THE OSTEOLOGY AND TAXONOMIC POSITION OF THE WHITE-BACKED DUCK, *THALASSORNIS LEUCONOTUS*

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THE White-backed Duck (*Thalassornis leuconotus*) of Africa and Madagascar is one of the least-studied members of the family Anatidae. There appears to be little detailed information as to its general behavior in nature, except that it is an inhabitant of quiet ponds, feeding both on the surface and by diving (Delacour, 1959). The food includes both plant and animal materials (Clancey, 1964). Until recently little was known about its structure and habits, but current studies suggest that its original classification was in error. Eyton (1838, not seen) allied it with the stifftail ducks, which are currently listed as the tribe Oxyurini of the subfamily Anatinae (Johnsgard, 1968). Verheyen (1955) classified the Anatidae on the basis of comparative osteology, but was unable to determine the relationships of *Thalassornis*, which he listed as Incertae Sedis, though possibly related to the stifftail genus *Oxyura*. Delacour and Mayr (1945) presented a thorough revision of the Anatidae in which they retained *Thalassornis* in the Oxyurini, but noted the resemblance of its call to that of *Dendrocygna*. Most recently Johnsgard (1967) argued that *Thalassornis* is not related to the Oxyurini at all, but instead bears a close affinity to the whistling ducks (*Dendrocygna*) of the subfamily Anserinae, and subsequently (1968) placed both genera in the tribe Dendrocygnini. This opinion is based upon several features, including the absence of stiffened rectrices and inflatable throat pouches, the reticulate tarsal pattern, the structure of the trachea, and numerous behavioral characters, including sexual, aggressive, and maintenance behavior patterns.

In this paper I will evaluate the skeleton of this species both from the standpoint of its taxonomic significance and its locomotor specializations. Together these should add to our understanding of the phylogenetic history of this little known form.

METHODS AND ACKNOWLEDGMENTS

I compared a skeleton of *Thalassornis leuconotus* with representatives of all three subfamilies of Anatidae, including *Anseranas semipalmata* (Anseranatinae); *Cygnus columbianus*, *Anser* (*Chen*) *caerulescens*, *Branta canadensis*, *Dendrocygna autumnalis*, *D. bicolor*, and *D. javanica* (Anserinae); and *Anas platyrhynchos*, *Heteronetta atricapilla*, *Oxyura jamaicensis*, and *Biziura lobata* (Anatinae). The last three species represent the tribe Oxyurini, with which *Thalassornis* was originally associated. All specimens except those listed below are from the collection of the Museum of Vertebrate Zoology, University of California, Berkeley. I am grateful to Dr. Richard L. Zusi of the United States

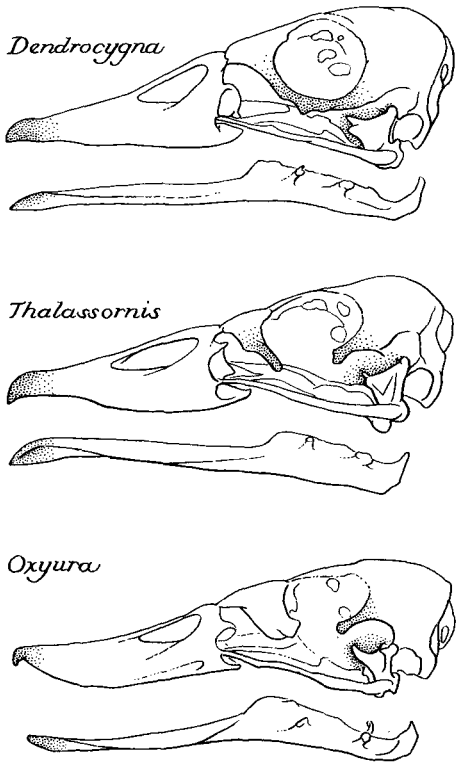

FIG. 1. Lateral views of the skulls of *Dendrocygna autumnalis, Thalassornis leuconotus,* and *Oxyura jamaicensis. Thalassornis* resembles *Dendrocygna* in the straight dorsal margin of the quadrate, the decurved mandibular symphysis, the straighter retroarticular process, and the more vertically oriented maxillae (not apparent in this view). It differs in lacking a complete suborbital bar. (Not to scale.)

