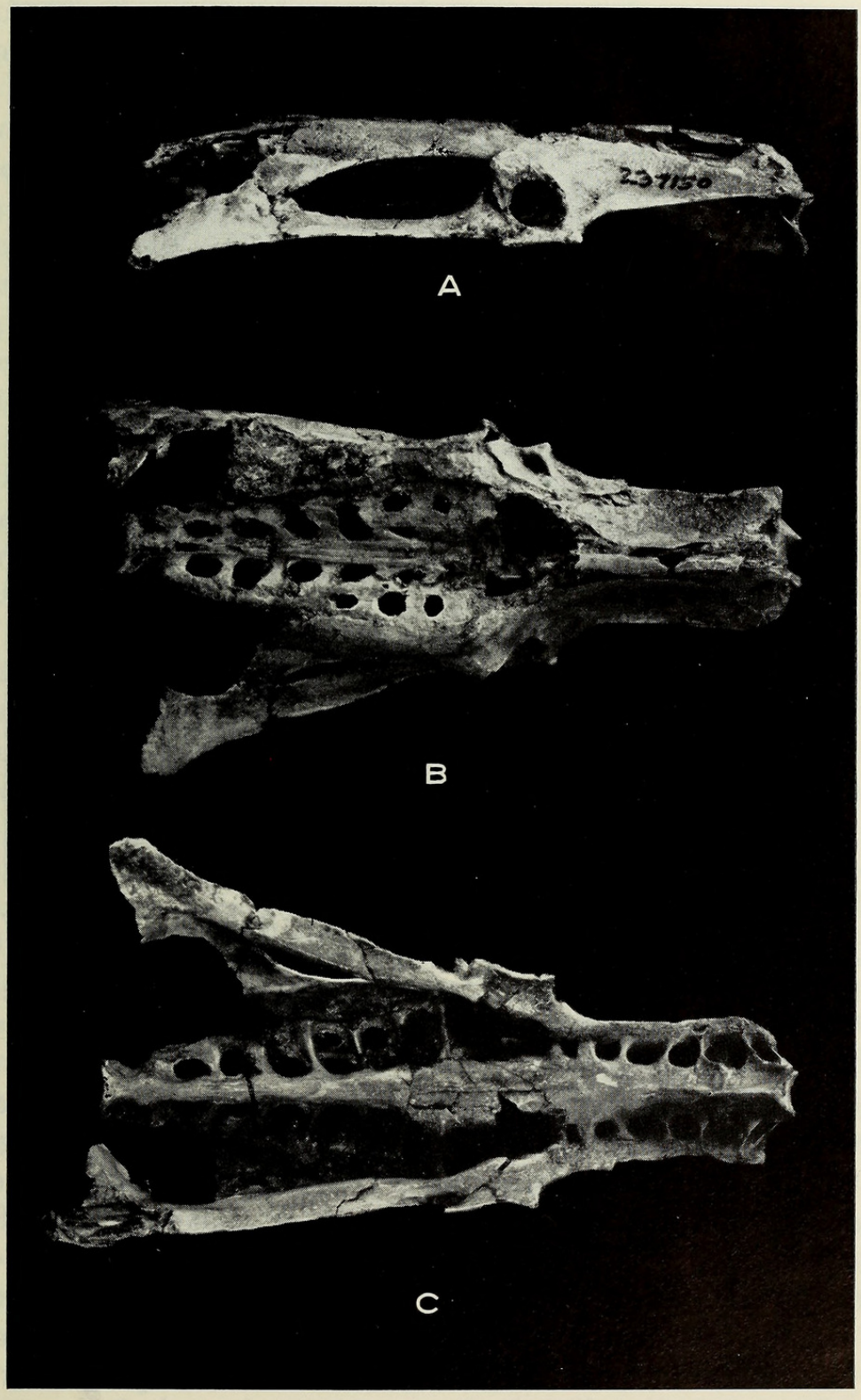

Fig. 2. Pelvis of holotype of *Mergus miscellus* (USNM 237150). a, right lateral view; b, dorsal view; c, ventral view. All figures about natural size.

flat and relatively straight in anterior view, showing little curvature proximally or distally; inner extensor groove shallow; posterior metatarsal groove broad; distal portion of shaft only slightly expanded; trochleae very narrow, giving the distal end of the bone a compressed appearance; outer

