

THE SCLERAL OSSICLES OF *OPISTHOCOMUS* AND THEIR PHYLOGENETIC SIGNIFICANCE

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ABSTRACT.—Dried scleral rings of *Opisthocomus*, Galliformes, Cuculiformes, and other birds were examined to determine the pattern of ossicle overlap in *Opisthocomus* and its bearing on the phylogenetic relationships of this taxon. Although *Opisthocomus* shares a derived number of 12 scleral ossicles with cuculid Cuculiformes, the pattern of ossicle overlap differs. Nevertheless, fewer modifications are required to derive the number and pattern of ossicles in *Opisthocomus* from the conditions in cuculid or musophagid Cuculiformes than from the conditions in any galliform. Our findings also indicate that the scleral rings of birds, unlike those of lizards, often do not conserve overlap relations between adjacent ossicles during phylogeny. Received 2 March 1987, accepted 23 July 1987.

THE phylogenetic relationships of the Hoatzin (*Opisthocomus hoazin*) have been the subject of a long-standing controversy in systematic ornithology. An enigmatic inhabitant of the flooded forests of Amazonia, *Opisthocomus* has been regarded as most closely related to many avian taxa, but most commonly to either Cuculiformes or Galliformes (Olson 1985; reviewed by Sibley and Ahlquist 1972, 1973). One character that has been used to support a close relationship between the *Opisthocomus* and Cuculiformes is the morphology of the sclerotic ring, a ring of small bones that develops within the sclera in the corneal hemisphere of the eye in birds and many other vertebrates (Edinger 1929). Lemmrich (1931) found that the scleral ring of *Opisthocomus* consists of 12 ossicles per eye, which is lower than the 13–16 ossicles he found in 10 species of cracid and phasianid Galliformes (all of which showed a modal number of 14) but is identical to that found in a single cuculiform, *Cuculus canorus*.

In addition to ossicle number, the pattern in which the scleral ossicles overlap varies among avian taxa (Lemmrich 1931, Curtis and Miller 1938). Because the same number of ossicles may have been derived independently, simple counts can be misleading. The pattern of ossicle overlap provides evidence about ossicle homologies and hence about cases in which the same number of ossicles has been derived through the loss of different individual ossicles.

Although the pattern of scleral ossicle overlap is known for many birds, it has been unknown for *Opisthocomus*. We compared the numbers of ossicles and their patterns of over-

lap in the scleral rings of larger samples of *Opisthocomus*, Cuculiformes, Galliformes, and other relevant avian taxa. Our findings have implications both for the relationships of *Opisthocomus* and for the manner in which scleral rings evolve.

MATERIALS AND METHODS

Twenty-four scleral rings from 14 *Opisthocomus* individuals were compared with rings from 42 galliform and 36 cuculiform species representing all of the recognized families, subfamilies, and tribes (Morony et al. 1975) in those groups (Table 1). To understand variation in scleral ossicle overlap patterns for a given number of ossicles, we also examined representatives of other avian groups with the same number of ossicles as *Opisthocomus* (Spheniscidae, Sulidae, Psittacidae, and Todidae).

We examined only the dried, detached scleral rings from museum skeletal specimens; no rings were examined *in situ*. In many cases scleral ossicle patterns could be distinguished in these rings without further preparation, but in others adherent connective tissue was removed. This was accomplished by immersing the rings in water or ethanol to soften the adherent tissue, which was then removed with forceps. Because we used only detached scleral rings, the side of the head from which each ring came had to be inferred. We used the patterns in the same or closely related taxa observed by Lemmrich (1931) in conjunction with the fact that the widest ossicles occur at the temporodorsal edge of the ring (best seen in Fig. 1D) to determine whether a given ring was from the right or left side.

We followed Lemmrich's (1931) conventions for numbering ossicles and describing patterns of ossicle overlap. Lemmrich recognized two basic patterns of ossicle overlap, which he designated Types A and B.

