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REFLECTANCE SPECTRA OF PLUMAGE AREAS COLORED BY GREEN FEATHER PIGMENTS

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ABSTRACT.—Only rarely are green plumage colors due to the presence of green pigments. The best known is turacoverdin. Two galliform species (*Ithaginis, Rollolus*), *Jacana* and some anseriform species (*Somateria, Nettapus*) also have green pigments. The reflectance spectra of plumage pigmented by turacoverdin are characterized by distinct minima at about 570 and 610 nm. These minima represent absorption bands as confirmed by a transmittance spectrum of a turacoverdin extract. Surprisingly, the spectra of the two galliform species and *Jacana* also exhibit the characteristics of the turacoverdin spectrum, while that of *Somateria* is different. I show that the pigments of *Ithaginis, Rollolus,* and *Jacana* also resemble turacoverdin in containing copper in relatively high concentration, and conclude that these pigments are identical with or closely related to turacoverdin. Intra- and interspecific variation in reflectance spectra is assumed to be largely determined by the presence of dark, nongreen pigments in the plumage. The spectrum of turacoverdin supports the hypothesis that the pigment is closely related to the well-known red pigment of turacos (Musophagidae)—turacin. However, the chemical constitution of turacoverdin remains unknown. The presence of turacoverdin and turacin in the plumage of the Musophagidae hitherto has been considered an autapomorphy of the turacos. The fact the turacoverdin also is present in two possibly related galliform taxa argues for phylogenetic relationships between the Musophagidae and the Galliformes. *Received 3 April 1991, accepted 10 January 1992.*

GREEN, noniridescent plumage colors can be produced in a number of ways (Auber 1957). The combination of a structural blue color with yellow pigments, as found in parrots, is best known (Frank 1939, Dyck 1971). The olive-green colors obtained by the juxtaposition of yellow and blackish pigments (apposition colors; Auber 1957, Dyck 1978) also are widespread. Central to my two studies is the question of the evolution of plumage colors that resemble the green colors of leaves, without chlorophyll being available as a feather pigment (Needham 1974:81). In principle, the simplest way to produce a green plumage color is to deposit a green pigment within the feather keratin. This possibility has been realized in only a limited number of cases.

The best-known green feather pigment is turacoverdin. This is found in some turacos (Musophagidae), especially the species of *Tauraco* and *Musophaga*, and possibly also in the Great Blue Turaco (*Corythaeola cristata*; Krukenberg 1882, Moreau 1958). Preliminary chemical studies have been carried out (Moreau 1958). Other known green pigments are zooprasinin in the remiges of the Jacana (*Jacana spinosa*, Jacanidae; Rensch 1925), phasianoverdin in belly feathers of the Blood Pheasant (*Ithaginis cruentus*, Phasianidae; Götz 1925), and a green pigment in much of the plumage of the Roulroul (Crested Wood-Partridge, *Rollolus roulroul*, Phasianidae), especially the female (Völker 1961). The green pigments in some anseriform species (*Nettapus, Somateria*; Auber 1957) are poorly known (Brush 1978).

I describe the reflectance spectra of green plumage areas in several species and discuss factors that influence the shapes of the spectra. I compare the reflectance spectra with the spectrum of turacoverdin in extract and from this infer the probable identity of some of the pigments.

MATERIALS AND METHODS

Most measurements were performed on study skins from the Zoological Museum, University of Copenhagen, and the British Museum (Natural History). A few measurements were also carried out on mounted specimens. The spectrum of the nape of an adult male Eider (*Somateria mollissima*) was scanned on feathers taken from a newly dead bird. Feathers plucked from live birds were obtained from the Zoological Garden, Copenhagen, and kept four months in the dark before measurement.

Reflectance spectra were obtained on a Beckman DK-2A spectrophotometer with a reflectance attachment and using a reference of magnesium oxide. The illuminated spot was approximately 8 × 8 mm.

