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THE SYSTEMATIC POSITION OF THE COCOS FLYCATCHER

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ABSTRACT.—The Cocos Flycatcher (*Nesotriccus ridgwayi*), traditionally allied with *Myiarchus,* was recently placed in another subfamily, Fluvicolinae, near *Empidonax* and *Cnemotriccus.* A comparative study of the skull and syrinx demonstrates that the nearest relatives of *Nesotriccus* are *Phaeomyias murina* and *Capsiempis flaveola* in the subfamily Elaeniinae, since all three genera share unique derived character states of the nasal septum and of the supporting elements of the syrinx.

In 1891 Charles Townsend collected a new flycatcher on Cocos Island, which he later named *Nesotriccus ridgwayi* (Townsend 1895). He called attention to the zoogeographic and, inferentially, the morphological relationship between his new monotypic genus from Cocos, over 500 kilometers off the Pacific coast of Costa Rica, and an equally interesting flycatcher in the Galapagos Islands, *magnirostris,* which Ridgway (1893) had recently removed from *Myiarchus* and placed in its own genus, *Eribates.* Hellmayr (1927) similarly was impressed with the affinity of *Nesotriccus* and *Eribates* and placed both close to *Myiarchus,* the widespread and successful mainland genus. As recently as 1955, Eisenmann followed Hellmayr in placing *Nesotriccus* next to *Myiarchus* in a list of species of Middle American birds. Subsequent recommendations (Swarth 1931; Lanyon 1978; Zimmer, unpubl. notes, Amer. Mus. Nat. Hist.) that *magnirostris* should be returned to *Myiarchus* left unresolved the systematic position of *Nesotriccus.*

The alleged affinity between *Nesotriccus* and *Myiarchus* was rejected by Swarth (1931) and Zimmer (unpubl. notes) on the basis of external morphology. In a study of cranial anatomy, Warter (1965) concluded that *Nesotriccus* "appears intermediate in structure between the *Myiarchinae* (s.s.) and *Todirostrum,* but otherwise is probably more closely related to the former." Ames (1971) reported the syrinx of *Nesotriccus* to be unlike the syringes of *Myiarchus, Empidonax, Contopus,* and *Cnemotriccus,* but made no recommendation as to how *Nesotriccus* should be classified on the basis of syringeal morphology. In the only definitive classification of the Tyrannidae since Hellmayr (1927), Traylor (1977) removed *Nesotriccus* from its traditional position among the myiarchine flycatchers and placed it in the subfamily Fluvicolinae, between *Empidonax* and *Cnemotriccus,* on the basis of external morphology.

At the time that I was completing my revision of the genus *Myiarchus* (Lanyon 1978), I had decided on the basis of external morphology alone to exclude *Nesotriccus* from *Myiarchus.* I doubted that nests of *Nesotriccus,* when discovered, would be located within tree cavities and lined with fur and feathers, the derived nesting behavior that defines the myiarchine flycatchers (Lanyon 1982, Lanyon and Fitzpatrick, 1983). Subsquently I examined the skull of *Nesotriccus* and, contrary to the findings of Warter (1965), found it to be very distinct from the skull of *Myiarchus.* My interest in *Nesotriccus* was revived with the descriptions of the first known nests (Sherry, in press) and the availability of alcoholic specimens taken by Sherry. I was certain that a careful study of the skull and syrinx would provide meaningful clues to the nearest relatives of *Nesotriccus.* This paper presents the results of that study.

METHODS

Research on the skull (Warter 1965) and the syrinx (Ames 1971) has demonstrated the utility of these structures in determining relationships within the suboscines. I have been influenced greatly by both of these important studies and I follow the terminology of these authors. Two complexes in particular have proven effective in diagnosing groups of tyrant flycatchers: (1) the nasal septum, and notably the degree to which there is ossification and buttressing with internal and/or laterally projecting supporting elements, and (2) the morphology of the bony and cartilaginous supporting elements in the syrinx, and in particular the number, shape, and position of the internal cartilages (Lanyon 1982, Lanyon and Fitzpatrick 1983).

