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Pterylography of Birds-of-paradise and the Systematic Position of Macgregor's Bird-of-paradise (*Macgregoria pulchra*)

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Macgregor's Bird-of-paradise (*Macgregoria pulchra*) is a poorly known species that occurs higher in the mountains of New Guinea than any other member of its family (Gilliard 1969, Cooper and Forshaw 1977). *Macgregoria* was originally discovered in 1896 and observations on its breeding behavior were first made by Rand (1940), who located the species in 1933 and 1938. More recently, Beehler (1983, 1991) visited its habitat on several occasions and reported on the species' behavior and ecology. As far as is known, *Macgregoria* habitat is cloud forest and subalpine *Dacrycarpus* (*Podocarpus*) forest at the edge of alpine grasslands between 2,800 and 4,000 m. Although the species appears to be sedentary, relatively easy to observe, and fairly common in *Dacrycarpus* groves when

the trees are fruiting, the high mountains where *Macgregoria* lives are difficult of access and the birds disappear to unknown habitat when *Dacrycarpus* is not fruiting (Beehler 1991).

Because the species is little studied and rare in collections, knowledge of the morphology of *Macgregoria* is limited. When Bock (1963) published a study of the Paradisaeidae based on skull morphology and jaw musculature, no specimen of *Macgregoria* then existed in alcohol; Bock's only material for that genus was a skull taken from a study skin. He found that, within the family, *Macgregoria* was the only genus that did not clearly fall into either the large subfamily of typical birds-of-paradise (Paradisaeinae) or the small group (Cnemophilinae) that Bock proposed for *Cne-*

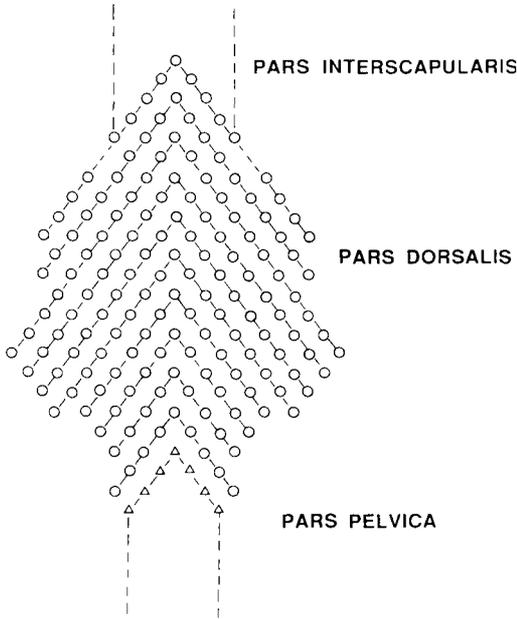


Fig. 1. Diagrammatic representation of Pteryla Spinalis in *Macgregoria pulchra*. Individual feathers of pars dorsalis are indicated by circles, those of first row of pars pelvica as triangles.

mophilus, *Loria*, and *Loboparadisea*. *Macgregoria* shared many skull characters with the cnemophilines, but also had a few that were similar to the true birds-of-paradise. Bock concluded that *Macgregoria* was most similar to the Cnemophilinae and included it in that subfamily.

Mayr (1962) recognized the subfamilial divisions, but although he was familiar with Bock's (1963) study and noted that the genus might belong in the Cnemophilinae, he placed *Macgregoria* as the first genus of the Paradisaeinae for Peters' Check-list. Perhaps because *Macgregoria* is large-bodied and almost solidly black, but with orange-yellow eye wattles and wing patches, and *Paradigalla* is also large and black with yellow wattles at the base of the upper mandible, Mayr (1941) had placed the two genera between the similarly large but all-black *Manucodia* and *Phonygamus* in an earlier work on the New Guinea avifauna. Mayr may have been more persuaded by *Macgregoria*'s outward appearance than by its cranial characteristics. Since the early 1960s, therefore, the systematic position of the genus has remained in question. Probably because further evidence has not become available, most subsequent authors have followed Mayr's placement (e.g. Schodde 1976).