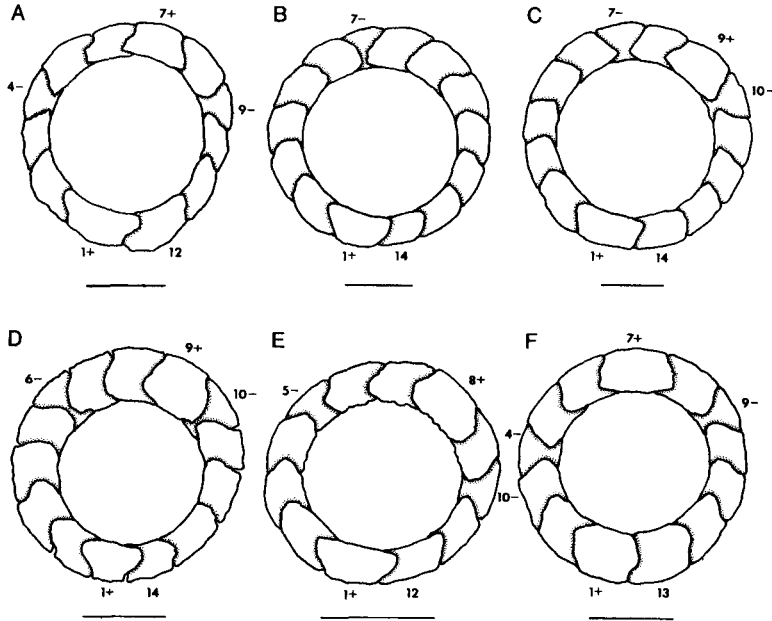


Fig. 1. Modal patterns of scleral rings in *Opisthocomus*, Galliformes, and Cuculiformes. (A) *Opisthocomus hoazin* (Opisthocomidae), (B) *Alectura lathami* (Megapodiidae), (C) *Aburria aburri* (Cracidae), (D) *Numida meleagris* (Phasianidae), (E) *Crotophaga ani* (Cuculidae), (F) *Tauraco hartlaubi* (Musophagidae). All rings are (from the right side, seen in corneal view). Scale equals 5 mm.

In Type A two ossicles in each ring overlap, and two others are overlapped by, the immediately adjacent ossicles; all others have one edge above and one beneath the adjacent ossicles (Fig. 1A, C-F). Lemmrich pointed out that the most dorsal ossicle in Type A rings always overlaps both its neighbors, and he referred to such overlapping ossicles as "+" elements. Approximately opposite this dorsal "+" element is another "+" element that he designated ossicle number 1. He counted ossicles around the ring postero-dorsally from this ventral "+" element, clockwise on the right ring and counter-clockwise on the left. He then recorded the positions of the "+" elements and those overlapped by both of their neighbors, the "-" elements, by listing the positions of the "+" elements separated by commas, then a semicolon, followed by the positions of the "-" elements separated by commas. The ossicles overlapped by one neighbor and overlapping the other ("imbricating" ossicles) are excluded in this notation. In this way, the ring in Fig. 1A would be recorded as 1,7;4,9. In Lemmrich's Type B pattern, only a single ventral "+" element and a single dorsal "-" element are present. Hence, the pattern in Fig. 1B is designated 1;7.

Hypotheses of phylogenetic relationship were based on the tenet that only shared derived characters contain useful information about recency of common ancestry (Hennig 1966). Character polarity was deter-

mined by outgroup comparison (e.g. Maddison et al. 1984).

RESULTS

The distribution of scleral ossicle number and pattern in Galliformes, Cuculiformes, and *Opisthocomus* is listed in Table 1. *Opisthocomus* (Fig. 1A) showed a modal number of 12, with a range from 11 to 13. Galliformes (Fig. 1B-D) showed a modal number of 14, with only about 15% of the specimens having 13 or 15, often on a single side. No specimens were observed to have 16 ossicles, a number seen rarely in *Gallus gallus* (Lemmrich 1931). Lemmrich examined only a single cuculiform, *Cuculus canorus*, with 12 ossicles; all 25 cuculid species we examined agreed with this finding (Fig. 1E). All musophagids examined (Fig. 1F) had 13 ossicles.