Thus far I have examined the skulls of 83 genera and the syringes of 86 genera of the 91 genera of tyrant flycatchers (sensu Traylor 1977) in a larger, ongoing study of the phylogeny of the Tyrannidae. In addition to the anatomical collections at the American Museum of Natural History (AMNH), material has been borrowed from the Carnegie Museum

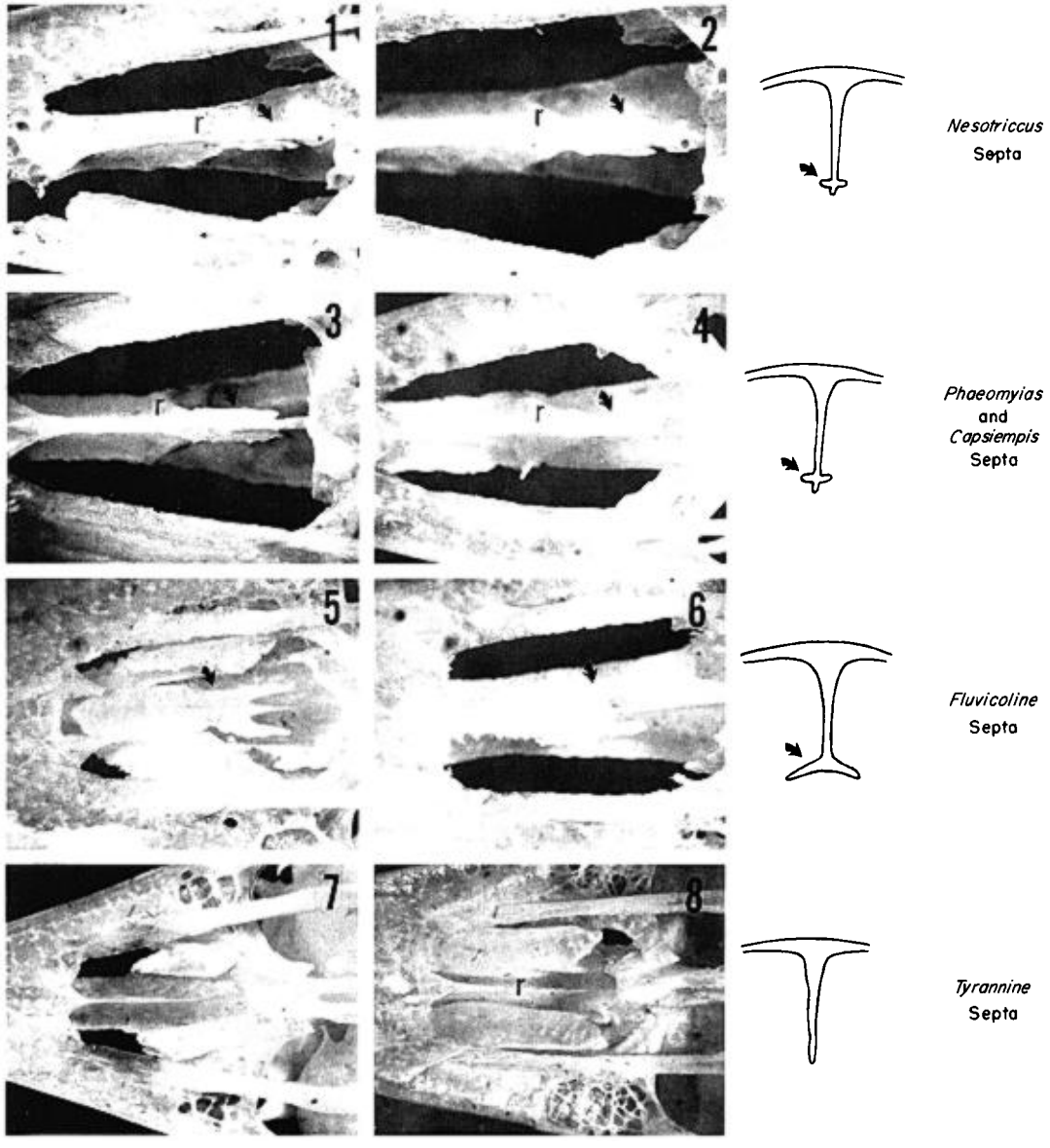

FIGURE 1. Photographs of the skulls of selected tyrant flycatchers (ventral aspect; anterior end to the left) and diagrammatic representations of cross sections of the corresponding nasal septa (projecting downward from the roof of the nasal capsule): 1, 2 *Nesotriccus ridgwayi* (AMNH 9210), 15× and 20×; 3, *Phaeomyias murina* (AMNH 7306), 20×; 4, *Capsiempis flaveola* (UMM 200869), 20×; 5, *Empidonax euleri* (AMNH 6934), 15×; 6, *Cnemotriccus fuscatus* (AMNH 6685), 15×; 7, *Myiozetetes similis* (AMNH 7173), 10×; 8, *Myiarchus tuberculifer* (AMNH 7175), 10×. Arrows indicate presence of trabecular plates on the nasal septa of all skulls except those of the two tyrannines (7 and 8).

of Natural History in Pittsburgh, the Field Museum of Natural History in Chicago (FMNH), the Museum of Zoology at Louisiana State University in Baton Rouge (LSU), the Museum of Zoology at the University of Michigan in Ann Arbor (UMMZ), the National Museum of Natural History in Washington, D.C., and the Peabody Museum of Natural History, Yale University, in New Haven. Specimens cited here are identified to collection by the abbreviations given above. Syringes were stained with alcian blue and alizarin red (after Dingerkus and Uhler 1977) to facilitate the study of the supporting elements and to differentiate between bony and cartilaginous tissue.

RESULTS AND DISCUSSION

NASAL SEPTUM

The nasal septum of *Nesotriccus* is characterized by having (1) a well-developed internal supporting rod that presumably serves to buttress the septum ("r" in photographs 1 and 2, Fig. 1), and (2) a trabecular plate in the form

of short and narrow lateral projections from the septum, elevated above the ventral edge of the septum and located near the ventral end of the internal supporting rod (indicated by arrows in photographs 1 and 2 and the corresponding cross-sectional diagram in Fig. 1). The posterior ends of these lateral projections extend caudally in close proximity to, but more or less free from, the septum.

