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THE RELATIONSHIPS OF THE HOATZIN

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THE taxonomic position of the Hoatzin (*Opisthocomus hoazin*) of South America has long been one of the most debated problems in avian systematics. It has usually been placed in the Galliformes, but some authors have allied it with the African turacos (Cuculiformes: Musophagidae), the pigeons (Columbidae), or the rails (Rallidae), and others have placed it in its own monotypic order. The Hoatzin occurs in riparian vegetation along the streams of the Orinoco and Amazon river drainages in northern South America. It is a slender bird, about 25 inches in length and generally brownish in color, somewhat resembling a chachalaca (Cracidae). The small head bears a ragged, bristly, reddish-brown crest and the bare facial skin is bright blue. As is apparent from the Frontispiece, the Hoatzin is actually most like the smaller Guira Cuckoo (*G. guira*) in coloration; in fact, the two species are remarkably similar, except in size.

This paper reviews the taxonomic history of the Hoatzin and presents new evidence from a study of the egg-white proteins indicating that the resemblance to *Guira* is due to a close relationship, not merely to convergence or coincidence. The correct position of the Hoatzin is as a genus within the neotropical subfamily Crotophaginae (Cuculidae) and its closest relatives are *Guira* and *Crotophaga*. The long association with the Galliformes, we believe, was based upon little more than the prejudice established by the original description as *Phasianus hoazin* (Müller 1776) and the inability of subsequent workers to interpret their anatomical data. The link to the Musophagidae seems to be based upon the common possession of a number of anatomical characters (see Verheyen 1956), the vegetarian diets, poor flying ability, general proportions, and similar size. In the turacos and in the Hoatzin the young have wing claws and clamber about near the nest before they can fly.

THE TAXONOMIC HISTORY OF THE HOATZIN

In general appearance a museum specimen of the Hoatzin resembles a galliform bird and it is not surprising that Müller (1776) originally named

The Hoatzin (lower figure) and the Guira Cuckoo drawn to the same size.
Insert shows relative sizes of the same birds.
From an original acrylic painting by Jon Ahlquist.

TABLE 1

SOME OPINIONS ON THE SYSTEMATIC POSITION OF *OPISTHOCOMUS*

Placed in Galliformes	Placed in separate order	Placed near Musophagidae	Evidence of relationship to Cuculidae
Müller, 1776			
Linnaeus, 1788			
Illiger, 1811			
Cuvier, 1817	L'Herminier, 1837[2]	Nitzsch, 1829, 1840	
Carus, 1868	Huxley, 1868[2]	Gray, 1844–49, 1869–71	
	Garrod, 1879[1]		
Reichenow, 1882	Sclater, 1880[1]	Cabanis, 1847[6]	
	Newton, 1884[2]		
Fürbringer, 1888[4]	Elliot, 1885[3]		Goodchild, 1886 (secondary coverts)
	Sharpe, 1891[5]		
Gadow, 1892, 1893[4]	Beddard, 1898[1]		Pycraft, 1895 (pterylography)
Shufeldt, 1904	Stresemann, 1927–34, 1959[3]		Beebe, 1909 (behavior)
			Lemmrich, 1931 (sclerotic ossicles)
Wetmore, 1930, 1934, 1940, 1951, 1960			
Peters, 1934			
Berlioz, 1950			
Mayr and Amadon, 1951	Barnikol, 1953	Verheyen, 1956	
Storer, 1960			
Verheyen, 1961			Sibley and Ahlquist, 1972

[1] Between Galliformes and Cuculiformes.
[2] Between Galliformes and Columbiformes.
[3] Next to Galliformes.
[4] Noted ties to Musophagidae.
[5] Between Columbae and Ralli, following Seebohm (1888, 1890, 1895) who believed that *Opisthocomus* had gruiform affinities.
[6] Cabanis was apparently the first to note the similarity in color and pattern between *Opisthocomus* and *Guira*.

it *Phasianus hoazin*. Apparently this was enough to establish a bias in favor of galliform affinities, and in most classifications to the present time, the Hoatzin has been placed in or near the Galliformes. Some of the opinions concerning the classification of the Hoatzin are summarized in Table 1.

The first suggestion that the Hoatzin might be related to the Musophagidae was that of Nitzsch who found similarities in the carotid arteries (1829) and pterylography (1840). In both papers Nitzsch placed *Opisthocomus* with *Colius* and the Musophagidae in the "family" Amphibolae.