During his field studies of *Macgregoria*, Beehler (1983, 1991) color-tagged and attached radios to a few birds to follow their daily movements. Fortunately

for morphologists, one individual caught in a net was accidentally killed by a dog and, thus, was preserved in formalin: USNM No. 541230, an adult male from Papua New Guinea, Northern Province, English Peaks, 3,650 m (8°46'S, 147°29'E); 23 July 1986; testes 3 × 2 mm, mass 253 g, no molt. I am grateful to B. M. Beehler and to S. L. Olson of the National Museum of Natural History for being allowed to skin and examine this and other recently obtained material.

When I published a study of the body pterylosis (feather tracts) of the birds-of-paradise (Clench 1985), my series of specimens included all the known genera of the family except *Macgregoria*, *Lycocorax*, and *Drepanornis*. *Drepanornis*, an undoubted member of the Paradisaeinae, remains unavailable, but with a recently collected specimen of *Lycocorax* (USNM No. 507559) and a better specimen of *Loboparadisea* (a cage bird from the National Zoological Park; USNM No. 507321), a fairly complete record of the body pterylosis of the family is now available. I also thank M. LeCroy of the American Museum of Natural History, who arranged to lend me a recently collected specimen of *Melampitta* (AMNH No. 4384), a New Guinea "log-runner" that Sibley and Ahlquist (1990) found to be a primitive paradisaeid.

In this study, I have followed the flat-skin technique previously described (Clench 1970, 1985), examining the underside of a skin with a binocular dissecting microscope (10–40×). The pterylae studied and pterylographic terminology used here are the same as in Clench (1985). In brief, the Pteryla Spinalis (the Dorsal Tract of Clench 1970) extends down the dorsal surface from the base of the skull to the uropygial gland. It contains three parts: the pars interscapularis (formerly, anterior element), a narrow band of feathers extending down the midline of the body from the base of the skull to the upper back; the pars dorsalis (saddle), an expanded area of feathering that covers the back; and the pars pelvica (posterior element), a narrow band that covers the rump. The Pteryla Ventralis (Ventral Tract) is composed of a mirror-image double band of feathers covering the breast and abdomen on either side of the midline. It contains two parts: the pars pectoralis (flank element) and the pars abdominalis (main element). In most passerines, the Pteryla Spinalis, especially the pars dorsalis, shows more variation and, therefore, is of the greatest taxonomic interest.

Macgregoria is uniformly heavily feathered in the Pteryla Spinalis. The central pars dorsalis contains 10 chevron-shaped rows, with a total of 158 feathers (Fig. 1). The feathering is closely arranged with no suggestion of a space or apertium at the junction of the pars dorsalis and pars pelvica, which is also heavily feathered. The Pteryla Ventralis has a maximum width of eight feathers and the separation between the pars pectoralis and pars abdominalis is three or four rows long; the pars abdominalis had lost too many feathers to count.

TABLE 1. Dorsal pterylosis of Paradisaeidae.*

Taxon	Pteryla Spinalis, pars dorsalis			No. specimens examined
	No. rows	No. feathers	Basal gap	
Cnemophilinae				
<i>Loria</i>	13	225, 254	No	2
<i>Loboparadisaea</i>	13	245	No	2
<i>Cnemophilus</i>	13	—	No	2
<i>Macgregoria</i>	10	158	No	1
<i>Melampitta</i>	12	254	Yes	1
Paradisaeinae				
<i>Lycocorax</i>	8	115	Yes	1
<i>Manucodia</i>	8	92, 116	Yes	3
<i>Phonygammus</i>	7	105	Yes	1
<i>Ptiloris</i>	9	147	Yes	1
<i>Semioptera</i>	7	89	Yes	1
<i>Seleucidis</i>	7	97	Yes	1
<i>Paradigalla</i>	7	—	Yes	1
<i>Epimachus</i>	10	172, 180	Yes	2
<i>Astrapia</i>	11	200, 201	Yes	2
<i>Lophorina</i>	8	119	Yes	1
<i>Parotia</i>	10	142	Yes	1
<i>Pteridophora</i>	10	150	Yes	1
<i>Cicinnurus</i>	7	83	Yes	1
<i>Diphyllodes</i>	8	102, 128	Yes	2
<i>Paradisaea</i>	9, 10	144, 155	Yes	3

