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PHYLOGENETIC RELATIONSHIPS OF THE ZIGZAG HERON (*ZEBRILUS UNDULATUS*) AND WHITE-CRESTED BITTERN (*TIGRIORNIS LEUCOLOPHUS*) ESTIMATED BY DNA-DNA HYBRIDIZATION

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ABSTRACT.—Recently, we acquired DNA of two rare species of heron, the Neotropical Zigzag Heron (*Zebrilus undulatus*) and the African White-crested Bittern (*Tigriornis leucolophus*). To estimate their phylogenetic relationships to other herons, we compared these species with representatives of the major heron clades using DNA-DNA hybridization. Even though the Zigzag Heron resembles a tiger-heron in its barred plumage and forest habitat, it is most closely related to bitterns. The White-crested Bittern is monophyletic with the New World tiger-herons (*Tigrisoma*) and, thus, is better termed the White-crested Tiger-Heron. These findings accord well with phylogenetic analyses based on osteology. The remaining uncertainties in higher-level heron phylogeny are principally: (1) the position and composition of some enigmatic genera (e.g. *Gorsachius, Agamia, Pilherodius,* and *Ardeola*); and (2) the identification of the basal heron lineage, which appears to be either tiger-herons or the Boat-billed Heron (*Cochlearius*). *Received 15 June 1994, accepted 27 January 1995.*

THE HERONS (Ciconiiformes: Ardeidae) may be divided ecologically into groups that: (1) feed largely in open areas either by day (e.g. *Egretta, Ardea, Bubulcus,* and *Butorides*) or night (*Nycticorax, Nyctanassa,* and *Cochlearius*); (2) live and nest in marshes (bitterns); or (3) live in forested areas (tiger-herons and *Gorsachius* night-herons). Of these groups, the least known are the forest-dwelling species, which generally are rare and difficult to observe. In comparison to other herons, they are poorly represented in museum collections, have received little ecological and behavioral study, and have obscure phylogenetic relationships (Payne and Risley 1976, Hancock and Elliott 1978, Hancock and Kushlan 1984). They also exemplify some intriguing evolutionary issues and problems. Forest-dwelling herons have undergone marked adaptive changes in apparent response to their habitat (especially in terms of their plumage), and they have relictual tropical distributions—the tiger-herons occur in the Neotropics, Africa, and New Guinea, and *Gorsachius* occurs in Africa and Asia.

In this paper we present DNA-DNA hybridization evidence of the phylogenetic relationships of members of one of these little-known groups, the tiger-herons. This study supplements a previous DNA-DNA hybridization effort to estimate the intergeneric phylogenetic relationships of herons (Sheldon 1987a, see also Sheldon and Kinnarney 1993). At the time of the 1987 study, DNA was available from only one tiger-heron species—the Rufescent Tiger-Heron (*Tigrisoma lineatum*)—and, as a result, little could be said about the relationships among members of this group. Also, because the determination of the position of the tiger-heron clade within the heron family relied on a single species, the overall estimate of heron phylogeny potentially suffered from the limited sample representing this important group. Since the earlier study, we have obtained DNA of two more tiger-heron genera (sensu lato): the White-crested Bittern (*Tigriornis leucolophus*) of Africa and the Zigzag Heron (*Zebrilus undulatus*) of South America. With *Tigrisoma lineatum,* these new species constitute three of the four traditional tiger-heron genera. Unfortunately, a sample of the fourth tiger-heron, the Forest Bittern (*Zonerodius heliosylus*) of New Guinea, is still lacking.

The inclusion of two more tiger-heron genera not only improves the likely accuracy and use-

TABLE 1. Species and samples used in study.

Name	Country	Preparation no.
Egretta thula (Snowy Egret)	USA	3705
Cochlearius cochlearius (Boat-billed Heron)	Ecuador	3281
Tigrisoma lineatum (Rufescent Tiger-Heron)	Ecuador	3165, 4507
Tigriornis leucolophus (White-crested Bittern)	Liberia	1910
Zebrilus undulatus (Zigzag Heron)	Ecuador	3170
Ixobrychus exilis (Least Bittern)	USA	409
Plegadis falcinellus (Glossy Ibis)	USA	852

fulness of the DNA-DNA estimate of phylogeny, but it permits a more substantial comparison between the DNA-DNA hybridization results and other studies of heron phylogeny (e.g. Bock 1956, Curry-Lindahl 1971, Payne and Risley 1976). Payne and Risley's (1976) study is particularly useful as a sounding board, because it is a thorough cladistic and phenetic analysis of heron osteology and, thus, may be compared to the DNA-DNA hybridization results via taxonomic congruence analysis (e.g. Cracraft and Mindell 1989, Bledsoe and Raikow 1990).