Gray (1844–49, 1869–71) followed a similar scheme, placing these three groups, along with the Bucerotidae and several passerine families, in the Conirostres.

Huxley (1867) first examined only an incomplete skull and the feet of a Hoatzin. He found that the slender vomer bifurcates anteriorly in an unusual way but he considered the palate to be schizognathus, as in the Galliformes, rather than desmognathous, as are the cuckoos. Huxley considered the tarsometatarsus to be galliform and assigned *Opisthocomus* to a "special subdivision," Heteromorphae, in his large "suborder" Schizognathae. He placed the Heteromorphae between the sandgrouse ("Pteroclomorphae") and the pigeons ("Peristeromorphae"), not far from the galliforms ("Alectoromorphae"). Huxley soon obtained a complete skeleton and (1868) decided that in the majority of its osteological characters the Hoatzin resembles the Galliformes and the Columbiformes and that where it differs from these it is either unique or like the Musophagidae. He concluded that *Opisthocomus* is a highly modified form derived from "Gallo-columbine" stock, worthy of distinction in his monotypic "Heteromorphae."

Huxley's prestige and influence were great and these pronouncements must have had a strong effect upon subsequent workers. The galliform affinities of the Hoatzin seemed confirmed, but an alliance to the cuckoos, via the turacos, had been left open. This basic concept has prevailed to the present day, in spite of evidence to the contrary.

Garrod (1879) was among the first to follow Huxley's lead by placing the galliform and cuculiform birds together in his Galliformes (which also included the ratites, tinamous, rails, seriemas, and bustards). Garrod expressed his belief that *Opisthocomus* is an intermediate form, linking the Cuculidae and Musophagidae to the typical galliforms. He thus emphasized that *Opisthocomus* has a relationship to the cuckoos, although he retained the supposed link to the Galliformes as well.

Others who adopted *Opisthocomus* as the evidence for a galliform-cuculiform alliance included Fürbringer (1888) who placed the family Opisthocomidae next to the Gallidae in the "gens" Galli, but also noted a dozen characters linking *Opisthocomus* with the Musophagidae.

Gadow (1892: 229) also considered *Opisthocomus* to be a connection between the cuckoos and the galliforms but (1893) he placed the Opisthocomi in the Galliformes. Like Fürbringer, Gadow consistently emphasized the alliance to the cuckoos. Gadow (1893: 177) noted the following characters in comparisons among the three groups:

I. *Opisthocomus* agrees with the Galliformes and differs from the Cuculiformes in: 1) downy precocial young, not blind at hatching, 2)

schizognathous palate, 3) fusion of many dorsal vertebrae, 4) syrinx, 5) foot structure, 6) large crop.

II. *Opisthocomus* agrees with the Cuculiformes and differs from the Galliformes in: 1) deep temporal fossae, 2) short mandibular processes, 3) lack of basipterygoid processes, 4) lack of spina interna, 5) metasternal configuration, 6) large procoracoid, 7) spotted eggs, 8) 10 rectrices.

III. *Opisthocomus* differs from both Galliformes and Cuculiformes in: 1) lacking apteria on the sides of the neck, 2) arrangement of the adult downs, 3) number of cervical vertebrae, 4) small thoracic haemapophyses, 5) shape of the liver, 6) other specialized characteristics, for example, sternum, stomach, crop.

Because virtually all subsequent classifications, including those of Stresemann (1927–34), Wetmore (1930, 1934, 1940, 1951, 1960), Peters (1934) and Mayr and Amadon (1951) are based upon Gadow and Fürbringer, it is easy to understand why the Hoatzin has been placed so consistently in the Galliformes.

The anatomical evidence indicating a relationship to the Cuculidae includes a few additional points. Pycraft (1895: 362) found a general resemblance in the pterylography of the spinal tract among *Opisthocomus*, *Tauraco*, and *Centropus* but declined to offer an opinion on their relationships.

Lemmrich (1931) studied the bony platelets of the sclerotic ring in several groups of birds. He found that all of the 10 species of galliforms he examined had 13 to 15 plates but that *Opisthocomus* has only 12. Lemmrich noted (p. 534) that such a difference is "very remarkable" because there tends to be little variation within a group. Among the few other birds with 12 plates is *Cuculus*.