* Data for all except *Macgregoria*, *Melampitta*, *Lycocorax*, and *Loboparadisaea* from Clench (1985).

Lycocorax is much more lightly feathered, showing the pattern typical of the Paradisaeinae; the pars dorsalis has 115 feathers in eight rows. There is a small but distinct apterium at the base of the pars dorsalis (the central feather of row 8 is absent). The pars pelvica is similarly weakly feathered, with 12 short rows of mostly five feathers each.

Loboparadisaea is typically cnemophiline, with heavy plumage (245 feathers in 13 rows) and no gap or apterium at the base of the pars dorsalis. The pars pelvica is also heavily feathered but too damaged to count.

The Paradisaeinae are characterized by a relatively small and sparsely feathered pars dorsalis (Clench 1985). In addition, at the junction between the pars dorsalis and the pars pelvica is a small gap which is universal in the Paradisaeinae but found in none of the Cnemophilinae (Table 1). The three accepted genera of Cnemophilinae are generally small birds-of-paradise and, like *Macgregoria*, are also uniformly feathered, but more heavily. The pars dorsalis is 13 rows long in them all and contains from 225 to 254 feathers in the two *Loria* and one *Loboparadisaea* that could be counted fully. The wide range of body sizes in the Paradisaeinae probably accounts for the equally wide range found in that subfamily in the number of rows (7 to 11) and the number of feathers (83 to 201) in the pars dorsalis.

Unfortunately, the Pteryla Ventralis of the Paradisaeidae adds little useful information. Aside from the extraordinary development of the pars pectoralis

in the flank-plumed paradisaeines (especially *Paradisaea*), the tract is unremarkable in both subfamilies (Clench 1985). Cnemophilines have a maximum width of nine feathers, the separation between the two pars is three or four rows long, and most of the rows of the pars abdominalis contain four feathers. Paradisaeines have a maximum width of 7 to 10 feathers (11 to approximately 28 in the flank-plumed forms), the separation is from three to seven rows long (again, longer separations are associated with the specialized flank plumes), and the abdominal rows contain 3 to 5 feathers. *Macgregoria* does not differ in any important way from either subfamily in this tract.

Figure 2 shows the general correlation between the number of rows and number of feathers in the Pteryla Spinalis, pars dorsalis, based on data from all birds-of-paradise studied. Not surprisingly, the species with more rows also contain more feathers in the pars. *Macgregoria* (asterisk) is intermediate in both number of rows and number of feathers.

As indicated by wing length (Fig. 3A), general body size of *Macgregoria* is large, falling within the range of the Paradisaeinae. The genus also falls in or near the high range of the Paradisaeinae, but closer to the values of the Cnemophilinae in numbers of rows (Fig. 3B) and feathers (Fig. 3C) in the pars dorsalis. More importantly, in my experience, is the fact that the pattern type (with a basal apterium or gap) agrees with that of the Cnemophilinae (Table 1). Patterning in pterylae and, to a lesser extent, the degree (heavi-

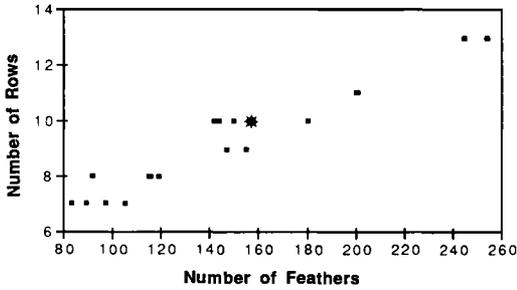


Fig. 2. Number of feathers versus number of rows in pars dorsalis of Paradisaeidae genera examined. The two points in upper right represent Cnemophilinae; asterisk represents *Macgregoria*.

