ON THE SYSTEMATIC POSITION OF THE BOAT-BILLED HERON

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THE close relationship of the Boat-billed Heron (*Cochlearius cochlearius*) to ardeids has long been accepted, but the taxonomic rank to be assigned to *Cochlearius* has been the subject of much discussion. Thus, while all authorities recognize a monotypic genus for the Boat-bill, opinions vary on whether the genus should be placed in the tribe Nycticoracini or in a separate tribe, a separate subfamily, or a separate family. E. Mayr and D. Amadon (*Amer. Mus. Novitates*, no. 1141, 1951; see p. 6) placed *Cochlearius* in the Ardeidae, but did not discuss in any detail its relationships within the family. In his generic review of the Ardeidae, W. J. Bock (*Amer. Mus. Novitates*, no. 1779, 1956) concluded that the external features and behavioral characters of the Boat-bill warranted no more than separate generic ranking for the species, and he placed *Cochlearius* in the tribe Nycticoracini with the remark (p. 32): "A further study of the anatomy and behavior of the herons may reveal that *Cochlearius* differs more from the night herons than the presently studied characters indicate. If so and if also the proposed use of tribes in the Ardeinae is accepted, it may be best to established a separate tribe, the Cochleariini, for the Boat-bill, but it is extremely doubtful that it is distinct enough to warrant its being given subfamily rank." A. Wetmore (*Smiths. Misc. Colls.*, 139[11]: 9–10) was of the opinion that the enlarged bill, four pairs of powder-down patches, and the peculiar features of the skull made the Boat-bill distinct enough to be recognized as a monotypic family. R. Verheyen (*Bull. Inst. Roy. Sci. Nat. Belg.*, 37: 20, 1961), on the basis of Wetmore's discussion, retained *Cochlearius* in a separate family. Other authors (see R. W. Storer, p. 69 *in Biology and comparative physiology of birds*, vol. 1 [A. J. Marshall, ed.], New York, Academic Press, 1960) have favored including *Cochlearius* in the Ardeidae.

The purpose of the present paper is to discuss certain postcranial osteological characters of *Cochlearius* with respect to any evidence they give about the relationships of *Cochlearius*. The question is posed: What is the magnitude of the differences between *Cochlearius* and its supposedly nearest relative, *Nycticorax*, as compared with other genera that are considered to be closely related to *Nycticorax*?

In an attempt to answer that question, I examined the following species: *Cochlearius cochlearius* (3 specimens), *Nycticorax nycticorax* (4), *Pilherodius pileatus* (2), *Gorsachius melanolophus* (1), and *Nyctanassa violacea* (2). Also, although details are not given here, I examined

Botaurus lentiginosus (3), *Leucophoyx thula* (2), *Hydranassa tricolor* (1), *Tigrisoma lineatum* (2), *Ardea herodius* (2), and *Butorides virescens* (1).

OBSERVATIONS

There is perhaps unanimous agreement among ornithologists that the genus *Nyctanassa* is closer to *Nycticorax* than is any other ardeid; indeed, many consider them "good" congeners. *Nyctanassa* is very similar to *Nycticorax* in the postcranial skeleton but differs as follows (see H. Howard, *Univ. California Publs. Zool.*, 32: 318–324, 1929, for terminology and diagrams): *humerus*, deltoid crest is slightly better developed; *ulna*, no consistent differences were found; *carpometacarpus*, no consistent differences were found; *femur*, trochanteric ridge is usually better developed; *tibiotarsus*, distal end of the external condyle is slightly less round and the inner and outer cnemial crests are less separated; *tarsometatarsus*, the bone is longer and thinner; from anterior view the area below the internal cotyla on the medial side is depressed more; the intercotylar prominence is usually less bulbous; and the anterior metatarsal groove is slightly better developed; *pelvis*, the pelvis is relatively wider posteriorly and the posterior iliac crest is less well developed; *sternum*, no consistent differences were found; *coracoid*, no consistent differences were found.