The skull musculature and its innervation in *Opisthocomus* were studied by Barnikol (1953). He compared the Hoatzin with representative species of galliforms, turacos, and pigeons and summarized the study in a table (p. 520) listing 40 anatomical characters. Of these *Opisthocomus* shared 8 with the Galliformes, 9 with the Columbidae and 13 with the Musophagidae. Barnikol concluded that *Opisthocomus* is an isolated species deserving recognition as the sole occupant of the order Opisthocomae.

Verheyen (1956) defined 66 osteological characters of the Hoatzin and found that 50 of them are shared with the Musophagidae. This led him to combine the two groups as the order Musophagiformes, placed near the Galliformes and the "Anhimiformes." However, in his later (1961) classification Verheyen included *Opisthocomus* next to the Cracidae in his Galliformes, "owing to new information" (p. 21).

Some especially convincing sets of data arguing against a galliform alliance for *Opisthocomus* have appeared in recent years. In 1959 Hudson, Lanzillotti, and Edwards found 13 aspects of the hind limb musculature in which the Hoatzin differs from all galliforms and in 1964 Hudson and Lanzillotti listed 21 important differences between the pectoral musculature of *Opisthocomus* and that of the galliforms. They concluded (p. 111) that "*Opisthocomus* has either been erroneously associated with the Galliformes, or has diverged so far from the original ancestral condition, that there is little or no justification for retaining it in that order."

Because of his long interest in the *Opisthocomus* problem, the opinion of E. Stresemann is of particular significance. In his classifications of 1934 and 1959 he followed Fürbringer, placing the Hoatzin with the Galliformes and attributing resemblances to the turacos to convergence. But in recent studies of pterylosis and molt patterns E. Stresemann (1965) and E. and V. Stresemann (1966) discovered that *Opisthocomus* differs from all galliforms in four ways: 1) the nestling plumage lacks flight feathers; 2) the first flight feathers grow to nearly adult size and are not molted before the bird reaches maturity; 3) the two outer secondaries are not shorter than the adjacent ones and all develop at the same time; and, 4) the primaries are replaced in a continuous, stepwise process, not in the galliform sequence. These findings prompted E. Stresemann (1965: 64) to conclude (transl.): "If *Opisthocomus* is related to the gallinaceous birds it is only by way of Adam and Eve."

Life History and Behavioral Evidence

Accounts of the natural history of the Hoatzin have been published by Goeldi (1886), Quelch (1890), Beebe (1909), Chubb (1916) and Young (1929). A popular article by Grimmer (1962) is one of the most informative, including excellent photographs, and Sick (1964) presented a summary. From these accounts a fairly complete life history can be constructed.

The Hoatzin lives in the permanently flooded forests along the banks of some of the larger rivers and their tributaries in northeastern South America. The birds feed primarily, and perhaps exclusively, on the leaves, flowers, and fruits of certain marsh plants, including the genera *Montrichardia* (Araceae) and *Avicennia*, the arboreal White Mangrove. Grimmer found them feeding only on plants; others have recorded small animals (fish, crabs) as part of the diet. When feeding the birds fill the large, specialized crop, the resultant weight of which makes balance difficult and the bird often rests the sternal area on a branch to support the heavy crop. A special epidermal callosity has evolved in the area of contact.

Hoatzins are usually described as clumsy, poor fliers, their feet not well adapted for grasping branches and their weak wings restricting flight to short distances. The wings are used in clambering about in the vegetation and the weak flight is correlated with the reduction in the sternum and pectoral musculature associated with the exceptionally large crop.

When not breeding the Hoatzin forms flocks of up to 40 individuals which break up into smaller groups of 2 to 6 birds when nesting. The discovery (Grimmer 1962) that the Hoatzin forms communal nesting associations is of particular interest because the three species of anis (*Crotophaga*) and the Guira Cuckoo also build communal nests (Young 1929, Skutch 1935, 1966, Chapman 1938, Davis 1940a, b).

With the first rains the members of a nesting group build a flat nest of loosely organized dry twigs in branches overhanging the water. Mating seems to be indiscriminate and may be polygamous, and all members of the group participate in incubation and care of the young. The 2 to 5 buff-colored eggs have pink, brown, or bluish spots, and incubation takes about 28 days. The young have two successive coats of down and are fed from the crops of the adults, apparently on plant material.

The young remain in the nest for a considerable time but soon begin to undertake climbing excursions nearby, using the well-known wing claws, as well as the feet and beak. When frightened the young Hoatzin drops into the water and either dives or swims into the vegetation and hides. Later it climbs back to the nest.