Only two genera of tyrant flycatchers other than *Nesotriccus* have the unusual characteristics of the nasal septum described above. These are the monotypic *Phaeomyias* and *Capsiempis,* both placed by Traylor (1977) in the subfamily Elaeniinae. Their nasal septa, illustrated in photographs 3 and 4, Figure 1, are remarkably similar to that of *Nesotriccus.*

Traylor (1977) placed *Nesotriccus* in his subfamily Fluvicolinae, between *Empidonax* and *Cnemotriccus.* All of the genera in this subfamily, except *Nesotriccus,* have a large, conspicuous trabecular plate located along the ventral edge of the nasal septum, i.e., not elevated above the ventral edge (indicated by arrows in photographs 3 and 4 and the corresponding cross-sectional diagram in Fig. 1). Moreover, the plate in the fluvicolines is noticeably concave when viewed in cross section.

All of the genera in Traylor's (1977) third subfamily, the Tyranninae (which includes *Myiarchus* and relatives), have nasal septa that lack a trabecular plate. When viewed from below, the ventral edge of the septum in all tyrannines is thin and almost knife-like as illustrated in photographs 7 and 8, Figure 1, and there are no lateral projections of any kind.

SYRINX

For the purposes of this study, the significant characteristics of the supporting elements of the syrinx of *Nesotriccus* are: (1) the fusion of the bony elements A2 through A4 into a drum ("d" in photograph 1, Fig. 2), (2) the presence of a well-developed bony rod or pessulus in the tracheo-bronchial junction ("p" in photograph 1, Fig. 2), and (3) a single pair of relatively narrow internal cartilages, attached anteriorly to the dorsal ends of the A1 elements and the drum, and moderately forked at the free end. These cartilages are slightly curved, with the forked end pointing away from the medial plane ("c" designates the right internal cartilage in photograph 1, Fig. 2).

I know of only two tyrant genera that share with *Nesotriccus* the combination of syringeal characteristics described above. These are the monotypic *Phaeomyias* and *Capsiempis,* and their syringes are illustrated in photographs 2 and 3 in Figure 2.