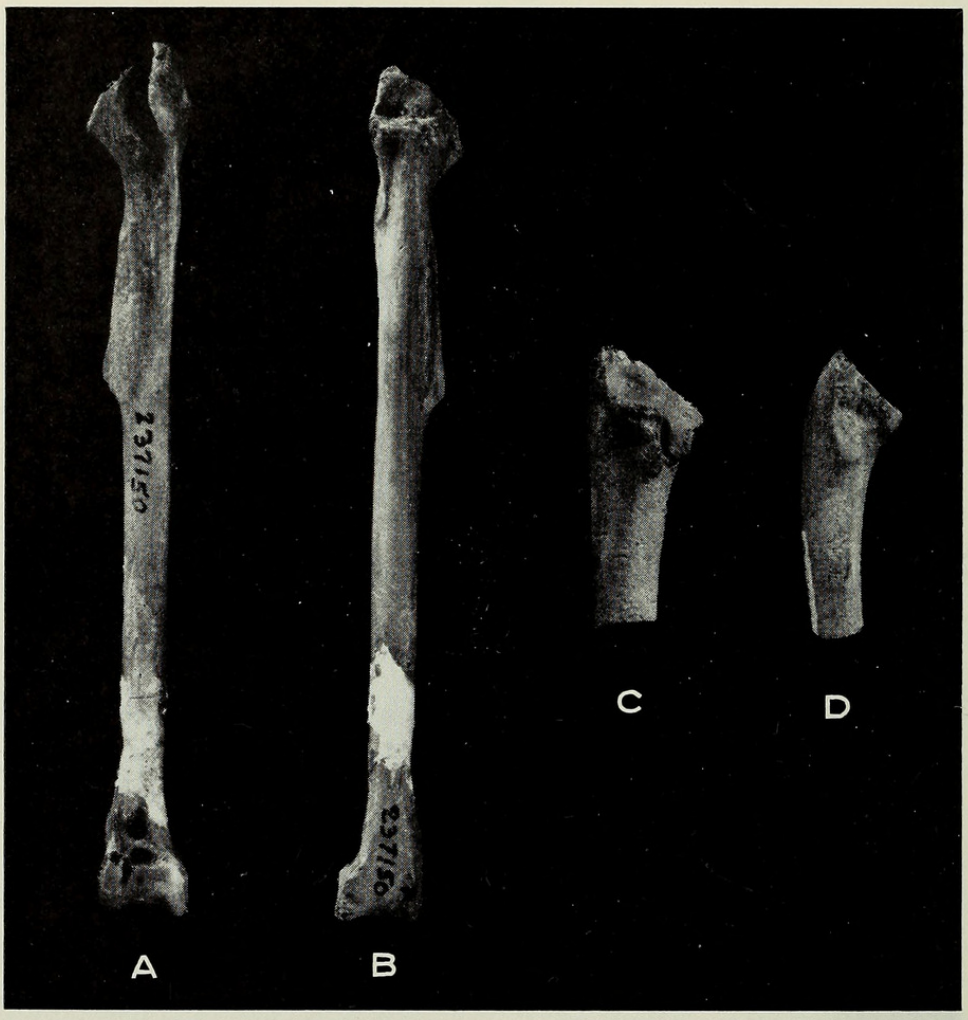

Fig. 3. a, right tibiotarsus of holotype of *Mergus miscellus* (USNM 237150), anterior view (inner cnemial crest warped laterally); b, same, posterior view; c, proximal end of left ulna of Tadornini gen. et sp. indet. (USNM 25926), internal view; d, same, anconal view. All figures about natural size.

extensor groove narrow and fairly deep; region anterior to excavation on lateral surface of outer trochlea flat; in lateral view the lateral edge of the middle trochlea extending farther anteriorly than the medial edge of the outer trochlea; and posterior surface of shaft depressed at base of middle trochlea.

Tibiotarsus in posterior view with the area beneath the internal articular surface deeply excavated; surface posterior to inner cnemial crest and directly anterior to internal articular surface with a deep, circular pit; internal ligamental attachment proximal to fibular crest; and posterior intercondylar sulcus flat.

Tibiotarsus in lateral view with outer cnemial crest laterally directed, its proximal edge nearly parallel to external edge of fibular crest; medial edge of shaft elevated above lateral edge toward distal end of bone; and external ligamental prominence moderately developed.

Tibiotarsus in anterior view with upper and lower margins of supratendinal bridge curved; groove for M. peroneus profundus very narrow, nearly obsolete; distal opening of tendinal groove oval; anterior intercondylar sulcus traversed by a conspicuous, narrow groove at the level of the apex of the internal ligamental prominence; and distal extensions of internal and external condyles equal.

Tibiotarsus in medial view with inner cnemial crest wide and bluntly flattened at its proximal apex; internal ligamental prominence moderately developed; and internal condyle extending farther anteriorly than external condyle.

Pelvis relatively wide; posterior iliac crest smoothly rounded directly above the ilioischiatic fenestra; and pectineal process short and sharply pointed.

Remarks.—Of the seven Recent species of mergansers, two are Holarctic in distribution (*Mergus serrator*, *M. merganser*), two Palearctic (*Mergellus albellus*, *Mergus squamatus*), one Nearctic (*Lophodytes cucullatus*), one has a limited distribution in southern Brazil and adajacent regions of Argentina and Paraguay (*Mergus octosetaceus*), and one extinct form (*Mergus australis*) is known historically from the Auckland Islands and from subfossil remains in New Zealand (Kear and Scarlett, 1970). *Mergus miscellus* provides the only Tertiary record of a merganser and the earliest record for the tribe Mergini.[1]

Although most authorities (Delacour, 1959; Johnsgard, 1960) now place the genera *Lophodytes* and *Mergellus* in *Mergus*, Woolfenden (1961) considered the differences in postcranial osteology of these forms sufficient to warrant the recognition of all three genera. Our observations confirm that these differences do indeed exist. We have continued to use the terms *Lophodytes* and *Mergellus* as a means of facilitating discussion and description; we reserve judgment on the actual generic value of these distinctions. The term *Mergus* is used in this paper only to refer to the five larger species of mergansers (i.e., *Mergus* in the strict sense of Woolfenden and many earlier authors).