METHODS

The taxa and samples used in this study are listed in Table 1. Because of the n^2 problem noted by Barrowclough (1992), in which the required number of pairwise DNA-DNA hybridization comparisons increases geometrically with the number of taxa (n), we limited the number of species in this study to save money and time. Our selection of species for comparison (in addition to *Tigrisoma lineatum, Tigriornis leucolophus,* and *Zebrilus undulatus*) was based on the following observations. Sheldon (1987a) identified three fundamental lineages of herons: "typical" herons (including day-herons and night-herons); bitterns; and tiger-herons. Therefore, we decided to include representatives of each of these clades. *Egretta thula* was selected because it is a common typical heron. Similarly, *Ixobrychus exilis* is a common bittern. Sheldon (1987a) also found that *Cochlearius cochlearius* was genetically remote from other herons and possibly monophyletic with tiger-herons. Thus, *Cochlearius* was included in the study. Night-herons were excluded because they were found to be unambiguously monophyletic with day-herons and distant from all other lineages, including *Cochlearius* (contra Bock 1956, Cracraft 1967, Payne and Risley 1976). Finally, the Glossy Ibis (*Plegadis falcinellus*) was selected as an outgroup; DNA-DNA hybridization studies of various ciconiiform birds suggest that ibises are as close or closer to herons than any group of birds (Sibley and Ahlquist 1990, Sheldon and Kinnarney 1993). Moreover, within reason, outgroup choice appears to have remarkably little effect on DNA-DNA hybridization estimates of phylogeny (e.g. Sheldon 1994, Slikas et al. 1996).

With the exception of *Tigrisoma*, only one individual of each species was compared. For *Tigriornis* and *Zebrilus*, only one sample was available; for the other species, samples from more individuals were available, but degrees of individual variation were expected to be well below genetic differences among species (Sheldon 1987a, Bleiweiss and Kirsch 1993, Sheldon and Winkler 1993). We compared two individuals of Ecuadorian *Tigrisoma:* one from the eastern (Amazonian) lowlands (tissue no. 3165; ANSP catalog 183558); and one from 1,500 m elevation on the eastern slopes of the Andes (tissue no. 4507; ANSP catalog no. 185105). DNA of the latter was received late in the study and was included because we believed it to represent a separate species, the Fasciated Tiger-Heron (*T. fasciatum*). Now, we are not certain about the species of the specimen, but suspect it to be *lineatum*. This individual is a juvenile bird, whose powderdown pattern suggests *lineatum*, but was collected at an altitude more typical of *fasciatum*. We include its data in this paper because the specimen ultimately will be identified.

Methods of DNA preparation and hybridization were based on those of Sibley and Ahlquist (1990), with the modifications of Sheldon and Winkler (1993) and Slikas et al. (1996). Hybrids were fractionated in a 35-column machine from 60°–95°C in 2.5°C increments. All DNA samples were radiolabeled and compared as drivers (targets), except for *Tigrisoma* sample 4507, which was radiolabeled but not used as a driver in reciprocal comparisons. Data are available from the authors.

The indexes of hybrid stability (T_m, T_{mode}, ΔT_m, and ΔT_{mode}) and normalized percent reassociation (NPR) were computed by the methods of Sheldon and Bledsoe (1989). Individual hybrids were excluded from further analysis if they exhibited technical problems or less than 60% NPR (rationale discussed in Sheldon and Winkler 1993). Trees were built using the Fitch, Kitch, and neighbor-joining options of PHYLIP 3.4 (Felsenstein 1989). Because measurement error is not correlated with genetic distance (Fig. 1A), the fitting option was set to unweighted least squares (Cavalli-Sforza and Edwards 1967). Branch robustness was tested by bootstrapping with the program of A. Dick-

TABLE 2. Mode and ΔT_{mode} matrix.