An extract of turacoverdin was obtained as follows: Green feathers plucked from a 46-year-old study skin of *Tauraco schalowi livingstoni* were cleaned by ultrasonic treatment and dried. The green parts of the barbs were cut off and 0.10 g of these placed in 6 ml of 0.8 M aqueous ammonia at room temperature in the dark for one week. Likewise, extracts were prepared of the grey-brown proximal parts of the feathers from which the green barbs had been removed, of grey-brown feathers of *Gallinula chloropus*, and of white belly feathers of *Larus ridibundus*. It was necessary to add 1:5,000 of commercial sulfonate-free detergent to the latter feathers during the extraction in order to wet the feathers. Absorption spectra were obtained on a Beckman Acta C III spectrophotometer.

The copper determinations by flame atomic absorption (Perkin-Elmer) were done on extracts of pigments in 0.8-M ammonia. From 2 to 12 mg of feather material were extracted with 1 ml of solvent at room temperature for about one month. Only green feather parts were used; in *Rollolus* the melanized barbules were scraped off.

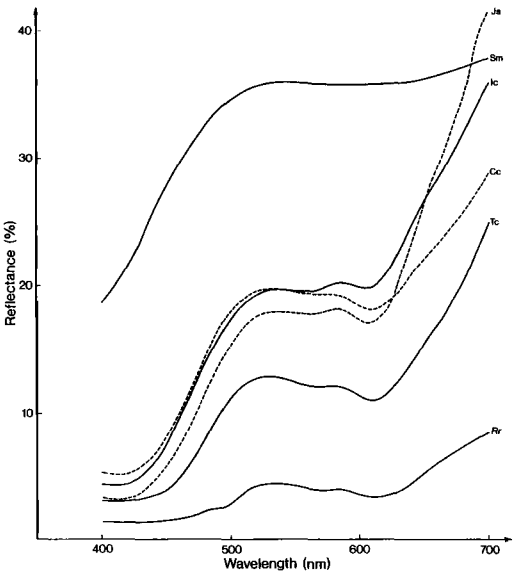

Fig. 1. Reflectance spectra of green-pigmented plumage areas for six species: *Rr, Rollolus roulroul; Tc, Tauraco corythaix; Cc, Corythaeola cristata; Ic, Ithaginis cruentus; Sm, Somateria mollissima;* and *Js, Jacana spinosa.*

RESULTS

The reflectance of the green *Tauraco* breast rises from a minimum at 412 nm to a maximum at 530 nm (*Tc* in Fig. 1, Table 1), only to fall to two minima at 568 and 612 nm (Figs. 1 and 2, Table 1) and rise again rather steeply to 700 nm. Overall, the reflectance spectra of *Corythaeola, Jacana* and *Ithaginis* show higher reflectances than the spectrum of *Tauraco,* but with similar shapes (*Cc, Js, Ic,* Figs. 1 and 2). The minima occur at similar wavelengths (Fig. 2, Table 1). Some of the spectra did not show all three minima (Table 1), but in these cases an incurvation always was observed on the spectrum in the relevant wavelength region.

The shape of the *Rollolus* reflectance spectrum is similar to that of *Tauraco* with overall lower reflectance (*Rr,* Fig. 1). The positions, however, of the three minima are more variable (Table 1), with a less-distinct middle minimum seen only as an incurvation on four of the five spectra. The spectra of *Rollolus* differ from those of *Tauraco* in the presence of an incurvation at 490 to 495 nm. Also, the maximum in the green is more marked, and three of the five spectra have a weak minimum at 535 nm (not shown).

Contrary to results for the above-mentioned species, the *Somateria* spectrum shows little resemblance to the *Tauraco* spectrum. The three minima are lacking. Instead, there is a wide, indistinct minimum at 580 to 590 nm and a faint incurvation at 415–420 nm (*Sm,* Fig. 1).

Figures 3 and 4 illustrate the influence of age and light exposure on the spectrum of *Tauraco.* The study skin and mounted specimen both were 139 years old at the time of measurement.

TABLE 1. Reflectance minima of green-pigmented plumage areas.