ness) of feathering are conservative within the Passeriformes (Clench 1970, 1985); in other families, pattern differences like those between *Macgregoria* and the Paradisaeinae have proved to be important distinctions supported by other morphological characters (e.g. Ames et al. 1968). Convergence of *Macgregoria* with some of the Paradisaeinae in certain aspects (such as numbers of rows and feathers) may result from similarity in body size.

In his extensive studies of birds-of-paradise, Beehler (1983) pointed out that *Macgregoria* differs from most or all of the Paradisaeinae in having a limited vocal repertoire, in being monomorphic and monogamous, in maintaining a strong pair bond throughout the year by continued ritualized behavior patterns and by close physical contact (members of a pair allopreen), and in being a fruit specialist. Later work (Beehler 1991) suggests that the last characteristic may not hold at all times. Although the female alone builds the nest and incubates the single egg, she is closely accompanied by the male throughout that period, and he appears to take the major part in feeding the chick. Even when fully grown, a juvenile remains with its parents, begging for food as the adults forage together. A pair of birds has also been shown to occupy a home range of about 12 ha, where fruit other than that of *Dacrycarpus* is eaten when the favored food is not immediately available (Beehler 1991).

Of the species of Paradisaeinae that *Macgregoria* is placed next to in most taxonomic lists (e.g. Mayr 1962; see Table 1), *Lycocorax* (a Moluccan genus whose biology is almost unknown), *Manucodia*, and *Phonygamus* are also monomorphic in plumage. As far as is known, *Phonygamus*, *Manucodia*, and *Macgregoria* have relatively similar breeding behavior that includes monogamy, simple courtship, and some participation by the male in raising the young. *Manucodia* and *Phonygamus* are fruit specialists (on figs), but until further field work can show what *Macgregoria* feeds on during periods when *Dacrycarpus* fruits are not available, its status as a fruit specialist (Beehler 1983) remains to be confirmed. In addition, *Manucodia* and

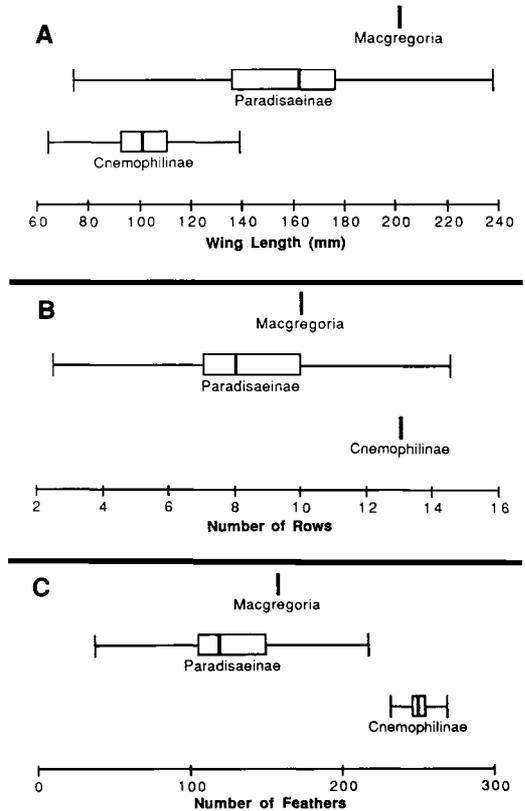


Fig. 3. Comparison of *Macgregoria* with data for Paradisaeinae and Cnemophilinae: (A) wing length; (B) number of rows in pars dorsalis; (C) number of feathers in pars dorsalis. For the two subfamilies, means (vertical line) and two standard deviations (horizontal line) indicated.