The young of the Groove-billed (*Crotophaga sulcirostris*) and Smooth-billed (*C. ani*) Anis have a similar pattern of behavior according to Skutch (1959, 1966). The flightless ani youngster also uses the beak, feet, and wings (which are clawless) in clambering about near the nest. When frightened it either moves away through the branches or drops to the ground and hides in the vegetation, later returning to the nest. Both Beebe (1909) and Skutch (1959: 294) commented upon the behavioral similarities between the Hoatzin and the anis.

THE EGG-WHITE PROTEIN EVIDENCE

Egg white of the Hoatzin was first received in 1961 through the kindness of J. Lear Grimmer and Woodbridge Williams. Additional material came from Ram E. Singh in 1972.

It was obvious from the first comparisons using starch gel electrophoresis (Sibley and Ahlquist, 1972, but see Sibley 1970 for a description of the technique) that *Opisthocomus* is not a galliform and is probably a cuckoo, but the resolving power of the starch-gel technique was insufficient to provide an unequivocal answer. A study of the literature on the natural history of the Hoatzin and of museum skins caused us to feel fairly certain

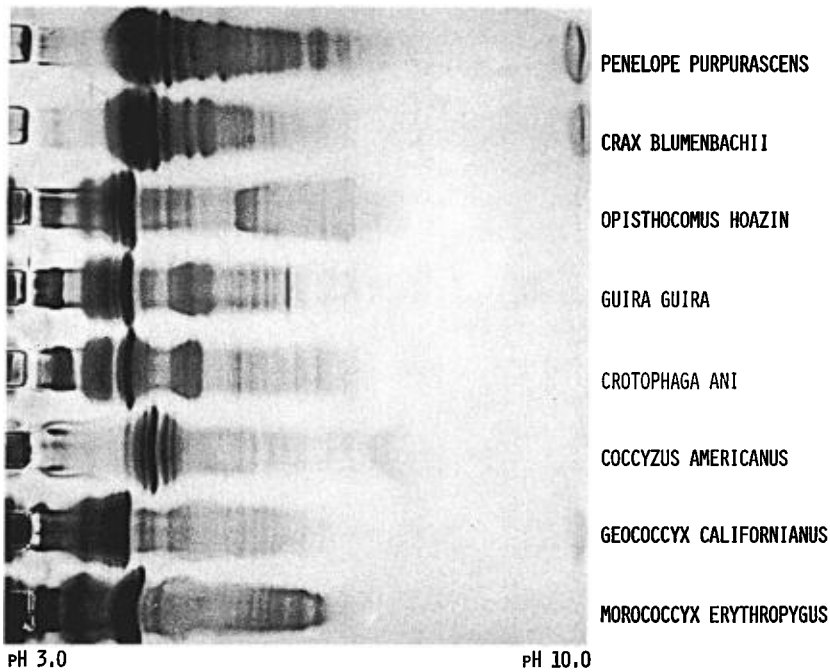

Figure 1. The egg-white proteins of *Opisthocomus* compared with those of some New World cuckoos and cracids using the technique of isoelectric focusing in acrylamide gel. The similarities among *Opisthocomus*, *Guira*, and *Crotophaga* are greater than between any one of these and the other genera compared. The patterns were produced using an Ampholine range of *p*H 3–10.

that the neotropical crotophagine cuckoos (*Guira*, *Crotophaga*) were the most likely relatives. In 1972 we felt confident enough to suggest such an alliance, but proof still seemed elusive. During 1972 we began work with the electrophoretic technique of isoelectric focusing in acrylamide gel (IFAG) (see Sibley and Frelin 1972, for a description of the technique), which has much greater resolving power than that of starch gel electrophoresis. Using the IFAG technique we compared the egg-white proteins of *Opisthocomus* with those of *Guira*, *Crotophaga*, other cuckoos, various galliforms, pigeons, and many other groups of nonpasserine birds. It quickly became clear that the patterns produced by Hoatzin egg white were most similar to those of the Crotophaginae. We now feel confident in stating, without qualification, that *Opisthocomus* is a close relative of *Guira*, which it resembles in plumage coloration, although it is a much larger bird. If the two had been more alike in size, or if the Hoatzin had possessed the typical cuculiform foot, we feel confident that this relation-