Species (*n*)	Reflectance minima (nm)[a]		
Tauraco corythaix (10)	412 (411–419)	570 (567–575)	612 (611–613)
Corythaeola cristata (belly, 4)	414 (412–416, *n* = 3)	564 (562–564, *n* = 3)	610 (609–611)
Ithaginis cruentus (3)	411 (409–411)	561 (559–563, *n* = 2)	606 (605–606, *n* = 2)
Rollolus roulroul (5)	416 (404–438)	574 (*n* = 1)	626 (607–628)
Jacana spinosa (4)	411 (407–415)	566 (565–566, *n* = 2)	606 (604–612)

[a] Median value and range (in parentheses) for each of three minima. Each specimen represented by one spectrum. Where given minimum not observed on all spectra, the number of spectra on which it was present is indicated. Positions of minima determined with accuracy of ±1–2 nm.

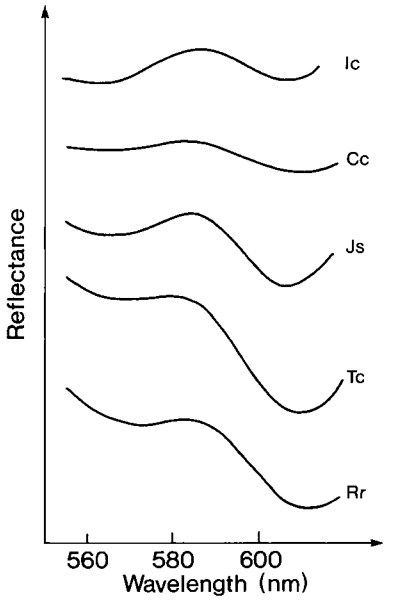

Fig. 2. Detailed reflectance spectra in region 560–615 nm. Measurements of same specimens as used in Figure 1, but not on exactly same plumage spot. Spectra displaced arbitrarily along reflectance axis. Ordinate unit is similar for spectra, but not exactly so. Species abbreviations as in Figure 1.

The former probably had been kept in darkness for the entire period. The latter is likely to have been on exhibition, exposed to light, up to 120 years. The minimum at ≈610 nm of the spectrum of fresh feathers is more pronounced than on the spectra of the old specimens. The difference is both relative, to the minimum at 565 to 570 nm, and absolute, with the result that the maximum in the green part of the spectrum occurs at shorter wavelengths than in the old specimens. Figures 3 and 4 further indicate that the spectrum of the mounted specimen (exposed to light) differs more from the spectrum of the fresh feathers than from that of the study skin. In *Jacana*, marked differences between the

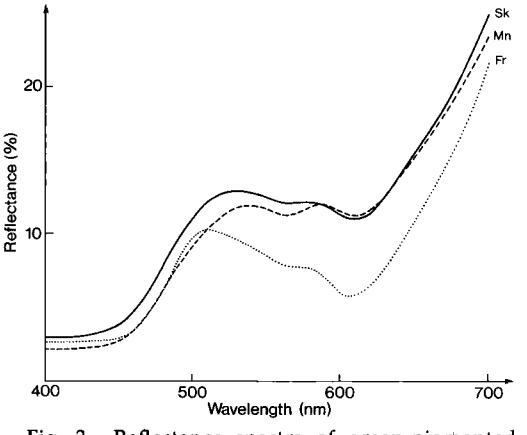

Fig. 3. Reflectance spectra of green-pigmented plumage of *Tauraco corythaix*: *Fr*, sample of fresh feathers; *Sk*, study skin; *Mn*, mounted specimen.