	Cochlearius		*Egretta*		*Ixobrychus*		*Tigriornis*		*Tigrisoma* 1		*Zebrilus*		*Tigrisoma* 2		*Plegadis*	
	Mode	ΔT_{mode}	Mode	ΔT_{mode}	Mode	ΔT_{mode}	Mode	ΔT_{mode}	Mode	ΔT_{mode}	Mode	ΔT_{mode}	Mode	ΔT_{mode}	Mode	ΔT_{mode}
Cochlearius																
n	4	4	3	3	4	4	3	3	4	4	4	4	4	4	4	4
$\bar{x}$	85.86	0.00	81.04	5.38	80.20	6.05	79.56	5.12	80.84	4.89	80.98	5.46	81.48	4.46	76.53	9.06
SD	0.35	0.35	0.12	0.12	0.20	0.20	0.22	0.22	0.17	0.17	0.22	0.22	0.21	0.21	0.05	0.05
Egretta																
n	3	3	4	4	7	7	4	4	5	5	3	3	4	4	4	4
$\bar{x}$	80.64	5.22	86.49	0.00	80.66	5.29	78.99	5.69	80.32	5.48	81.84	4.59	80.77	5.17	75.61	9.98
SD	0.07	0.07	0.09	0.03	0.53	0.19	0.05	0.05	0.35	0.26	0.08	0.08	0.21	0.21	0.11	0.11
Ixobrychus																
n	4	4	4	4	7	7	4	4	5	5	3	3	4	4	3	3
$\bar{x}$	79.72	6.14	81.37	5.12	85.95	0.00	78.29	6.39	79.77	6.03	82.13	4.30	79.83	6.11	75.50	10.09
SD	0.20	0.20	0.39	0.33	0.43	0.21	0.06	0.06	0.30	0.22	0.10	0.10	0.10	0.10	0.16	0.16
Tigriornis																
n	4	4	2	2	4	4	4	4	4	4	4	4	4	4	4	4
$\bar{x}$	80.57	5.29	80.25	6.17	79.38	6.88	84.68	0.00	81.24	4.49	80.27	6.16	82.09	3.85	76.40	9.20
SD	0.21	0.21	0.13	0.13	0.09	0.09	0.30	0.30	0.17	0.17	0.17	0.17	0.10	0.10	0.03	0.03
***Tigrisoma* 1[a]**																
n	4	3	3	3	3	4	4	3	3	4	4	4	4	4	4	4
$\bar{x}$	80.27	5.59	80.52	5.90	80.13	6.12	80.28	4.40	85.85	0.00	80.57	5.86	85.17	0.76	76.96	8.63
SD	0.15	0.15	0.04	0.04	0.18	0.18	0.14	0.14	0.23	0.21	0.19	0.19	0.20	0.20	0.17	0.17
Zebrilus																
n	4	4	2	2	4	4	3	3	4	4	3	3	4	4	3	3
$\bar{x}$	80.36	5.51	81.86	4.56	81.89	4.36	79.23	5.45	80.17	5.57	86.43	0.00	80.94	4.99	76.16	9.43
SD	0.12	0.12	0.08	0.08	0.12	0.12	0.14	0.14	0.20	0.20	0.47	0.47	0.00	0.00	0.03	0.03
***Tigrisoma* 2[a]**																
n	—	—	—	—	—	—	—	—	—	—	—	—	4	4	—	—
$\bar{x}$	—	—	—	—	—	—	—	—	—	—	—	—	85.94	0.00	—	—
SD	—	—	—	—	—	—	—	—	—	—	—	—	0.40	0.40	—	—
Plegadis																
n	3	3	5	5	6	6	4	4	6	6	3	3	4	4	4	4
$\bar{x}$	76.72	9.14	76.50	9.98	75.37	10.53	75.53	9.15	77.06	8.74	76.50	9.93	77.57	8.37	85.60	0.00
SD	0.11	0.11	0.12	0.13	0.17	0.09	0.15	0.15	0.13	0.12	0.19	0.19	0.20	0.20	0.10	0.10

[a] *Tigrisoma* 1 is *Tigrisoma lineatum*. *Tigrisoma* 2 is either *T. lineatus* or *T. fasciatum*.