The syringes of the fluvicolines with which Traylor (1977) associated *Nesotriccus,* i.e., *Empidonax* and *Cnemotriccus,* have a very different morphology: (1) the tracheal elements are not fused into a drum, (2) the pessulus is cartilaginous, narrow, and not well-developed, and (3) the internal cartilages are large, very broad, and nearly straight (photographs 4 and 5 in Fig. 2). Since none of the genera in Traylor's Fluvicolinae has a well-developed drum, as seen in *Nesotriccus,* I was puzzled by Ames's (1971:61) description of a drum in the syrinx of *Cnemotriccus poecilurus* (=*Knipolegus poecilurus* in Traylor 1977). I reexamined the specimen (AMNH 6743) that he had dissected and found that it had been mislabeled; it was actually *Mecocerculus leucophrys,* which belongs in the Elaeniinae and has a well-developed drum.

The syrinx of *Myiarchus* and near relatives (Lanyon 1982, Lanyon and Fitzpatrick 1983) differs from that of *Nesotriccus* in (1) the lack of fusion of tracheal elements into a drum, (2) the absence of a well-devloped bony pessulus, and (3) the presence of two pairs of internal cartilages, the larger of which attaches to the ventral portion of the tracheo-bronchial junction and is L-shaped (photograph 6 in Fig. 2).

TAXONOMIC CONCLUSIONS

The first conclusion to be drawn from this study of the nasal septum and the syrinx of *Nesotriccus* is that the notion of close relationship with the myiarchine flycatchers, through *Myiarchus magnirostris* of the Galapagos Islands, should be put to rest once and for all. There simply is no morphological support for this old contention, and therefore Traylor (1977) was correct in removing *Nesotriccus* from his subfamily Tyranninae.

What did Warter (1965) see in the septum of *Nesotriccus* that suggested myiarchine characteristics? I borrowed the single *Nesotriccus* skull (LSU 42902) that he examined and found it to be like the one I described above (AMNH 9210). I suspect that, when Warter (1965, Table II) classified the nasal septa of *Nesotriccus, Phaeomyias* and *Capsiempis* as the same type that he found among the myiarchine flycatchers (Type 2), he did so because of the conspicuous internal supporting rod. This feature, though present in the myiarchines (see "r" in photograph 8, Fig. 1), is not unique to that group; many other tyrants have a comparable structure, though usually not nearly as conspicuous and well-developed. What distinguishes the myiarchines from all other flycatchers is the presence of the conspicuous internal supporting rod *in the absence of* any