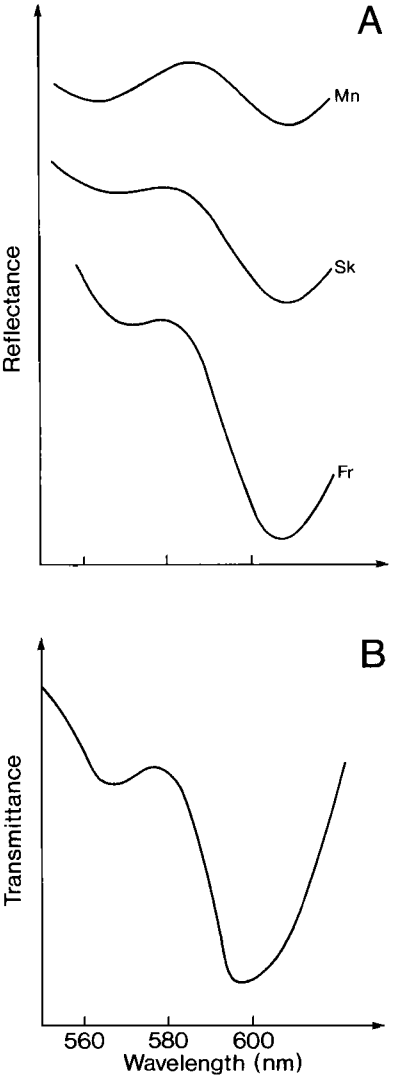

Fig. 4. (A) Detailed reflectance spectra in region 560–615 nm. Measurements of same specimens as used in Figure 3, with only spectrum *Fr* on exactly same plumage spot. Abbreviations as in Figure 3. (B) Detail of transmittance spectrum 1 (Fig. 5). Ordinate unit chosen so that 3% transmittance = 1% reflectance.

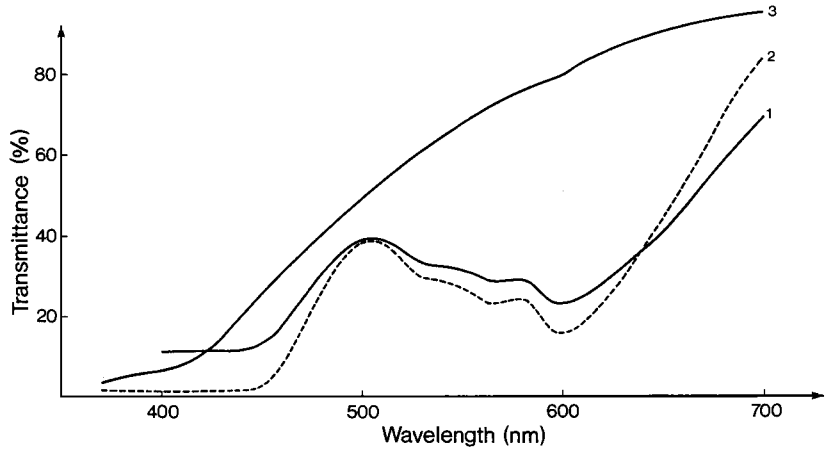

Fig. 5. Transmittance spectra: (1) freshly prepared extract of *Tauraco* turacoverdin; (2) same extract two months later; (3) extract of pigment from grey-brown *Tauraco* feathers.

reflectance spectra of fresh feathers, study skins, and a mounted specimen were not detected.

The transmittance of an extract of turacoverdin prepared from *Tauraco* (with 21% solvent added before measurement) rises from a low plateau at 400 to 440 nm to a maximum at 504 nm, falls to two minima at 565 and 597.5 nm (with an additional minimum indicated at 530 nm), and rises again rather steeply up to 700 nm (Figs. 4 and 5).

After storage at 4°C for two months, the absorption of the extract increased markedly (Fig. 5). Also, the positions of the two minima shifted slightly (to 566 and 600 nm), and there was then a minimum in the short-wave region of uncertain position due to the high absorption. The diluted extract (1:3) had this minimum at 404 nm, and the other two at 564 and 597 nm.

The transmittance of grey-brown *Tauraco* feathers increased smoothly with wavelength, except for weak incurvations at ≈415 and ≈600 nm (Fig. 5). The transmittance spectrum of grey-brown *Gallinula* feathers strongly resembles this spectrum, but lacks the incurvations, which makes it probable that these originate from contamination with green feather parts in the sample of grey-brown *Tauraco* feathers. The extract from white *Larus* feathers had an absorption close to zero.

The transmittance spectra of extracts in dilute aqueous ammonia of the pigments of *Corythaeola, Ithaginis, Jacana,* and *Rollolus* show, in general, the characteristics of the *Tauraco* spectrum. However, the minima in the 550 to 600 nm region were faint and the spectra somewhat variable. This was due to having too little feather material available and melanized feather parts that were not removed prior to extraction.

The copper concentrations of feathers showing *Tauraco*-like spectra are relatively high (Table 2). Dark and white reference feathers have low concentrations, close to the detection limit.

DISCUSSION

The reflectance spectra of plumage areas colored by green pigments differ markedly from both the spectra of a green parrot or an olive-green passerine (Fig. 6). The *Somateria* spectrum differs in the very gradual increase from 400 nm up to the maximum in the green region, while the other spectra display a strong mini-

TABLE 2. Copper concentrations (μg/mg) in green feather parts and in reference feathers.