Opisthocomus, Cuculiformes, and cracid and phasianid Galliformes all characteristically possess Lemmrich's (1931) Type A pattern of ossicle overlap. The modal ossicle distribution pattern in *Opisthocomus* (Fig. 1A) was 1,7;4,9, although five other patterns were observed (Table 1). Within Galliformes, three major patterns were

TABLE 1. Numbers and patterns of scleral ossicles in representative species of Galliformes, Cuculiformes, and *Opisthocomus*. Pattern designations are described in the Methods. Numbers in parentheses indicate subsample size. Modal configurations for variable species are in boldface.

Taxon	Specimens/rings examined	No. of ossicles	Pattern
Megapodiidae			
<i>Aepyodius arfakianus</i>	1/2	14	1;7
<i>Alectura lathamii</i>	1/2	14	1;7
<i>Macrocephalon maleo</i>	1/2	14	1;7
<i>Megapodius freycinet</i>	6/10	14	1;6 (1)
		14	1;7 (9)
Cracidae			
<i>Aburria aburri</i>	2/4	14	1,9;7,10
<i>A. pipile</i>	4/6	14	1,9;7,10
<i>Chamaepetes goudotii</i>	2/3	14	1,9;7,10 (2)
		15	1,9;7,11 (1)
<i>Crax daubentoni</i>	1/2	15	1,9;7,10
<i>C. mitu</i>	1/2	14	1,9;7,10
<i>C. pauxi</i>	2/3	14	1,9;7,10
		15	1,9;7,10
		15	1,10;8,11
<i>C. rubra</i>	2/4	13	1,8;6,9 (2)
		14	1,9;7,10 (1)
		15	1,9;7,10 (1)
<i>Nothocrax urumutum</i>	1/2	14	1,9;7,10
<i>Ortalis canicollis</i>	3/3	14	1,9;7,10
<i>O. cinereiceps</i>	1/2	14	1,9;7,10
<i>O. garrula</i>	1/1	14	1,9;7,10
<i>O. motmot</i>	2/4	14	1,9;7,10
<i>O. vetula</i>	3/6	14	1,9;7,10
<i>Penelope albipennis</i>	1/2	14	1,9;7,10
<i>P. jacquacu</i>	6/10	14	1,9;7,10
<i>P. purpurascens</i>	2/4	14	1,9;7,10 (3)
		15	1,9;7,11 (1)
Phasianidae			
Meleagridinae			
<i>Agriocharis ocellata</i>	1/2	14	1,9;6,10
Tetraoninae			
<i>Bonasa umbellus</i>	1/2	14	1,9;6,10
<i>Dendragapus obscurus</i>	3/4	14	1,9;6,10
<i>Lagopus lagopus</i>	1/1	14	1,9;7,10
<i>Tympanuchus cupido</i>	1/1	15	1,10;8,11
<i>T. phasianellus</i>	1/2	14	1,9;7,10
		15	1,10;8,11
Odontophorinae			
<i>Colinus cristatus</i>	1/1	14	1,9;6,10
<i>C. virginianus</i>	1/2	14	1,9;6,10
<i>Dactylortyx thoracicus</i>	2/3	14	1,9;6,10
<i>Callipepla californicus</i>	16/29	14	1,8;6,10 (2)
		14	1,9;6,10 (23)
		14	1,9;6,11 (1)
		15	1,9;6,10 (1)
		15	1,9;7,11 (2)
<i>Philortyx fasciatus</i>	1/2	14	1,9;6,10
Phasianinae			
Perdicini			
<i>Coturnix coturnix</i>	1/1	14	1,9;6,10
<i>Perdix perdix</i>	1/1	14	1,9;6,10
Phasianini			
<i>Gallus gallus</i>	1/1	14	1,9;6,10

TABLE 1. Continued.