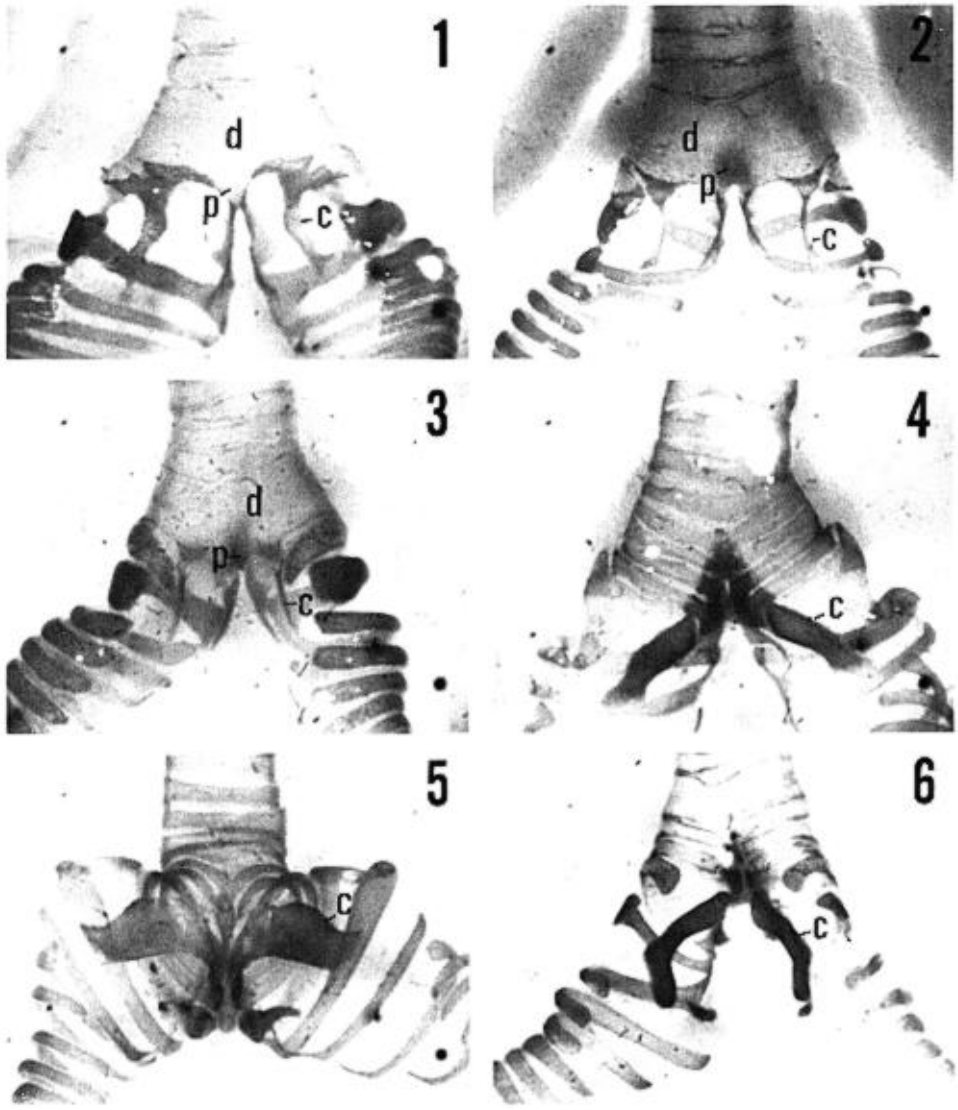

FIGURE 2. Photographs of the syringes of selected tyrant flycatchers (dorsal aspect): 1, *Nesotriccus ridgwayi* (AMNH 8067), 20×; 2, *Phaeomyias murina* (FMNH 291280), 20×; 3, *Capsiempis flaveola* (AMNH 7709), 20×; 4, *Empidonax euleri* (LSU 102573), 20×; 5, *Cnemotriccus fuscatus* (LSU 101499), 20×; 6, *Myiarchus swainsoni* (AMNH 7991), 15×. Letters designate structures as follows: d, fusion of bony supporting elements into a drum; p, well-developed bony rod or pessulus in the tracheo-bronchial junction; c, right internal cartilage.

kind of trabecular plate. *Nesotriccus, Phaeomyias* and *Capsiempis* all have a small but distinctive trabecular plate.

A second conclusion is that *Nesotriccus* cannot be assigned to the Fluvicolinae. No genus in that subfamily, as constituted by Traylor (1977), is known to have a trabecular plate elevated above the ventral edge of the nasal septum, or to have the bony supporting elements of the syrinx fused into a well-developed drum. Traylor (1977:162) was aware that *Nesotriccus* lacks features of the nasal septum that characterize the Fluvicolinae, but chose to override this consideration with emphasis upon external morphology. I believe the additional syringeal evidence presented here, which also denies relationship with the fluvicolines, provides a compelling and convincing argument.

Thirdly, *Nesotriccus ridgwayi* alone, of those species studied thus far, shares with *Phaeomyias murina* and *Capsiempis flaveola* derived states of the nasal septum and of the supporting elements of the syrinx. The concordance between these two very different character complexes in all three genera is truly impressive and cannot, I think, be accounted for other than by relatedness. The suggestion that *Nesotriccus* and *Phaeomyias* are near rel-

atives, though novel, is compatible with considerations of external morphology, nesting behavior (Haverschmidt 1970; Sherry, in press) and zoogeography. *Nesotriccus* is a somewhat larger edition of *Phaeomyias,* sharing with that widespread mainland form (Panama and widely scattered regions of South America) the dull brownish upperparts, a pale superciliary line, and buffy wingbars. The most obvious difference in their appearance is the proportionately longer, more spatulate bill of *Nesotriccus,* a characteristic that might easily be acquired under the insular conditions of Cocos, and one that would enable greater exploitation of the available food supply in the absence of competitors (Grant 1968).