Species	Cu concentration
Tauraco schalowi	1.2
Corythaeola (belly)	0.3
Corythaeola (tail)	0.2
Ithaginis	0.5
Rollolus	0.4
Jacana	0.2
Reference feathers	
Tauraco (tail, dark)	≤0.03
Fulica (black)	≤0.03
Larus (white)	≤0.03

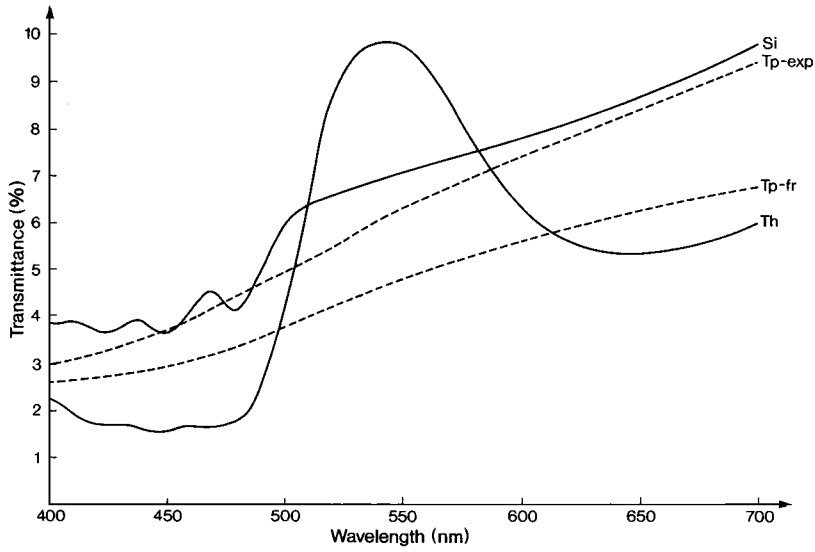

Fig. 6. Reflectance spectra: *Th*, green back of *Trichoglossus haematodus*; *Si*, olive-green back of *Satrapa icterophrys*; *Tp*-fr, fresh grey-brown back feathers of *Turdus philomelos*; and *Tp*-exp, same feathers after 13 months exposure to light.

mum at 410 to 420 nm and two weaker ones at ≈570 and ≈610 nm. Also, the green-pigment spectra do not resemble the spectra of other types of green plumage areas where green pigments are not involved (Dyck 1966, 1987, and unpublished spectra). The implication is that the characteristics of the spectra are largely due to the green pigments present.

Identity of pigments.—Turacoverdin is soluble in weak base (Krukenberg 1882) as is turacin (Church 1870). The absorption bands of the turacoverdin extract (Figs. 4 and 5) match the reflectance minima of the corresponding reflectance spectrum (Figs. 1 and 4) both with respect to the relative intensity and the position on the wavelength scale. The exact wavelengths at which the bands occur are somewhat shorter in extract as compared to pigment *in situ*. This phenomenon is general for pigments (Bellin 1965) and has been reported also for other feather pigments (Dyck 1966, Völker 1942), including turacin (Keilin 1926). Therefore, I conclude that the shape of the reflectance spectrum of *Tauraco* is determined primarily by the light-absorption profile of turacoverdin.

Since the reflectance spectra of *Corythaeola, Ithaginis,* and *Jacana* show the distinctive features of the *Tauraco* spectrum, this strongly indicates that their pigments are identical with or similar to turacoverdin. The *Rollolus* spectrum shows most of the characteristics of the *Tauraco* spectrum, with additional features as well. Völker (1961) reported, in a preliminary investigation of the *Rollolus* pigment, that the feathers also contain small amounts of yellow carotenoids, mainly lutein. Feathers with lutein as the dominant pigment show a marked reflectance minimum at ≈490 nm (unpubl. data on *Oriolus oriolus*; cf. Völker 1960). The weak reflectance minimum at 490 to 495 nm of the *Rollolus* plumage, therefore, may be due to lutein.