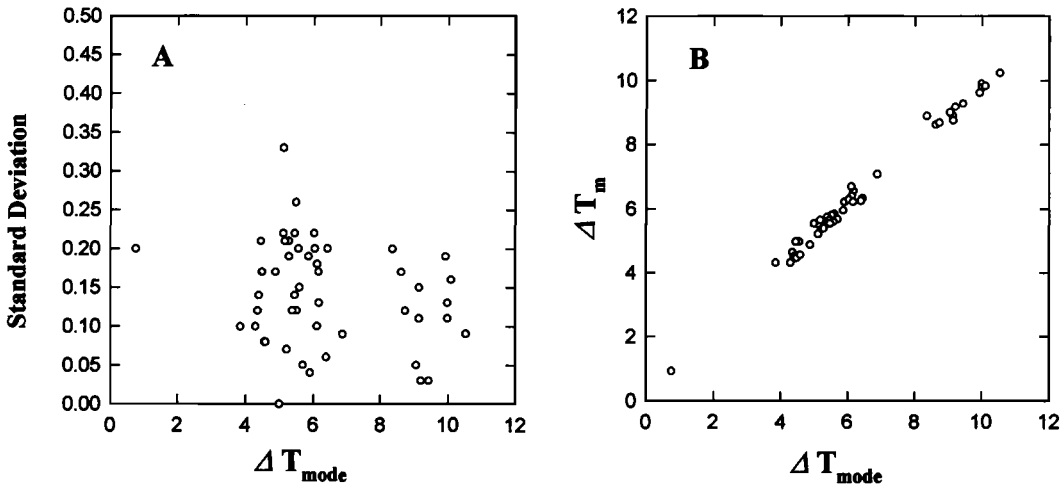

Fig. 1. (A) ΔT_{mode} versus standard deviation for each ΔT_{mode} value (from Table 2). (B) ΔT_{mode} versus ΔT_m, showing high correlation between the two distance measures ($R = 0.995$, $n = 49$).

erman (pers. comm.; Krajewski and Dickerman 1990) and jackknifing (Lanyon 1985).

Results

The phylogenetic analysis was based on 467 hybrids consisting of 7,005 thermal fractions. Because ΔT_m and ΔT_{mode} were highly correlated (Fig. 1B), we summarize in Table 2 only the ΔT_{mode} values, which have some better properties (e.g. Sarich et al. 1989). All Fitch and neighbor-joining trees and tests of branch robustness (bootstrapping and jackknifing) using those tree-building methods produced a single, fully resolved branching pattern (Fig. 2). This tree depicts two major heron groups—tiger-herons and other herons. The tiger-heron clade includes *Tigrisoma* and *Tigriornis*. The other herons are divided into three clades: *Cochlearius, Egretta,* and *Ixobrychus/Zebrilus*. *Egretta* is the sister taxon of *Ixobrychus/Zebrilus* and together they form the sister group of *Cochlearius*.

A relative-rate test (Sarich and Wilson 1967) was performed with *Plegadis* as the outgroup. *Ixobrychus* appears to have evolved faster, and *Cochlearius* and tiger-herons slower, than *Egretta* (ANOVA, $P < 0.001$). This result is concordant with previous determinations of heron rates

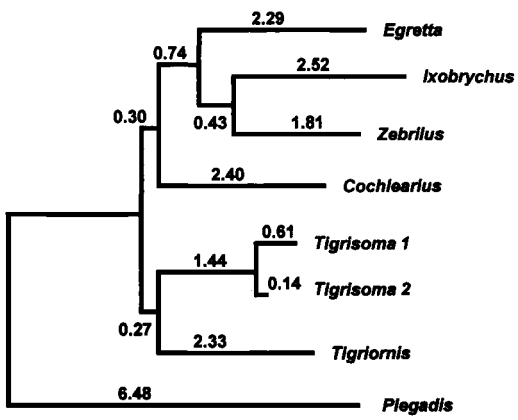

Fig. 2. Estimate of heron phylogeny. Modal distances fitted by unweighted least squares using the Fitch program of Felsenstein (1989). All branches 100% resolved after bootstrapping 1,000 times and jackknifing.

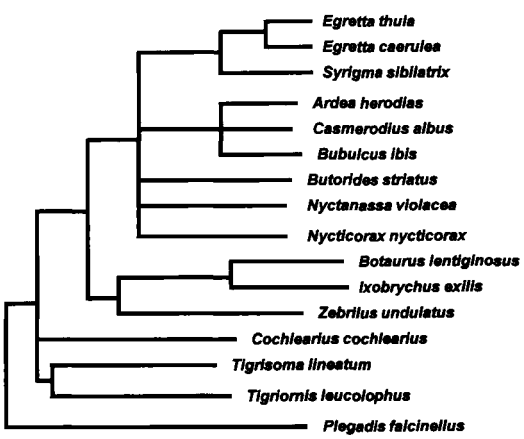

Fig. 3. Consensus tree derived by merging tree in Figure 3 with tree in Sheldon (1987a:fig. 1).