Phonygamus differ from *Macgregoria* behaviorally by their having a vocal repertoire of loud calls and complex songs. They also differ morphologically in having highly specialized, strikingly elongated tracheas (Clench 1978). Table 1 also shows that, typical of the pterylosis of their subfamily, *Lycocorax*, *Manucodia*, and *Phonygamus* all have relatively few feathers in seven or eight rows with gapping at the base of the pars dorsalis, which is clearly different from the condition in *Macgregoria*.

In addition, *Macgregoria* shares several traits with the Cnemophilinae, although the biology of species in that subfamily is poorly known: all are monogamous, have relatively simple courtship behavior, and are frugivorous (Beehler 1985, Gilliard 1969). The cnemophilines, however, are sexually dimorphic, but without the plumes and other specialized ornate feathering of paradisaeines.

It is unfortunate that the rarity of *Macgregoria* material has limited the knowledge of its morphology

and other factors that would contribute to a better understanding of its systematic position. Borecky (1977) did not have a specimen for his study of the appendicular myology of the Paradisaeidae; Borecky did, however, support the division of the family into the primitive Cnemophilinae and more highly evolved Paradisaeinae (Cooper and Forshaw 1977). Similarly, Sibley and Ahlquist (1990) have examined neither *Macgregoria* nor any of the cnemophilines, although they did find strong similarities among *Epimachus*, *Astrapia*, *Cicinnurus*, *Diphyllodes*, *Pteridophora*, *Ptiloris*, and *Paradisaea*, and a clear divergence between that sexually dimorphic group and *Manucodia*. They also found that the monomorphic, terrestrial *Melampitta*—heretofore customarily considered a logrunner (Muscicapidae, Orthonychinae; Deignan 1964)—was a primitive bird-of-paradise. This may well be the case.

My examination of the pterylosis of a specimen of *Melampitta lugubris* (prompted by Mary LeCroy after she refereed the present paper) showed a clear similarity between the feather tracts of this small, all-black New Guinea species and typical cnemophilines, yet also with paradisaeine characters. The pars dorsalis is heavily feathered in 12 rows with a total of 254 feathers, but unlike *Macgregoria* and the accepted cnemophiline genera, and like the Paradisaeinae, *Melampitta* also has a small gap (the equivalent of a single midline feather) at the base of the pars dorsalis, and a weak pars pelvica. The latter contains 10 chevron-shaped rows, predominantly with three feathers except for the last 3 or 4 rows which are longer and form an expanded base for the tract. The Pteryla Ventralis has a maximum width of 9 or 10 feathers, the separation between the pars pectoralis and pars abdominalis is 2 rows long, and the rows in the pars abdominalis are five or six feathers long. In *Melampitta*, therefore, we find another form that is intermediate between the two subfamilial types of the Paradisaeidae. Unfortunately, the pterylosis of orthonychine genera is not yet well known. Nitzsch (1867) and Forbes (1881) reported that *Cinclosoma* and *Eupetes macrocerus*, respectively, had the "typical passerine" pattern, an expanded pars dorsalis without a central apterium (a description I doubt that either man would have applied to *Melampitta*). I have not yet examined any logrunners, but timaliines (*Leiothrix*, *Stachyris*) agree with the categorization used by Nitzsch and Forbes. Clearly, *Melampitta* deserves further investigation, and DNA-DNA hybridization studies of this genus and both subfamilies of birds-of-paradise would be useful. After their recent field studies of *Melampitta lugubris*, Frith and Frith (1990) suggested that if the species is a bird-of-paradise, its nesting biology indicates a much closer relationship to the cnemophilines, and particularly *Cnemophilus* (*Macgregoria*), than to the paradisaeines.