The weak reflectance minimum at ≈535 nm on some *Rollolus* spectra may correspond to the weak minimum at ≈530 nm on the turacoverdin transmittance spectrum. Völker (1961) remarked on the similarity in hue between the pigment of *Rollolus* and turacoverdin, but found that they differed in solubility in alkaline extracts and in their reactions with concentrated sulphuric acid (without specifying the differences). He did not state whether he considered the pigments chemically related.

The pigments of *Corythaeola, Ithaginis, Rollolus,* and *Jacana* further agree with turacoverdin in being readily soluble in weak aqueous base and in containing copper in relatively high concentration. The value obtained here for *T. schalowi* is very similar to that obtained by Shaw and Bather (in Moreau 1958) for *T. corythaix*—0.8 μg Cu/mg feather.

Brunet et al. (in Moreau 1958) reported that turacoverdin "appears to consist of two pigments, one less soluble than the other." They gave no further details.

Based on the above findings, I conclude that the pigments of *Corythaeola, Ithaginis, Rollolus,* and *Jacana* are closely related, if not identical to turacoverdin of *Tauraco.* This conclusion is not changed materially if turacoverdin is a mixture of pigments. Thus, earlier statements that the pigments of *Ithaginis, Rollolus,* and *Jacana* are carotenoids (Götz 1925, Rensch 1925, Auber 1957) are probably erroneous.

As shown by its spectrum, the *Somateria* pigment is probably unrelated to turacoverdin. Brush (1978) found its spectrum to be like other xanthophylls. J. Hudon (pers. comm.), from characteristics such as spectrum and shape of crystals, suggested the *Somateria* pigment to be a porphyrin, but one of unusual nature.

The inter- and intraspecific differences among the reflectance spectra of *Tauraco, Corythaeola, Ithaginis, Rollolus,* and *Jacana* can be attributed to a number of factors. These are addressed briefly below.

Variation in overall level of reflectance.—In *Tauraco,* the green pigment is deposited in the rami. The barbules are reduced terminally and grey-brown basally. These grey-brown barbules are in part visible between the green rami. In *Rollolus,* the green pigment likewise is found in the rami. The lower reflectance is due to the black-pigmented barbules. In the remiges of *Jacana,* a species with relatively high reflectance values, the green pigment is present in both barbules and rami with a high pigment concentration in the distal barbules. There is very little, if any, dark pigment in these feather parts. The feather vane also is continuous, and there are no clefts through which light can pass and be absorbed underneath. Altogether, these facts explain the overall high reflectance of the *Jacana* spectrum.

All things considered, it appears that the overall level of reflectance is determined primarily by the presence of dark, nongreen pigments in the visible portion of the plumage.

Intraspecific variation in shape of spectra.—Variation in the shape of spectra obtained from a series of study skins of *T. corythaix* is slight. The variation recorded probably is mainly attributable to the degree of visibility of the grey-brown barbules in the measured plumage area.

Variation among spectra of feathers differing in age and previous exposure to light (Figs. 3 and 4) is more marked. However, age and exposure to light were not solely responsible for the differences between the spectrum of fresh feathers and the two other spectra. The sample of fresh feathers was prepared so that the terminal parts of the green rami with the grey-brown barbules reduced dominated in its center. Thus, the color of the barbules contributed considerably less to the overall reflectance than in the intact plumage. This factor undoubtedly explains why the reflectance spectrum of fresh feathers matches the transmittance spectrum more closely than do the other reflectance spectra (Fig. 4).

Additional factors may explain the differences between the three spectra. (1) One possible factor is a change in the reflectance properties of the melanized feather parts with time and exposure to light. Figure 6 shows the reflectance spectrum of a sample of grey-brown back feathers of *Turdus philomelos* when fresh and after 13 months of exposure to daylight filtered through a window glass. Reflectance increases and so does the inclination of the spectrum. If it is assumed that the reflectance properties of melanized feather parts of *Tauraco* respond similarly, then a change in the shape of spectrum in the sequence "fresh to study skin to mounted specimen" (Figs. 3 and 4) is to be expected. The fact that the mounted specimen shows slightly lower reflectance than the study skin does not fit, however. (2) A second possibility is a change of light absorption by turacoverdin with time and exposure to light. The changes observed with the pigment extract (Fig. 5) point to this as a possible cause. (3) Third, a change of the keratin with time and exposure to light may cause a change in the shapes of the spectra, because this may affect binding of the pigment to keratin. Such binding affects the absorption spectrum of the pigments (Bellin 1965).