Another genus considered by some authors to be congeneric with *Nycticorax* is *Pilherodius* (Bock, *op. cit.*: 29–31). It differs from *Nycticorax* in the following characters: *humerus*, the external condyle is slightly flattened distally, is less round in palmar view; the internal condyle is usually less elevated distally relative to external condyle; when viewed from distal end the internal condyle is wider, less round; bicipital furrow is usually less deep and less well marked; the deltoid crest is more developed; the ligamental furrow is less deep; *ulna*, no consistent differences were found; *carpometacarpus*, the process of metacarpal I is stubbier; from posterior view the internal edge of the carpal trochlea projects farther posteriorly relative to the external edge; *femur*, the obturator ridge is less well developed; the trochanteric ridge is usually (?) better developed distally; *tibiotarsus*, the external condyle is flatter distally, and less rounded posteriorly; from anterior view the external condyle is less broad and heavier; the internal condyle is less developed, and the anterior edge is directed more distally; the ridge on which the flexor attachment is located is much more well marked, more angular, less round; the inner and outer cnemial crests are less separated and the area between the crests is less elevated, especially proximally; *tarsometatarsus*, the anterior and posterior metatarsal grooves are much better developed; the intercotylar prominence is less bulbous and projects more, is more well defined; the trochlea for digit 3 projects less distally

relative to the trochlea for digit 4; *pelvis*, the pelvis is relatively wider anteriorly; *sternum*, the keel is not as deep anteriorly and its ventral edge curves more dorsally; the sternocoracoidal process is shorter and wider; the coracoidal sulcus is slightly better developed; *coracoid*, no consistent differences were found.

Bock (*op. cit.*: 27–29) placed the genus *Gorsachius* in the tribe Nycticoracini. *Gorsachius* is similar to *Nycticorax* but differs from it in some postcranial features, as follows: *humerus*, the distal end of the external condyle is much flatter, not rounded; the ligamental furrow is slightly less developed; the ectepicondyle projects more distally relative to the external condyle; the external tuberosity is slightly less developed; the bicipital furrow is less deep proximally; *ulna*, the external cotyla projects much less; *carpometacarpus*, the process of metacarpal I is stubbier; *femur*, the rotular groove is slightly less deep; when viewed from distal end the internal condyle projects less anteriorly relative to the external condyle; the area immediately distal to the obturator ridge is not depressed; *tibiotarsus*, the anterior margin of the external condyle (when viewed from side) meets the shaft less abruptly (?); the inner and outer cnemial crests are much less separated; *tarsometatarsus*, the anterior rim of the internal cotyla projects much less relative to the position of the intercotylar prominence; the intercotylar prominence projects less proximally; *pelvis*, the posterior iliac crest is less developed; *sternum*, the ventral manubrial spine is shorter; the coracoidal sulcus is slightly better developed; the sternocoracoidal process is shorter; *coracoid*, the area of the sternocoracoidal process is less pronounced laterally.

Finally, the postcranial skeleton of *Cochlearius* is very similar to that of *Nycticorax* but differs in the following characters: *humerus*, the ligamental furrow is less deep; the area around the external pneumatic fossa is more depressed; *ulna*, no consistent differences were found; *carpometacarpus*, the tip of process of metacarpal I projects less proximally; the anterior carpal fossa is slightly better developed and more well defined; *tibiotarsus*, the area between the inner and outer cnemial crests is usually more elevated, the groove being less well marked; the ridge on which the flexor attachment lies (from posterior view) is usually more well marked, more angular and less round; *tarsometatarsus*, the anterior metatarsal groove is slightly deeper and usually more well defined; the intercotylar prominence usually projects less proximally; the trochlea for digit 3 is less elevated relative to the trochlea for digit 4; the trochlea for digit 2 is less wide; *pelvis*, no consistent differences were found; *sternum*, no consistent differences were found; *coracoid*, the sternal facet is less well developed and less elongated.