National Museum for the loan of a skeleton of *Thalassornis* (U.S.N.M. 431502), and to Dr. Robert W. Storer of the University of Michigan Museum of Zoology for loaning me specimens of *Heteronetta.* The illustrations were drawn by Gene M. Christman.

THE SKULL

The most characteristic feature of the skull in *Dendrocygna* is that the foot of the lacrimal usually extends posteriorly to fuse with the postorbital process, forming a complete suborbital bar. This has otherwise been reported in the Anatidae only in some specimens of *Cereopsis* (Beddard, 1898:468). This fusion does not occur in *Thalassornis* (Fig. 1).

The quadrate of *Thalassornis* resembles that of *Dendrocygna* because its dorsolateral margin is straight, running from the otic process past the base

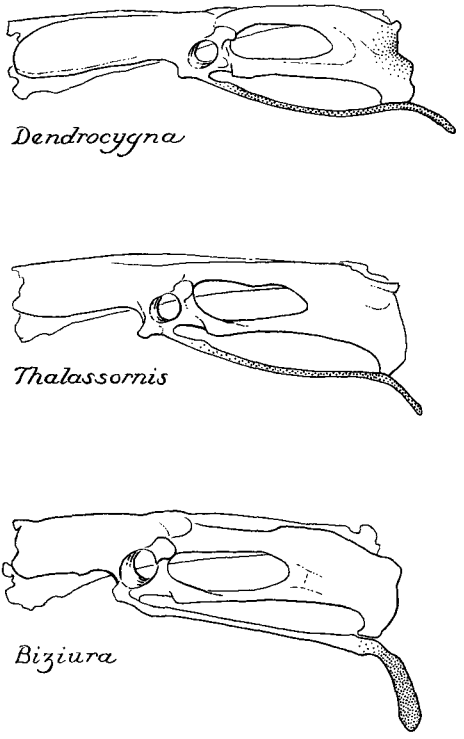

FIG. 2. Lateral views of the pelvic girdles in *Dendrocygna bicolor*, *Thalassornis leuconotus*, and *Biziura lobata*. *Thalassornis* resembles *Dendrocygna* in the form of the pubis, but otherwise is convergent to *Biziura*, especially in its relative proportions, which indicate a greater degree of adaptation for diving than in *Dendrocygna*. Further details are given in the text.

of the orbital process. In all other waterfowl examined this margin is concave, so that the orbital and otic processes are more distinctly set apart from the body of the quadrate.

The upper jaw of *Thalassornis* resembles that of *Dendrocygna* in that the maxillae are more vertically oriented than in the Oxyurini, where they diverge ventrally. Thus in *Dendrocygna* and *Thalassornis* the concave roof of the mouth is deeper than in stifftails.

The lower jaw of *Thalassornis* resembles that of *Dendrocygna* because the posterior edge of the retroarticular process is straight, while in the Oxyurini (except *Biziura*) it is rounded. Furthermore, in *Thalassornis* and *Dendrocygna* the mandibular symphysis is sharply decurved, while in the

Oxyurini it is not decurved at all (*Oxyura, Biziura*) or only slightly so (*Heteronetta*).

POSTCRANIAL SKELETON

The postcranial skeleton of waterfowl was studied by Woolfenden (1961) who included nearly all living genera, but not *Thalassornis*. In examining this genus I have used various criteria presented by Woolfenden by which the subfamilies and tribes of waterfowl may be distinguished. These criteria consist mainly of surface features and relative proportions of a number of bones, and I have chosen those which clearly distinguish the Oxyurini from *Dendrocygna*. Most require no explanation, and are listed in Table 1.

DISCUSSION

Woolfenden (1961:48) states that the coracoidal depression (Table 1, no. 14) will distinguish the coracoid of *Dendrocygna* from that of any other bird. A similar, but very shallow depression occurs also in *Thalassornis*, displacing the intermuscular line posteriorly exactly as in *Dendrocygna*, and indicating a relationship with that genus.

In general the postcranial skeleton of *Thalassornis* bears nearly as many similarities to that of the Oxyurini as to that of *Dendrocygna*. This could be interpreted as suggesting that the White-backed Duck is related to either one of these groups and convergent on the other. However, in view of the similarities of the quadrate and jaws, the findings of Johnsgard (cited above), and the presence of features highly characteristic of *Dendrocygna* (Table 1, nos. 14 and 30) according to the analysis of Woolfenden (1961), it seems most probable that *Thalassornis* is in fact a stifftail-like whistling duck.