Of these three factors I consider the first to be the most important. This is supported by the fact that *Jacana,* which has little or no dark pigment in the green-plumage area, showed no marked differences between reflectance spectra of fresh feathers, study skins, and a mounted specimen.

Interspecific variation in shape of spectra.—Variation among *Corythaeola, Ithaginis,* and *Jacana* is related to one or several factors. (1) First, it could be due to a variable contribution of feather parts

pigmented green to the overall reflectance of the measured spot; this, in turn, would depend on the concentration of green pigment and the area of the green-pigmented feather parts relative to the total area of the plumage spot. The spectra indicate that this contribution is largest in *Jacana* and smallest in *Corythaeola*. (2) Second, there could be variation in the chemical composition and concentration of the dark (grey-brown to blackish) pigments. (3) Third, variation may be present in the degree of reflection from the feather medulla and the spectral characteristics of the light reflected from the medulla. These characteristics are known to vary among species (Dyck 1978). In *Ithaginis*, the reflection of green light from the barbules is increased by the presence of air in the barbule cells (Schmidt 1961), which is exceptional as barbule cells are normally solid. (4) Fourth, there could be variation in the chemical composition of the green pigment(s).

Of these four factors, I consider (1) and (2) the most important. This is supported by the fact that interspecific variation in the shapes of the spectra resembles to a considerable extent the observed intraspecific variation.

Relationship between turacoverdin and turacin.—In Church's (1870, 1892) studies of the red feather pigment of touracos (turacin; copper-uroporphyrin III), he found that, when exposed to air and moisture or for extended periods of time to continued ebullition with water or alkaline liquids, turacin acquired a color closely resembling that of chlorophyll. He considered it likely that this alteration product of turacin was identical to turacoverdin. This possibility has been mentioned by more recent authors as well (Keilin and McCosker 1961, Brush 1978).

Table 3 compares the positions of the absorption bands of this "altered turacin" with those of turacoverdin, *Ithaginis* pigment, and turacin. Clearly, there is agreement between "altered turacin" and turacoverdin (and *Ithaginis* pigment). The table also shows that the α- and β-bands of turacin are retained in the alteration product as noted by Church (1870, 1892), and are present in turacoverdin.

Keilin and McCosker (1961) oxidized turacin and produced copper-uroporphyrin I *in vitro* with H_2O_2 formed during the copper-catalyzed oxidation of ascorbate. In both cases, a green pigment resulted with absorption bands corresponding to those of altered turacin (Table 3). However, the γ-band was not the strongest as in turacoverdin (Fig. 5). Church (1892) remarked that the γ-band of altered turacin is very distinctive, but always accompanied by the α-, β- and δ-bands.

The spectral data support the suggestion that turacoverdin is identical to or closely related to an oxidized form of turacin. Several additional facts suggest that turacin and turacoverdin are closely related: (1) In breast patches and crests of some species the two pigments intermingle within individual feathers (Moreau 1958). (2) Turacin, which has a much more limited distribution than turacoverdin, occurs only in the presence of the latter (Moreau 1958). (3) Both pigments contain copper. (4) The two pigments show similar appearances and deposition patterns in the feather cells under the transmission electron microscope (turacin, Schmidt and Ruska 1963; turacoverdin, my unpubl. observ.). However, the exact nature of this relationship still remains to be elucidated a century after the pioneer studies by Church (1870, 1892) and Krukenberg (1882).

Systematics.—The finding that the green pigment of *Corythaeola* is turacoverdin fits well with the widespread occurrence of the pigment within the Musophagidae. Brush and Witt (1983) found *Corythaeola* to be closely related to *Crinifer* and *Gallirex*. Both possess turacoverdin, although the former only has small amounts (Auber 1957). Moreau (1958) expressed doubt about the pigment in *Corythaeola*, because the plumage looks yellower than that of *Tauraco* spp. The more yellowish appearance can be attributed to an overall higher reflectance (Fig. 1; see Dyck 1966:65).