As a general rule, I question the utility of vocal characters for determining relationships among genera of tyrant flycatchers, and would insist on judging relatedness primarily upon the sharing of derived morphological characters. A consideration of vocal characters, however, may provide interesting supplemental arguments for confirming the clustering of genera. While I was still debating whether or not to acquire some field experience with *Nesotriccus,* as part of continuing studies of the putative relatives of *Myiarchus,* I received a copy of a recording of *Nesotriccus* vocalizations that F. Gary Stiles had made during a visit to Cocos in 1978. I subsequently played that recording for Theodore A. Parker (Museum of Zoology, Louisiana State University) and John W. Fitzpatrick (Field Museum of Natural History, Chicago), both of whom remarked on the great similarity between the vocalizations of *Nesotriccus* and *Phaeomyias.* I was impressed with their view, since I had just made a similar conclusion regarding the skulls of these genera.

A close relationship between *Nesotriccus* and *Capsiempis* is less evident on external morphological grounds, because the latter is olive-green above and bright yellow below, with pale yellow wingbars and superciliary line. Traylor (1977) recommended merging *Capsiempis* into a much enlarged genus *Phylloscartes,* although he voiced some hesitancy because of differences in ecology and nesting behavior. Consideration of the nasal septum and syrinx further argues strongly against this merger. With respect to these character complexes, *Phylloscartes ventralis, Phylloscartes orbitalis, Pogonotriccus eximius* and *Leptotriccus sylviolus* (all placed in *Phylloscartes* by Traylor) form a closely-knit group, while *Capsiempis flaveola* is completely distinct from this group and remarkably similar to *Nesotriccus* and *Phaeomyias* as indicated in this study. *Capsiempis* builds a cup-shaped nest and lays white eggs (Skutch 1960) as do *Nesotriccus* and *Phaeomyias,* and its distribution is compatible, extending as it does from Nicaragua through much of South America.

Presumably all three genera, *Nesotriccus, Phaeomyias* and *Capsiempis,* belong somewhere within the subfamily Elaeniinae as constituted by Traylor (1977). Since I have doubts about the monophyly and hence the composition of this assemblage, I can make no recommendation as to the relationship between them and other genera presently assigned to the Elaeniinae until we have a more satisfactory phylogeny of the family Tyrannidae.

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It was the field work of Thomas Sherry on Cocos Island that rekindled my interest in the endemic flycatcher there. I am indebted to him for comments on an earlier draft of this manuscript and for providing the alcoholic specimens (by way of the Field Museum of Natural History) that were crucial for this study. I thank F. Gary Stiles for sending me a copy of his Cocos Island recording, and for sharing with me his field experience with *Nesotriccus.* I am grateful to the following for arranging loans of specimens under their care: John W. Fitzpatrick, Storrs Olson, Kenneth C. Parkes, James V. Remsen, Charles G. Sibley, and Robert W. Storer. The photographs of skulls and syringes were made with equipment in the laboratory of Charles W. Myers, my colleague at the American Museum of Natural History.

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RECENT PUBLICATIONS

Check-list of North American birds, 6th edition.—American Ornithologists' Union. 1983. Am. Ornithol. Union, Washington, DC. 877 p. Deluxe edition, limited to 100 copies, bound in leather, signed by members of the check-list committee, $90.00; regular edition, $35.00 ($28.00 to AOU members). Source: Allen Press, P.O. Box 368, Lawrence, KS 66044. Long awaited, this new edition of the Check-list will surely be the most lasting and important memorial to the AOU Centennial. It differs from its 1957 predecessor chiefly in expanded geographic scope (now including Hawaii, Middle America, and the West Indies), restriction of coverage to the species level, and adoption of several major changes in classification. These last are not new proposals by the "Check-list" Committee but its acceptance of revisions that have already been published elsewhere. As explained in a carefully written preface, the Committee has striven to steer a course between traditional views and bold innovations. The specific entries themselves give in customary manner the recommended names, citation of the original description, habitat, and distribution. Additionally, in many cases they include notes on other nomenclature or taxonomy, thereby pointing out matters of uncertainty or controversy. While this check-list embodies many notable changes from the Fifth, it clearly looks toward further changes in the Seventh. The Committee and its longtime Chairman, the late Eugene Eisenmann (to whom the volume is fittingly dedicated) deserve great appreciation for the thought and work they have put into this book. Four appendices of special lists, list of AOU numbers, index, endpaper maps.