This view is supported by the fact that many of the stifftail-like characters listed in Table 1 are part of an adaptive specialization for swimming and diving. Thus in *Thalassornis* the sternum is relatively wide (Table 1, no. 13). This is possibly associated with a widening of the body to make it more stable when swimming on the surface. The sternum is comparatively wide in *Biziura* and *Oxyura*, both excellent divers, but is relatively narrow in *Dendrocygna*. It is also narrow in *Heteronetta*, a less specialized diver. *Dendrocygna* spends much time out of the water, but the stifftails and *Thalassornis* typically rest on the water, being nearly helpless on land.

The pelvic proportions (Table 2), with an elongated postacetabular region and a general lateral compression, are similar to those associated with an abducted hind limb posture in *Oxyura* and *Biziura*. This posture is efficient for swimming, but the splayed, posteriorly placed feet makes walking difficult or impossible. The form of the cnemial crest (Table 1, no. 24) also appears convergent to the condition in these genera, where it is associated

TABLE 1

COMPARISON OF FEATURES OF THE POSTCRANIAL SKELETON OF *DENDROCYGNA*, *THALASSORNIS*, AND THE *OXYURINI*

Feature	*Dendrocygna*	*Thalassornis*	*Oxyurini*
Humerus			
1. Capital shaft ridge.	Prominent.	Prominent.	Less prominent.
2. Elevated area of pectoral attachment.	Circular.	Circular.	Elongate.
3. Pneumatic fossa.	Deep, with numerous foramina.	Shallow, with few or no foramina. Most resembles *Biziura*.	Shallow, with numerous foramina.
4. Scar of *M. latissimus dorsi posterioris*.	Mediad to outer edge of pectoral attachment.	In line with outer edge of pectoral attachment.	In line with outer edge of pectoral attachment.
5. Entepicondyle.	Relatively large.	Relatively large.	Relatively small.
Carpometacarpus			
6. Upper surface of metacarpal II.	Relatively flattened.	Relatively flattened.	Relatively rounded.
7. Extensor attachment.	Limited to tip of process of metacarpal I.	More limited, as in *Dendrocygna*.	Extends onto distal edge of process.
8. Shape of metacarpal II.	Incurved.	Incurved.	Not incurved.
9. External rim of carpal trochlea.	Slightly notched.	Slightly notched.	More deeply notched.
Sternum			
10. Sternal basin.	Deep.	Intermediate.	Shallow.
11. Pneumatic foramen.	Present.	Lacking.	Lacking or minute.
12. Ventral manubrial spine.	Lacking.	Lacking.	Present (except *Biziura*).
13. Relative width of sternum (medial width/length).	0.45.	0.65.	0.39 (*Heteronetta*); 0.58 (*Biziura*); 0.63 (*Oxyura*).
Coracoid			
14. Depression on ventral surface in angle between sternal facet and intermuscular line.	Deep.	Shallow.	Lacking.

TABLE 1 (Continued)

Feature	*Dendrocygna*	*Thalassornis*	*Oxyurini*
Furculum			
15. Coracoidal tuberosity.	Minute.	Minute.	Larger.
Pelvic Girdle (Fig. 2)			
16. Posterior end of ischium.	Extends considerably posterior to end of ilium.	Extends to about the same level as end of ilium.	Extends to about the same level as end of ilium.
17. Relative proportions.	Poorly specialized for diving.	Highly specialized for diving (see discussion).	Highly specialized for diving.
18. Body of pubis.	Concave dorsally.	Concave dorsally.	Straight or convex dorsally.
19. Postischiac pubis.	Short, weak, and more caudally directed.	Short, weak, intermediate in orientation (see Figure 2).	Longer, stouter, more ventrally directed.
Femur			
20. Anterior ridge of external condyle.	Elevated from trend of shaft.	Intermediate.	Not elevated.
21. Anterior surface of femur.	Concavity present two-thirds of way from proximal end.	Concavity as in *Dendrocygna*.	Concavity with a different terminal configuration.
22. Popliteal fossa.	Shallow.	Shallow.	Deep.
23. Anterior edge of trochanter.	Extends some distance anterior to head of femur.	Reduced.	Reduced.
Tibiotarsus			
24. Axis of inner cnemial crest.	Rotated sharply anterior to axis of shaft.	More nearly parallel to axis of shaft.	More nearly parallel to axis of shaft (except *Heteronetta*).
27. Orientation of inner cnemial crest.	Strongly directed laterally.	Only slightly directed laterally.	Only slightly directed laterally (except *Heteronetta*).
28. Depression between cnemial crests.	Relatively shallow.	Relatively deep.	Relatively deep (except *Heteronetta*).
29. Internal condyle.	In line with edge of shaft when viewed anteriorly.	Extends medially beyond shaft, resembling *Oxyura*.	Extends medially well beyond shaft.
Tarsometatarsus			
30. Trochlea for digit II.	Not grooved.	Intermediate. Shallow groove does not reach posterior face of trochlea.	Well developed groove all around articular surface of trochlea.