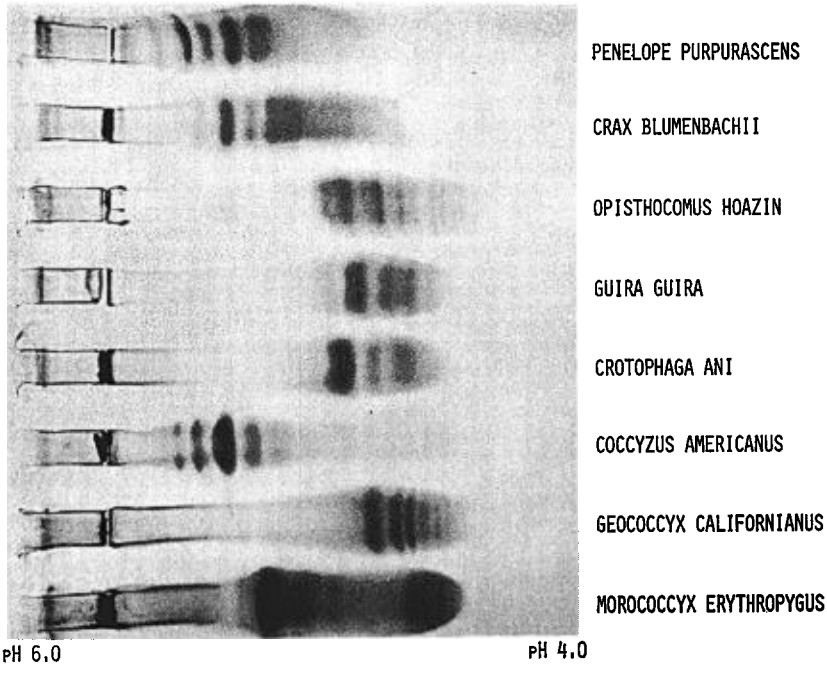

Figure 2. The same species as in Figure 1 but using an Ampholine range of *p*H 6–4.

ship would long ago have been recognized. The egg-white data confirm the relationship, but ample additional evidence from the plumage, anatomy, life history, and behavior supports this conclusion.

A detailed description of the IFAG patterns follows.

Figures 1 and 2 depict those egg-white proteins that have isoelectric points between *p*H 3 and 10. Because no egg-white proteins are known to be isoelectric below *p*H 3 and only lysozyme may be isoelectric above *p*H 10, nearly all components are resolved in these patterns. In these figures the egg white of *Opisthocomus* is compared to that of several species that have been suspected of being related to it. The pattern of *Opisthocomus* differs from those of the curassow *Crax* and the guan *Penelope* in nearly all aspects. In the cracids the ovalbumins and most other components are isoelectric near *p*H 5. This produces a "short" pattern with many bands close together. In *Opisthocomus* the ovalbumins are isoelectric near *p*H 4 and many components, mainly the ovotransferrins, are isoelectric at *p*H 6 or above. *Crax* and *Penelope* have a prominent lysozyme near *p*H 10 that *Opisthocomus* lacks.

In those features where the *Opisthocomus* pattern differs from those of the cracids it is like those of *Guira* and *Crotophaga*. This resemblance is