Ithaginis and *Rollolus* both belong to the Perdicinae (Smythies 1953, Stresemann and Stresemann 1966). *Ithaginis*, despite its English common name of Blood Pheasant, exhibits the adult tail-molt pattern characteristic of the Perdicinae (Stresemann and Stresemann 1966). Both species differ from the majority of perdicine species in showing marked sexual dimorphism in plumage color. Both species are found in Southeast Asia, but their ranges do not overlap and their habitats are very different. Their ranges are relatively close in Burma, where *Ithaginis* occurs at high altitudes in mountains in the north, and *Rollolus* in mature forest in lowland and on hills in the extreme south (Smythies 1953, Medway and Wells 1976).

Taking these facts into consideration, I find it likely that the presence of turacoverdin in-

TABLE 3. Absorption bands of extracts of green feather pigments, turacin and derivatives of turacin.

Pigment (solvent)	Absorption band (nm)[a]				Reference
	δ	β	α	γ	
Turacoverdin (2% Na_2CO_3)				+[b]	Krukenberg 1882
Turacoverdin (0.8 M NH_3)	—	530	565	597.5	This study
Green "altered turacin" (Na_2CO_3)	473–494	523	562	597	Church 1870, 1892
Oxidized copper-uroporphyrin I (phosphate buffer, pH = 6.4)	484	526	562	610	Keilin and McCosker 1961
Oxidized turacin (phosphate buffer, pH = 6.4)	484	526	562	610	Keilin and McCosker 1961
Turacin (faintly ammoniacal, fresh preparation)	475–496	523	562	—	Church 1892
Ithaginis pigment (2% KOH)	—	—	569	593	Götz 1925

[a] Terminology of Church (1870, 1892).

[b] "Scharfes dunkles Absorptionsband unmittelbar vor *D* [Sharp, dark absorption band very close to *D*]."

dicates a close relationship between the two species. The color patterns, however, are quite different and, therefore, I consider it unlikely that *Ithaginis* and *Rollolus* are each other's closest relatives. Instead, I assume that a common ancestor to a group of galliform species including *Ithaginis* and *Rollolus* had turacoverdin. Thus, turacoverdin becomes a symplesiomorphy for this group of species.

There seems to be consensus that the Jacanidae belong to the Charadriiformes/Charadrii (Fry 1983, Sibley et al. 1988). This makes it virtually impossible that turacoverdin in *Jacana* reflects a common ancestry with either the Musophagidae or a group of galliform species. The pigment must have evolved independently in *Jacana*. In support of this supposition is the fact that the pigment in *Jacana* is found in the remiges, primarily the barbules. In the musophagid and galliform species, it is found mainly in body feathers and possibly exclusively in rami (*Tauraco, Rollolus*), or in rami and barbules (*Corythaeola* [tail], *Ithaginis*).

The phylogenetic relationships of the Musophagidae are still uncertain (van Tuinen and Valentine 1986). In Sibley and Ahlquist's (1972) review, they listed the Galliformes as one of the more realistic possibilities in terms of closest relatives. Since then, several relevant studies have appeared. Some of these (Cerny 1972, van Tuinen and Valentine 1986, Brom 1991) support affinity to members of the Galliformes, while others (Gysels 1969, Sibley and Ahlquist 1972, 1985) do not.

The presence of turacoverdin and turacin in the feathers is often mentioned (e.g. Turner and Grimes 1985) as an autapomorphy of the Musophagidae. The fact that turacoverdin is present also in two galliform species (possibly related) is a further, strong argument for a relatively close phylogenetic relationship between the Musophagidae and the Galliformes. More specifically, the pigment data suggest that turacos evolved from a group of galliform species that have turacoverdin as a symplesiomorphy, and are represented by the extant genera *Ithaginis* and *Rollolus*. Judged from the appearance of the green feathers, *Rollolus* is closer to a possible ancestor than is *Ithaginis*. A transition from a bird living on the ground in the jungle, feeding partly on vegetable matter (as *Rollolus;* Robinson and Chasen 1936), to an arboreal forest bird almost exclusively vegetarian (as some turacos; Turner and Grimes 1985) is, in principle, easy to imagine.

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