Taxon	Specimens/rings examined	No. of ossicles	Pattern
<i>G. sonneratii</i>	1/1	14	1,9;6,10
<i>Lophura swinhoi</i>	1/2	14	1,9;6,10
<i>Phasianus colchicus</i>	1/1	14	1,9;6,10
Numidinae			
<i>Acryllium vulturinum</i>	4/6	13	1,9;6,10 (1)
		14	1,9;6,10 (4)
		15	1,9;6,11 (1)
<i>Guttera plumifera</i>	3/4	14	1,9;6,10 (3)
		14	1;10 (1)
<i>G. pucherani</i>	1/2	14	1,9;6,10
<i>Numida meleagris</i>	5/9	15	1,9;6,10
		14	1,9;6,10 (8)
		14	1,9;7,10 (1)
<i>N. mitrata</i>	2/2	14	1,9;6,10
Opisthocomidae			
<i>Opisthocomus hoazin</i>	14/24	11	1,6;4,7 (1)
		11	1,6;4,8 (3)
		11	1,7;4,8 (1)
		12	1,7;4,9 (11)
		12	1,7;5,9 (1)
		13	1,7;4,9 (5)
		13	1,8;4,10 (2)
Musophagidae			
<i>Corythaecola cristata</i>	2/3	13	1,7;4,9
<i>Corythaixoides leucogaster</i>	1/2	13	1,6;4,9
		13	1,7;4,8
<i>Crinifer piscator</i>	1/2	13	1,7;4,9
		14	1,7;4,10
<i>C. zonurus</i>	1/1	13	1,7;4,9
<i>Musophaga rossae</i>	2/4	13	1,7;4,9
<i>Tauraco corythaix</i>	4/7	13	1,7;4,9
<i>T. erythrolophus</i>	2/3	12	1,7;4,9 (1)
		13	1,7;4,9 (2)
<i>T. hartlaubi</i>	6/7	13	1,7;4,9 (6)
		14	1,7;4,9 (1)
<i>T. persa</i>	1/2	13	1,7;4,9
<i>T. porphyreolophus</i>	1/1	13	1,7;4,9
<i>T. schalowi</i>	2/4	11	1,6;4,8 (1)
		12	1,7;4,9 (1)
		13	1,7;4,9 (2)
Cuculidae			
Cuculinae			
<i>Cacomantis pyrrhophanus</i>	1/1	12	1,8;5,10
<i>Chalcites basalis</i>	2/2	12	1,8;5,10
<i>Clamator jacobinus</i>	3/6	12	1,8;5,10
<i>Cuculus pallidus</i>	1/2	12	1,8;5,10
<i>C. solitarius</i>	1/1	12	1,8;5,10
<i>Misocallius osculans</i>	1/2	12	1,8;5,10
Phaenocophaeinae			
<i>Coccyzus americanus</i>	3/4	12	1,8;5,10
<i>C. melacoryphus</i>	1/1	12	1,8;5,10
<i>Piaya cayana</i>	4/6	12	1,8;5,10
Crotophaginae			
<i>Crotophaga ani</i>	2/4	12	1,8;5,10
<i>C. sulcirostris</i>	5/9	12	1,8;5,10
<i>Guira guira</i>	10/15	12	1,8;5,10 (13)
		13	1,6;4,10 (1)
		14	1,8;5,10 (1)

TABLE 1. Continued.