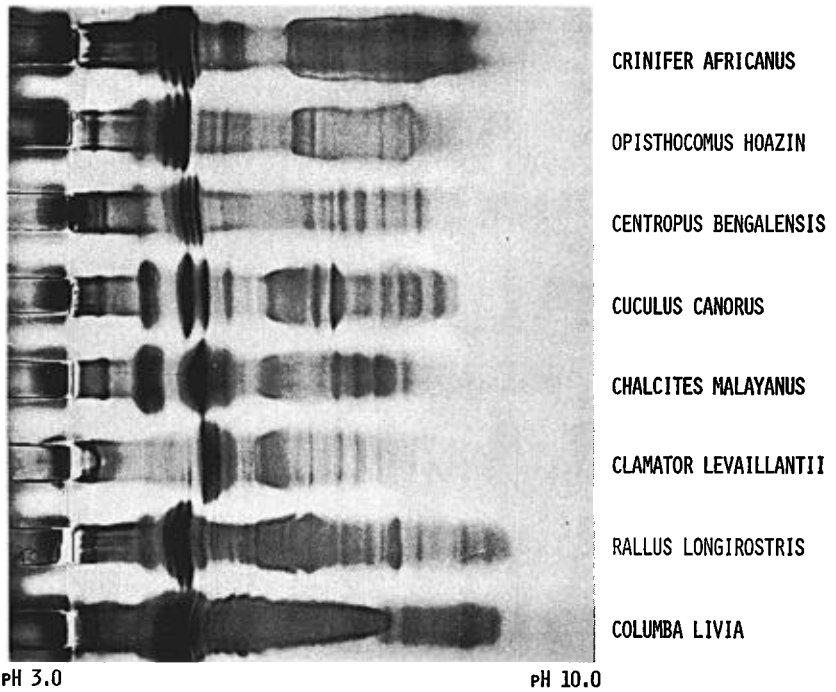

Figure 3. The egg-white proteins of *Opisthocomus* compared with those of some Old World cuculiforms, a rail, and a dove using isoelectric foscusing with an Ampholine range of *p*H 3–10. The similarities among *Opisthocomus* and the others are less striking than those among *Opisthocomus, Guira,* and *Crotophaga* in Figure 1.

most striking in the ovalbumin region around *p*H 4, but there are other components as well that have identical isoelectric points. The general pattern of *Opisthocomus* is similar to those of the musophagid *Crinifer* and the coucal *Centropus*, but few components have identical isoelectric points. The pattern of *Opisthocomus* differs considerably from those of the New World cuckoos *Coccyzus*, *Geococcyx*, and *Morococcyx*.

The patterns of *Coccyzus* and *Morococcyx* in turn resemble those of the Old World *Cuculus* and *Clamator*. Finally there are no similarities between *Opisthocomus*, *Rallus*, and *Columba*.

Figures 3 and 4 depict the egg-white proteins of the same species in the *p*H range 6 to 4. In these separations greater resolution of those components in the ovalbumin region is achieved. For example, in the *p*H 3–10 range four major bands and an additional four minor bands can be seen in the ovalbumin region of *Opisthocomus*. In the *p*H 6–4 patterns *Opisthocomus* has 18 components. *Opisthocomus* again bears the greatest resemblance to *Guira* and *Crotophaga*, although small differences in the

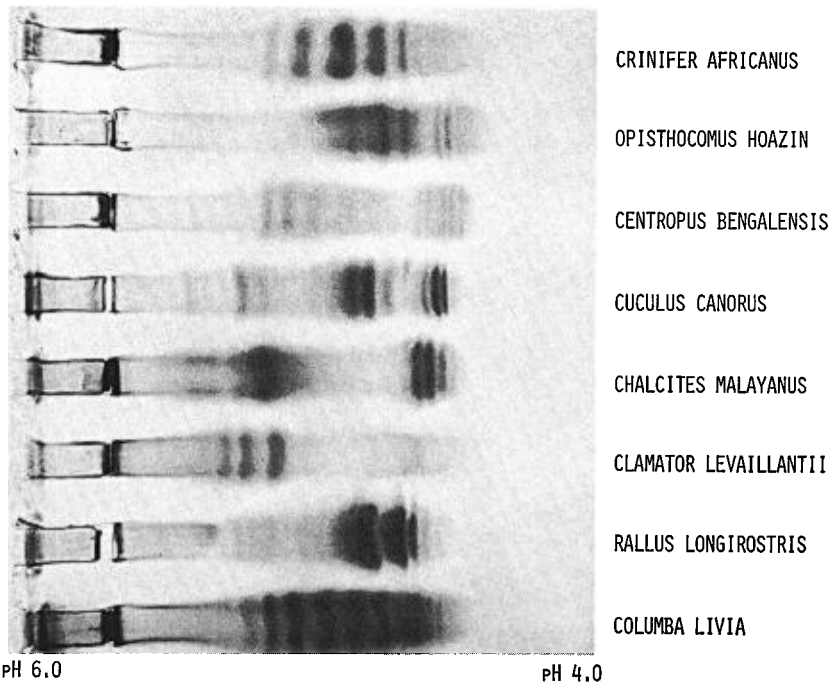

Figure 4. The same species as in Figure 3 but using an Ampholine range of *p*H 6–4.

isoelectric points of a number of proteins can be discerned. The *Opisthocomus* pattern shows some similarity to that of *Crinifer*, but less to those of *Centropus* and the other cuckoos, and is unlike those of the cracids, *Rallus*, or *Columba*.

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SUMMARY

The systematic relationships of the Hoatzin (*Opisthocomus hoazin*), long classified with the Galliformes, have been re-evaluated in the light of data from electrophoretic comparisons of the egg-white proteins. All

evidence has been found to be consistent with an assignment to the subfamily Crotophaginae of the Cuculidae. There is no substance to the long-accepted alliance to the Galliformes and the relationship to the Musophagidae is simply that of the two families within the Cuculiformes.

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