TABLE 1

SUMMARY OF THE DIFFERENCES OF *NYCTANASSA*, *COCHLEARIUS*, *PILHERODIUS*, AND *GORSACHIUS* FROM *NYCTICORAX*[1]

Character	Nyctanassa	Cochlearius	Pilherodius	Gorsachius
Humerus				
External and internal condyles	—	—	+	+
Deltoid crest	+	—	+	—
Ectepicondyle	—	—	—	+
Bicipital furrow	—	—	+	+
External tuberosity	—	—	—	+
Ligamental furrow	—	+	+	+
Pneumatic fossa	—	+	—	—
Ulna				
External cotyla	—	—	—	+
Carpometacarpus				
Process of metacarpal I	—	+	+	+
Carpal trochleae	—	—	+	—
Anterior carpal fossa	—	+	—	—
Femur				
Internal condyle	—	—	—	+
Trochanteric ridge	+	—	+ (?)	—
Obturator ridge	—	—	+	+
Rotular groove	—	—	—	+
Tibiotarsus				
External condyle	+	—	+	+ (?)
Internal condyle	—	—	+	—
Cnemial crests	+	+	+	+
Area of flexor attachment	—	+	+	—
Tarsometatarsus				
Intercotylar prominence	+	+	+	+
Metatarsal grooves	+	+	+	—
Cotylae	—	—	—	+
Digital trochleae	—	+	+	—
Pelvis				
Relative width	+	—	+	—
Posterior iliac crest	+	—	—	+
Sternum				
Keel	—	—	+	—
Ventral manubrial spine	—	—	—	+
Coracoidal sulcus	—	—	+	+
Sternocoracoidal process	—	—	+	+
Coracoid				
Sternal facet	—	+	—	—
Sternocoracoidal process	—	—	—	+

[1]Minus = character very similar; plus = character different.

DISCUSSION

The characters of the postcranial skeleton of *Cochlearius* are unquestionably those of an ardeid and are well within the range of variation seen in the family and in the subfamily Ardeinae. The similarities, not the differences, of *Cochlearius* and *Nycticorax* must be stressed. In fact, from the above data (summarized in Table 1) it can be seen that *Cochlearius* is only slightly more different from *Nycticorax* than is *Nyctanassa* and is certainly much less different than are both *Pilherodius*

and *Gorsachius*. Moreover, *Cochlearius* does not exhibit any greater degree of difference from *Nycticorax* than the other genera of the family that were examined. In a recent paper on the relationships of *Syrigma*, P. S. Humphrey and K. C. Parkes (Proc. XIII Intern. Orn. Congr., pp. 84–90, 1963) demonstrated distinct differences in the shape of the axis between the Ardeini and the Nycticoracini (based, however, on only a few genera), and in this character *Cochlearius* resembles *Nycticorax* very closely.

Thus, a comparison of the postcranial differences among the genera discussed leads me to the conclusion that neither a separate subfamily nor a separate family should be recognized for *Cochlearius*. While I agree that the cranial features, if taken by themselves, are certainly distinct enough for the recognition of a monotypic family, I do not think these differences adequately portray the relationships of *Cochlearius*. The broad bill, the wide palatines, and the changes in the shape of the quadrate and lacrimal are probably part of a single functional unit specialized for a unique feeding method (see Bock, *op. cit.*: 32–33). That this functional complex probably evolved rapidly and rather recently is suggested by the great similarities of *Cochlearius* to *Nycticorax* and other herons; that is, while the postcranial skeleton evolved apparently at the same rate in *Cochlearius* as in other herons, the cranial complex probably evolved much faster. The postcranial evidence seems to indicate that *Cochlearius* is not much older, if at all, than the other ardeid genera.

The question as to whether *Cochlearius* should be placed in the Nycticoracini or in a separate tribe is still unanswered, and it probably will remain a matter of opinion. On the basis of only the postcranial skeleton, *Cochlearius* probably should be placed in the Nycticoracini. However, I think it can be reasonably argued that the cranial features and the four pairs of powder-down patches warrant placing *Cochlearius* in a separate tribe. Further anatomical and behavioral studies (e.g., A. L. Rand, *Auk*, 83: 304–306, 1966) may give us more evidence on which to base a decision.

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