Osteological specializations for diving in ducks and other birds include a progressive elongation and narrowing of the pelvis (Raikow, 1970), and lateral compression of the tarsometatarsus with narrowing of the trochleae and a more posterior rotation of the inner trochlea. With respect to the manner in which these characters are manifested in mergansers, *Lophodytes*, which has the broadest pelvis and the shortest and least compressed tarsometatarsus, appears to be the most primitive, while the species of *Mergus* are the most derived, with *Mergellus* being intermediate. The tarsometatarsus in *Mergus* is more compressed, with narrower trochleae and a more posteriorly rotated inner trochlea than in any of the Mergini, or, for that

matter, than in any of the other diving ducks. The species *miscellus* shares with *Mergus* these same highly derived characters of the tarsometatarsus.

It is of interest, however, that the pelvis in *M. miscellus* is not as elongate and narrow as in the Recent species of *Mergus* but instead is most similar to that of *Mergellus*. This suggests that in *Mergus*, the diving specializations of the tarsometatarsus evolved before those of the pelvis. This in turn implies differential rates of evolution in the components of the pelvic assemblage and that the evolution of diving specializations of the foot is not linked to that of the pelvis as a single functional complex.

Woolfenden (1961:115) listed ten osteological characters that are shared between the mergansers and the goldeneyes (*Bucephala*) and which set this group apart from the other genera of Mergini. Of these, the straight external edge of the outer trochlea and the nearly straight diagonal line of the proximal edge of the outer cnemial crest are observable in *M. miscellus*, confirming its allocation to the merganser-*Bucephala* assemblage. We also found similarities between *M. miscellus* and *Bucephala* that are not shared by other mergansers. In the marked anterior extension of the anterolateral edge of the shaft of the tarsometatarsus, and the short rather than elongate pectineal process of the pelvis, *M. miscellus* agrees with *Bucephala* (and also with *Mergellus* in the case of the latter feature) and differs from *Lophodytes* and *Mergus*. These characters of *M. miscellus* tend to corroborate the relationship between the mergansers and *Bucephala* postulated by Delacour and Mayr (1945), Woolfenden (1961), and others, and which is supported as well by behavioral evidence (Johnsgard, 1960, 1961). Perhaps the most compelling evidence for such a relationship comes from the fact that *Bucephala clangula* has been known to hybridize with *Lophodytes cucullatus*, *Mergellus albellus*, and *Mergus merganser* (Johnsgard, 1960). This indicates a degree of genetic compatibility between *Bucephala* and the mergansers. *Mergus miscellus* shows that the divergence of mergansers from *Bucephala* had to have taken place prior to the Middle Miocene. Thus, the genetic compatibility between *Mergus* and *Bucephala* has persisted in excess of 14 million years, this being the approximate age of the Calvert Formation (Blackwelder and Ward, 1976).

Tribe Tadornini
Genus and Species Indeterminate

In order to complete the present record of the Anatidae in the Calvert Formation, we include mention of a specimen that is too imperfect to merit a name but that is still of interest. This is the proximal fourth of a left ulna (USNM 25926) collected by Albert C. Myrick on 22 June 1969 from Zone 14 in the Calvert Formation, 400 m south of Governor's Run Road, Calvert County, Maryland (Fig. 3c, d). The olecranon is somewhat abraded and the outer layer of bone on the shaft appears to have been etched away.

After examining a wide variety of anatid skeletons, we found this fragment to bear a decided resemblance to the Tadornini (sheldrakes), and particularly to *Tadorna*. It resembles *Tadorna* and differs from other tribes of Anatidae in the greater distal projection of the internal surface of the external cotyla and in the more elongate and more proximally situated prominence for the anterior articular ligament; a distinct ridge runs from this prominence to a transverse groove across the internal face of the olecranon. In size and proportions the fossil closely resembles the Recent species of *Tadorna*.

No members of the Tadornini occur in North America today, although the extinct genera *Anabernicula* Ross and *Brantadorna* Howard from the Pleistocene of western North America have been assigned to the Tadornini (Brodkorb, 1964). The significance of the present fossil lies mainly in adding another element to the Calvert avifauna.

Acknowledgments

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Footnote

[1] A worn cervical vertebra from the Lower Pliocene of India was referred to as "*Mergus* (?) sp." by Lydekker (1890:142) but this assignment is too dubious to merit consideration as Lydekker had only a specimen of *M. serrator* with which to compare it and from this the fossil was said to differ in being "shorter and wider."