In summary, pterylography adds additional evidence to Bock's (1963) cranial data and support to his conclusion that *Macgregoria* is morphologically inter-

mediate between the Cnemophilinae and the Paradisaeinae. Based on our respective experiences with the characters under consideration, however, I also agree with Bock (1963) that *Macgregoria* is more like the Cnemophilinae and should be included there, at least until further evidence can clarify the relationship. On balance, behavioral data also support the placement of *Macgregoria* in the Cnemophilinae. The comparatively great body size differences between *Macgregoria* and the genera accepted to be cnemophilines may be due to convergence with others in the family. *Melampitta* may well be another intermediate form of bird-of-paradise and related to *Macgregoria*.

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Differences in Song and Sexual Dimorphism between Cuban and North American Red-winged Blackbirds (*Agelaius phoeniceus*)

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In many species of birds, song is characteristic of the male (Nottebohm 1975). However, an increasing number of studies have also found that females sing (reviewed in Farabaugh 1982, Ritchison 1983). Usually, in such cases, male and female songs are distinctly different in structure but have similar functions, such as territory advertisement and defense (Armstrong 1963, Farabaugh 1982, Ritchison 1983). In temperate species, female song is relatively rare; however, it is more common in tropical species, where females often duet with their mates (Farabaugh 1982). Red-winged Blackbirds (*Agelaius phoeniceus*) are one of the few known species in which males and females sing different songs in temperate populations (Beletsky 1983, Searcy 1989a), whereas pairs duet in a tropical population (Farabaugh 1982, E. S. Morton pers. comm.). This intraspecific variation provides an opportunity to study the adaptive function of song and other sexually selected characteristics, such as plumage and body size.

We compared sexual differences in song, plumage and body size between temperate Red-winged Blackbirds in eastern North America (*A. p. phoeniceus*) and tropical Red-winged Blackbirds in Cuba (*A. p. assimilis*). Red-winged Blackbirds breed throughout most of North and Central America; the distribution of *A. p. phoeniceus* extends from north-central Ontario to northern Florida and from the Mississippi River to the Atlantic Ocean (Peters 1968, Power 1970), whereas *A. p. assimilis* is endemic to the western part of Cuba (Peters 1968, Garrido 1970, Bond 1985). In this paper we show that Cuban Red-winged Blackbirds exhibit relatively less sexual dimorphism in song, plumage and body size than North American Red-winged Blackbirds. We propose a hypothesis to account for these differences and suggest a possible test.

The songs of Cuban Red-winged Blackbirds were recorded in the Zapata Swamp at Treasure Lake (22°10'N; 81°50'W) during 9–10 April 1991. In Cuba, the birds were observed in bottle-brush trees (*Callistemon speciosus*) and tall grasses (*Phragmites* spp.) at the periphery of the lake. Two birds were observed carrying strips of vegetation, which suggested that April was the beginning of the breeding season for Cuban Red-winged Blackbirds. Temperate Red-winged Blackbird songs were recorded between April and June 1991 near Kingston, Ontario, Canada (44°33'N; 76°20'W). In Ontario, males were associated with breeding territories in cattail (*Typha* spp.) marshes, similar to other populations throughout North America (Nero 1956, Orians 1980).

Songs were recorded with an Audio-technica AT815a directional microphone and Sony Professional cassette recorder. Sonograms were analyzed on a Kay Elemetrics DSP Sonagraph Model 5500, using a 16-kHz frequency axis with a 512-point transform (117-Hz band-pass filter) and a time axis of 2 s with a 200-point transform (300-Hz band-pass filter). We analyzed duets of pairs in Cuba and solo songs of individuals in Cuba and North America. We considered a duet as one pair of songs, one song produced by each sex, overlapping or less than 1 s apart, and given repeatedly in sequence (e.g. Farabaugh 1982; Fig. 1). Duets were performed by one male and one female perched 0.5 to 2.0 m apart. In most cases the male was perched above the female and they were facing each other. For simplicity we refer to a duetting male and female as a pair; however, it was not known whether the two individuals were mates. Songs given in sequence by the same individual, but not closely followed by the song of another individual, were considered solo songs. For solo songs the following