Taxon	Specimens/rings examined	No. of ossicles	Pattern
Neomorphinae			
<i>Dromococcyx pavoninus</i>	1/2	12	1,8;5,10
<i>D. phasianellus</i>	1/2	12	1,8;5,10
<i>Geococcyx californianus</i>	3/6	12	1,8;5,10
<i>Morococcyx erythropygus</i>	3/6	12	1,8;5,10
<i>Neomorphus geoffroyi</i>	1/2	12	1,8;5,10
Couinae			
<i>Coua caerulea</i>	2/3	12	1,8;5,10
<i>C. cristata</i>	1/1	12	1,8;5,10
Centropodinae			
<i>Centropus bengalensis</i>	1/1	12	1,8;5,10
<i>C. goliath</i>	3/6	11	1,7;4,9 (2)
		12	1,8;5,10 (4)
<i>C. phasianius</i>	1/1	12	1,8;5,10
<i>C. senegalensis</i>	1/1	12	1,8;5,10
<i>C. sinensis</i>	2/4	12	1,8;5,10
<i>C. superciliosus</i>	3/5	12	1,8;5,10

seen: cracids (Fig. 1C) had primarily a 1,9;7,10 pattern, phasianids (Fig. 1D) had mostly 1,9;6,10, and megapodiids (Fig. 1B), the only examples in the present study of Lemmrich's Type B pattern, had 1;7. Most musophagid Cuculiformes (Fig. 1F) had 1,7;4,9 and most cuculids (Fig. 1E) 1,8;5,10.

In comparisons within families whose members vary widely in body (or eye) size (e.g. *Coturnix* vs. *Agriocharis* within Phasianidae), ossicle configuration did not correlate with size.

DISCUSSION

As pointed out by Lemmrich (1931), cuculids are more similar to *Opisthocomus* than is any group of Galliformes in having 12 ossicles per ring; however, other groups of birds share this number. Lemmrich found 12 ossicles in the spheniscid *Catarrhactes* (= *Eudyptes*) *chrysocome* (1,8;5,10), the sulid *Sula bassanus* (1,7;4,10), and the 11 psittacid species he examined (1,6;4,9/1,7;4,9/1,8;5,11). There are 12 ossicles in the trochilid *Selasphorus rufus* (1,6;4,8) (Curtis and Miller 1938). In addition, we observed 12 ossicles in *Sula capensis* (1,5;4,10), *S. serratator* (1,6,8;4,7,10), and *S. abbotti* (overlap patterns not determined), and in 1 out of 2 eyes in *Todus todus* (1,8;5,10).

Birds probably are derived from within Dinosauria, and thus the closest outgroups to birds are to be found among the nonavian members

of this monophyletic taxon (e.g. Ostrom 1976, Gauthier 1984, Gauthier and Padian 1985). We know of no complete scleral rings among non-avian Saurischia, but complete rings with a range from 13 to 15 ossicles occur in Ornithischia (Edinger 1929, Russell 1940, Ostrom 1961, Galton 1974). Heilmann (1926) reported 14 scleral ossicles in *Archaeornis* (= *Archaeopteryx*), although Wellnhofer (1974) counted "approximately 12" in a different specimen. Because Cuculiformes, Galliformes, and *Opisthocomus* are all neognaths, ratites plus tinamous constitute an even closer outgroup for the relationships under investigation in the present study (Prager et al. 1976, Sibley and Ahlquist 1981, Stapel et al. 1984, Cracraft 1986). *Struthio* and *Dromaius* have 15 ossicles (Lemmrich 1931). We observed 15-16 in the tinamous *Crypturellus cinnamomeus* and 15 in *Tinamotis pentlandii*. Twelve ossicles, as seen in *Opisthocomus* and Cuculidae, is a low number compared with that seen in the most significant outgroups and suggests that such a number is derived relative to the mode of 14 seen in Galliformes.

As noted above, various avian taxa possess what appears to be a derived number of 12 scleral ossicles. The positions of the "+" and "-" ossicles, however, often differ among taxa with the same total number of ossicles. For example, other taxa with a mode of 12 ossicles have the following modal patterns: *Eudyptes* (Lemmrich 1931) and *Todus* (this study) 1,8;5,10; *Sula* (3 spp.)