Bird Conservation, No. 1.—Edited by Stanley A. Temple. 1983. Published for the International Council for Bird Preservation, U.S. Section, by the University of Wisconsin Press, Madison. 148 p. Paper cover. $12.95. Source: University of Wisconsin Press, 114 North Murray St., Madison, WI 53715. This is the first in a projected series of annuals intended to publish information on bird conservation activities, primarily in the U.S. "Each annual will include several major reports on specific conservation programs written by the biologists who are involved directly with the projects. Usually these reports will focus on a single or a few key issues." This one, for example, focuses on falconiforms with specific articles on the Peregrine Falcon, Bald Eagle, and California Condor. A second regular section for news and updates will give current, concise reports on various bird populations, conservation activities, and international treaties. Finally, there will be a compilation of references from the recent literature that pertain to endangered birds or conservation topics. This yearbook itself valuably fills a niche between the scientific and the popular press by disseminating reliable information in a not-overly technical manner. The U.S. Section of the ICBP deserves applause for sponsoring this new publication as a way to advance knowledge and understanding of issues in bird conservation.

Perspectives in Ornithology/Essays presented for the Centennial of the American Ornithologists' Union.—Edited by Alan H. Brush and George A. Clark, Jr. 1983. Cambridge University Press, Cambridge. 560 p. $29.95 ($24.00 to AOU members). Source: Cambridge Univ. Press, 32 East 57th St., New York, NY 10022. The AOU has a useful tradition of sponsoring volumes of ornithological essays at intervals in its history, first in 1933, next in 1955, and now once again. While the subject matter itself is of course the focus, it is also revealing to compare the style and selection of topics in these collections. Most of the topics in the present volume were not mentioned at all in the previous one, clearly showing the areas of new growth in the field. Perhaps in awareness of this—and encouraged by the editors—the present authors are more open to the possibilities of further change. Their articles are not so much reviews of the state-of-the-art as examinations of some important questions and the ways of addressing them in future research. The existence of ferment and controversy is underscored by the commentaries that follow most of the chapters, giving alternative viewpoints, specific criticisms, or additional material. In his Introduction, Ernst Mayr offers insights about recent changes in ornithology as well as his comments on several of the chapter topics. The essays are as follows: Captive birds and conservation: William Conway; Research collections in ornithology: Jon C. Barlow and Nancy J. Flood; The study of avian mating systems: Douglas W. Mock (commentary by Sara Lenington); Cooperative breeding strategies: Stephen T. Emlen and Sandra L. Vehrencamp (J. David Ligon, Ian Rowley); Ecological energetics: Glenn E. Walsberg (William A. Calder III); Optimal foraging: John R. Krebs, David W. Stephens, and William J. Sutherland (J. P. Myers); Biochemical studies of microevolutionary processes: George F. Barrowclough (John C. Avise); Organization of the avian genome: Gerald F. Shields; Origin and early radiation of birds: Larry D. Martin (David W. Steadman, Pat V. Rich); Avian community ecology: John A. Wiens (James R. Karr); Biogeography: Daniel Simberloff (Joel Cracraft, Dennis M. Power); Bird song learning: P. J. B. Slater (Luis F. Baptista, Donald E. Kroodsma); and Bird navigation: Charles Walcott and Anthony J. Lednor (Kenneth P. Able). The essays differ in format almost as much as in content, yet the editors have seen to it that they are all well written. This is a stimulating and timely book, not just for those whose specialities are included, but for all ornithologists who care about the process and progress of their science. Lists of references accompany each chapter and commentary. Index.