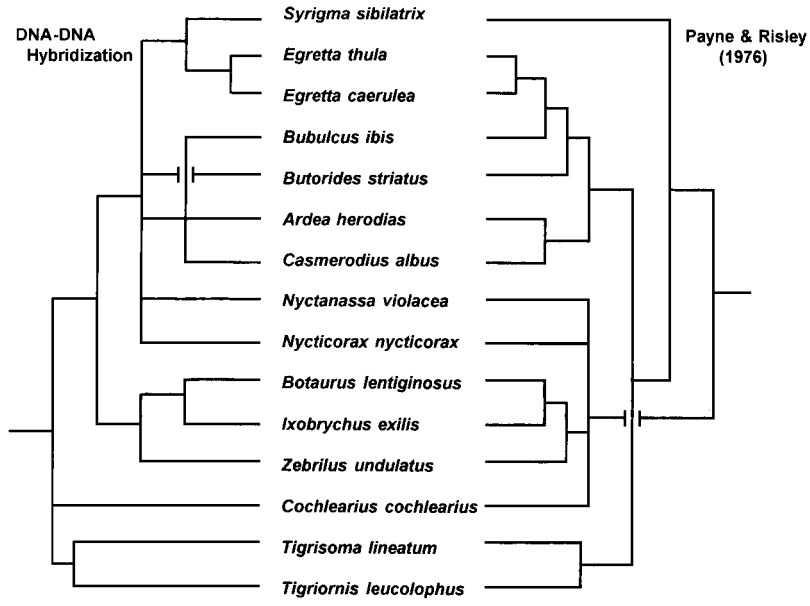

Fig. 4. Comparison of tree in Figure 3 and tree based on cladistic osteological analyses of Payne and Risley (1976:figs. 34 and 35).

(Sheldon 1987b, Sheldon and Kinnarney 1993). However, *Zebrilus*, which is monophyletic with *Ixobrychus*, does not exhibit the fast rate found in other bitterns. Because of the variability in rates of evolution, we did not use the Kitch option in PHYLIP, which assumes a molecular clock.

DISCUSSION

The only other rigorous effort to estimate heron phylogeny was the osteological cladistic and phenetic study of Payne and Risley (1976). Given the importance of tree congruence in assessing the accuracy of phylogenetic estimates (e.g. Cracraft and Mindell 1989, Bledsoe and Raikow 1990, Swofford 1991), we have aligned our tree (Fig. 3) with a consensus tree (Fig. 4) derived from the most-parsimonious Wagner trees of Payne and Risley (1976:figs. 34 and 35) to determine the extent of agreement. In Figure 4, we used Payne and Risley's (1976) cladistic parsimony results for this comparison, instead of their phenetic trees, because phenetic analyses of morphology are not generally useful in estimating phylogeny. Such analyses fail because overall similarity in morphology is not distributed hierarchically according to phylogeny (e.g. Ridley 1986). The same is not true of molecular-distance methods, such as DNA-DNA hybridization, as long as the data are fitted to a branching pattern without assuming a constant (or monotonic) evolutionary rate. DNA-DNA hybridization distances are inherently hierarchical and appear mainly to reflect phylogeny (e.g. Springer and Krajewski 1989, Bledsoe and Sheldon 1990, Sheldon 1994).

The two fundamental discoveries of our study are supported by congruence with Payne and Risley's (1976) phylogeny: *Tigrisoma* and *Tigriornis* are sister taxa; and *Zebrilus* is monophyletic with bitterns.

That *Tigriornis* is a tiger-heron (sensu stricto) is expected. Although *Tigriornis* differs from other large tiger-herons in some traditionally important morphological characters (e.g. it has two instead of three powderdown patches and a particularly distinct sternum), it is united with *Tigrisoma* by a series of osteological synapomorphies (e.g. sacral parapophyses with the synsacrum and ligamental furrow of the humerus; Payne and Risley 1976), as well as other characters (e.g. nesting; see below). Given the relationship between *Tigriornis* and other large tiger-herons, the common name of this species ought to be White-crested Tiger-Heron, not White-crested Bittern as in Sibley and Monroe (1990).