TABLE 2

RELATIVE PROPORTIONS OF THE PELVIC GIRDLE IN SEVEN SPECIES OF WATERFOWL
(Mean Values × 100)

Species and number	Post-acetabular length (Total length)	Anterior iliac width (Total length)	Interacetabular width (Total length)	Posterior ischiac width (Total length)
Thalassornis leuconotus (1)	61	19	17	42
Dendrocygna bicolor (3)	54	24	20	41
D. autumnalis (3)	56	24	20	40
D. javanica (1)	53	24	20	34
Heteronetta atricapilla (3)	60	22	23	53
Oxyura jamaicensis (21)	61	20	20	62
Biziura lobata (8)	68	21	14	48

with specializations of the shank musculature. Further details of these functional specializations in the Oxyurini are discussed in Raikow (1970).

There is one feature in which an adaptive convergence with the stifftails has apparently not occurred. In the Oxyurini the tail, with its long, stiffened rectrices, is used as an underwater rudder. In *Thalassornis*, however, the tail is very short. Delacour (1959:252) reported that the short rectrices are stiffened, but Johnsgard (1968:81) claimed that they are unstiffened. In any event, the structure of the caudal skeleton and pelvis suggests that the tail is probably not used as a rudder in *Thalassornis*. The pygostyle is relatively smaller than in the stifftails. The Oxyurini are characterized by a long and sturdy postischiac pubis (Table 1, no. 19), the area of origin of certain well-developed caudal muscles. This bone is quite feeble in *Thalassornis*, closely resembling that of *Dendrocygna* (Fig. 2).

The evidence thus suggests that *Thalassornis* is an aberrant whistling duck more highly specialized for swimming and diving than *Dendrocygna*, and convergent in this adaptation to the stifftail ducks of the tribe Oxyurini. Whistling ducks are notable for the fact that they are not highly specialized for walking, swimming, or diving, but are rather generalized in their locomotor habits. Their actions underwater are apparently not extremely efficient. Frith (1967) says of *Dendrocygna arcuata*: "Although it secures much of its food underwater, its movements and swimming are clumsy." An underwater photograph of this species (Frith, 1967, opposite p. 74) shows that it swims with the legs greatly adducted, whereas the most specialized diving ducks, including the stifftails, utilize a highly abducted leg posture (Raikow, 1970). Whether the latter posture is also utilized by *Thalassornis* is not known, but its skeletal structure and inability to walk on land suggest that this is likely.

It thus appears that *Thalassornis* is the only highly specialized diving form known in the subfamily Anserinae. It may be a remnant of a lineage which diverged from the line leading to *Dendrocygna* before that genus achieved its present form. This is suggested by the absence of a suborbital bar and the presence of a rudimentary coracoid depression.

Since *Thalassornis* is the only known member of the Anserinae which has become highly specialized for diving, it is possible that more such types failed to develop because this adaptive zone was being actively entered by several groups of true ducks (Anatinae), which were perhaps better fitted to exploit this way of life.

SUMMARY

Recent studies of behavior and external anatomy suggest that the White-backed Duck (*Thalassornis leuconotus*) is related to the Dendrocygnini rather than to the Oxyurini as formerly suggested. Several features of the cranial and postcranial osteology support this theory, but other characteristics of the postcranial skeleton resemble the condition in the Oxyurini. Most of these can be interpreted as being parts of a general adaptive specialization for efficient aquatic locomotion, and it is suggested that the resemblance to the Oxyurini is therefore attributable to convergence.

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