1,5;4,10/1,7;4,10/1,8;4,10/1,6,8;4,7,10 (Lemmrich 1931, this study); Psittacidae (5 spp.) 1,6;4,9/1,7;4,9/1,8;5,11 (Lemmrich 1931, Curtis and Miller 1938); and Trochilidae (1 sp.) 1,6;4,8 (Curtis and Miller 1938). These differences might be taken to suggest that reduction to 12 ossicles has been achieved independently in each of the taxa with "+" and "-" ossicles in different positions through the loss of different imbricating ossicles. In lizards, conservation of overlap pattern and loss of imbricating ossicles can account for most transformations between scleral rings with different overlap patterns (de Queiroz 1982, Underwood 1984). In birds, however, lack of conservation of overlap relationships between adjacent ossicles is supported by the occurrence of Type A and Type B rings with the same total number of ossicles within a single species (e.g. *Guttera plumifera*) or in closely related taxa (e.g. megapodes vs. other Galliformes), and by the occurrence within single species of rings conforming to the same basic type (A or B) but having the "+" and "-" ossicles at different positions in the ring (e.g. *Opisthocomus*) (Table 1). These differences presumably result from direct shifts in overlap between adjacent ossicles, with conservation of ossicle number.

Given the preceding considerations, we determined the minimum number of evolutionary events necessary to transform the scleral ring of one group into that of another. A cuculid-*Opisthocomus* transition requires only a single change, in which cuculid ossicle 1 becomes *Opisthocomus* ossicle 12 by shifting overlaps such that cuculid ossicle 1 no longer overlaps, but is instead overlapped by cuculid ossicle 2 (which then becomes *Opisthocomus* ossicle 1). Similarly, a musophagid-*Opisthocomus* transition requires only a single step, with an ossicle either added or lost between the "-" ossicle 9 and "+" ossicle 1. On the other hand, at least three changes, involving both losses and shifts in overlap of ossicles, are necessary between *Opisthocomus* and any of the galliform patterns.

Considerable individual variation was seen in ossicle overlap in certain taxa, notably *Opisthocomus* (Table 1). We examined this variation to determine if any of the nonmodal variants might be more similar (i.e. fewer changes) to any of the cuculiform or galliform patterns than was the modal, suggesting a possible transformation series. None of the *Opisthocomus* variants was any more similar to cuculids or musophag-

ids than was the modal pattern, however, nor did any of the variants make a galliform relationship more tenable; at least three changes were necessary to transform any of them to any of the galliform patterns.

The shared possession of a derived reduced number of ossicles per ring in conjunction with the minimum number of steps necessary between modal patterns suggests that *Opisthocomus* is more closely related to Cuculiformes than to Galliformes. As with an *Opisthocomus*-cuculiform transition, however, only one step is necessary between *Opisthocomus* and 12-ossicled Spheniscidae, Sulidae, and Todidae, 13-ossicled Coraciidae and Alcedinidae (Lemmrich 1931), or 11-ossicled Columbidae (Lemmrich 1931). It is therefore just as reasonable on the basis of scleral ring morphology to infer that *Opisthocomus* is allied with one of those groups as with Cuculiformes. Further, some 12-ossicled psittacids share an identical pattern to that of *Opisthocomus*.

We do not mean to suggest that the Hoatzin is closely related to penguins, boobies, todies, rollers, kingfishers, doves, or parrots. Comparisons with these taxa are provided only to illustrate that the evidence for the placement of *Opisthocomus* based on scleral ring morphology is equivocal. In general, limited conservation of overlaps between adjacent ossicles makes it difficult to determine homologies in the avian scleral ring, and this limits the usefulness of overlap patterns as systematic characters. Nevertheless, given the current lack of evidence supporting a close relationship to some other group of birds (Sibley and Ahlquist 1972, 1973), one might assume that *Opisthocomus* is allied either with Galliformes or Cuculiformes. Under this assumption, scleral ring morphology suggests a closer relationship to Cuculiformes.