The discovery that *Zebrilus* and bitterns are monophyletic also is not surprising, despite the

resemblance of *Zebrilus* to large tiger-herons in plumage and forest habitat, and the uniqueness of some of its osteological features (e.g. small size, shape of the bill, angle of the bill with the skull, and form of the sternal keel; Payne and Risley 1976). Like bitterns, *Zebrilus* has 10 tail feathers, instead of the normal 12, and it has scutellate tarsi (Payne and Risley 1976). In addition, *Zebrilus* and bitterns have pure white eggs (Hancock and Elliott 1978, English 1991). Large tiger-herons, in contrast, have eggs that are colored and blotched (e.g. beige-yellow with reddish brown or violet blotches in *Tigriornis* [Brown et al. 1982] and bluish white with pale-violet blotches in *Tigrisoma lineatum* [Hancock and Elliot 1978]). The nest of *Zebrilus* also is remarkably similar in some respects to those of certain bittern species. *Zebrilus* constructs a shallow round platform in trees or bushes between 1 and 3 m above water. Four of the five *Zebrilus* nests found by English (1991) were weaved with thorns to form an edge barrier. At least two species of forest-stream-dwelling bitterns, the African Dwarf Bittern (*Ixobrychus sturmii*) and the Black Bittern (*I. flavicollis*), are known to build nests in thorn bushes over water (Hancock and Elliot 1978). Tiger-herons construct nests in trees between 6 m (*Tigriornis*; Brown et al. 1982) and 15 m (*Tigrisoma mexicanum*; Hancock and Elliot 1978) above the ground or water.

Although DNA-DNA hybridization and morphological studies concur as to the phylogenetic position of *Zebrilus* and *Tigriornis*, they disagree in the placement of several other heron taxa. Payne and Risley's (1976) tree depicts *Cochlearius*, night-herons, and bitterns (including *Zebrilus*) as monophyletic. It also indicates the monophyly of day- and tiger-herons. DNA-DNA hybridization suggests a more asymmetrical tree. In particular, day- and night-herons are monophyletic; bitterns (including *Zebrilus*) are their sister taxon; and *Cochlearius* and tiger-herons are basal to these two groups. Although these differences between the morphological and DNA studies indicate substantial incongruence, in fact they are not well-founded. We have reanalyzed Payne and Risley's (1976) data (McCracken and Sheldon unpubl. analysis) using PAUP (Swofford 1993), a program that was not available to Payne and Risley. This reanalysis indicates that: (1) *Cochlearius* is highly diverged from other herons, including night-herons; indeed, based on morphology and a thorough consideration of outgroups, it is not even monophyletic with herons; (2) night-herons are not monophyletic with bitterns; and (3) tiger-herons and day-herons are not sister taxa. Following this reanalysis, the only major discrepancy between Payne and Risley's (1976) results and the DNA-DNA hybridization findings concerns the monophyly of day- and night-herons. The DNA-DNA hybridization data indicate that day- and night-herons are sister taxa, and Payne and Risley's (1976) data do not.

Our current study disagrees with Sheldon (1987a) in one respect. Formerly, *Cochlearius* appeared as the sister taxon of *Tigrisoma*; now it appears as the sister taxon of the lineage comprising bitterns/*Zebrilus* and "typical" herons. Because of this discrepancy, we have depicted the node from which *Cochlearius*, tiger-herons, and bitterns/typical herons emerge as a multifurcation in Figures 3 and 4. In terms of evolution, the discrepancy between the two DNA-DNA hybridization studies may simply reflect the inability of the technique to resolve this node given rapid origination of the three major heron groups over a short period of time (e.g. Sheldon 1987a). In terms of phylogenetic-reconstruction technique, the discrepancy may be the result of taxonomic sampling. In the 1987 study, fewer taxa bore on this node (viz. only one tiger-heron). Such incongruencies emphasize the need for as complete a set of taxa in phylogenetic reconstructions as possible (e.g. Lanyon 1994). Unfortunately, because *Cochlearius* is monotypic and genetically distant from all other herons, and only one more tiger-heron genus (*Zonerodius*) can be brought to bear on the problem, we cannot expect to increase our taxonomic sample substantially.

Several groups of birds are distributed pantropically, including tiger-herons, storks, finfoots, jacanas, trogons, and barbets. The cause of this distribution is one of the great mysteries of bird evolution. Moreover, certain of these groups are represented only by relicts (most notably the tiger-herons and finfoots), which raises tangential questions about the age of taxa and whether the same fundamental forces are responsible for shaping their distributions. At present, phylogenetic data are being gathered on all of these groups (Sibley and Ahlquist 1990, Lanyon and Hall 1994, Houde et al. 1995, B. Slikas pers. comm., S. Emlen pers. comm.), and the possibility of substantive comparative analyses of branching patterns and genetic distances is on the horizon.

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