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LITERATURE CITED

- CRACRAFT, J. 1986. The origin and early diversification of birds. *Paleobiology* 12: 383-399.
- CURTIS, E. L., & R. C. MILLER. 1938. The sclerotic ring in North American birds. *Auk* 55: 225-243.
- DE QUEIROZ, K. 1982. The scleral ossicles of sceloporine iguanids: a reexamination with comments on their phylogenetic significance. *Herpetologica* 38: 302-311.
- EDINGER, T. 1929. Über knocherne Scleralringe. *Zool. Jahrb. Abt. Anat.* 51: 163-226.
- GALTON, P. M. 1974. The ornithischian dinosaur *Hypsilophodon* from the Wealden of the Isle of Wight. *Bull. Brit. Mus. (Nat. Hist.) Geol.* 25: 1-152.
- GAUTHIER, J. A. 1984. A cladistic analysis of the higher systematic categories of the Diapsida. Ph.D. dissertation, Berkeley, Univ. California.
- , & K. PADIAN. 1985. Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight. Pp. 185-197 in *The beginnings of birds* (M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer, Eds.). Eichstatt, Proc. Int. *Archaeopteryx* Conf.
- HEILMANN, G. 1926. The origin of birds. London, H. F. & G. Witherby.
- HENNIG, W. 1966. *Phylogenetic systematics*. Urbana, Univ. Illinois Press.
- LEMMRICH, W. 1931. Der Skleralring der Vögel. *Jena. Z. Naturforsch.* 65: 513-586.
- MADDISON, W. P., M. J. DONOGHUE, & D. R. MADDISON. 1984. Outgroup analysis and parsimony. *Syst. Zool.* 33: 83-103.
- MORONY, J. J., JR., W. J. BOCK, & J. FARRAND JR. 1975. Reference list of the birds of the world. New York, *Am. Mus. Nat. Hist.*
- OLSON, S. L. 1985. The fossil record of birds. Pp. 79-238 in *Avian biology*, vol. 8 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- OSTROM, J. H. 1961. Cranial morphology of the hadrosaurian dinosaurs of North America. *Bull. Am. Mus. Nat. Hist.* 122: 33-186.
- . 1976. *Archaeopteryx* and the origin of birds. *Biol. J. Linn. Soc.* 8: 91-182.
- PRAGER, E. M., A. C. WILSON, D. T. OSUGA, & R. E. FEENEY. 1976. Evolution of flightless land birds on southern continents: transferrin comparison shows monophyletic origin of ratites. *J. Mol. Evol.* 8: 283-294.
- RUSSELL, L. S. 1940. The sclerotic ring in the Hadrosauridae. *Contrib. R. Ontario Mus. Paleontol.* 3: 1-7, 2 plates.
- SIBLEY, C. G., & J. E. AHLQUIST. 1972. A comparative study of the egg white proteins of non-passerine birds. *Bull. Peabody Mus. Nat. Hist.* 39: 1-276.
- , & ———. 1973. The relationships of the Hoatzin. *Auk* 90: 1-13.
- , & ———. 1981. The phylogeny and relationships of the ratite birds as indicated by DNA-DNA hybridization. Pp. 301-335 in *Evolution today*. Proc. 2nd Int. Congr. Syst. Evol. Biol. (G. G. E. Scudder and J. L. Reveal, Eds.). Pittsburgh, Carnegie-Mellon.
- STAPEL, S. O., J. A. M. LEUNISSEN, M. VERSTEEG, J. WATTEL, & W. W. DE JONG. 1984. Ratites as oldest offshoot of avian stem—evidence from alpha-crystallin A sequences. *Nature* 311: 257-259.
- UNDERWOOD, G. 1984. Scleral ossicles of lizards: an exercise in character analysis. Pp. 483-502 in *The structure, development and evolution of reptiles*. Symp. Zool. Soc. London No. 52 (M. W. J. Ferguson, Ed.). London, Academic Press.
- WELLNHOFER, P. 1974. Das fünfte Skelettexemplar von *Archaeopteryx*. *Palaeontographica* 147: 169-216.