SHORT COMMUNICATIONS

The Arrangement and Structure of Feather Melanin Granules as a Taxonomic Character in African Starlings (Sturnidae)

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It has long been known that the metallic colors of many birds arise from the physical structure of the feathers rather than from pigments (e.g. Strong 1902). The African starlings include many species noted for their brilliant iridescent plumage, and it has been demonstrated that these colors are due to the structure and arrangement of melanin granules in the barbules of the feathers (Durrer and Villiger 1967, 1970a).

The morphological basis of such colors must be considered a more reliable taxonomic character than the visual effects, since the physical arrangement of structures within the keratinized feather is produced under genetic control, but several different structural patterns can form the basis for the same color effects. Thus, in the African sunbirds (Nectariniidae) iridescence is produced by stacks of thin melanin platelets (Durrer and Villiger 1962), whereas in the American hummingbirds (Trochilidae) melanin platelets with a complex internal pattern of gas vacuoles are responsible for iridescent colors (Greenewalt 1960). Lattices of solid melanin rods are found in the Common Peafowl (*Pavo cristatus*) and the Congo Peafowl (*Afropavo congensis*, Durrer and Villiger 1975), and in the Emerald Cuckoo (*Chrysococcyx cupreus*, Durrer and Villiger 1970b). Air-filled melanin granules occur again in the trogons: in the genus *Pharomachrus* the melanin is organized in platelets, while in *Apaloderma, Galbula, Harpactes,* and *Trogon* the granules are round and hollow (Durrer and Villiger 1966).

Durrer and Villiger (1970a) investigated feather material from one or two species of all the extant genera of the Family Sturnidae, and commented briefly on relationships between the genera. We have examined material from all Afrotropical starlings (Table 1) except the oxpeckers (*Buphagus* spp.) by means of transmission electron microscopy.

All feathers were taken from the body plumage of museum specimens. For a few species, feathers from different body regions were investigated, but no important differences were found (except as described in the case of *Lamprotornis corruscus*). The feathers were dehydrated in a graded series of alcohols, then infiltrated and embedded in LR White resin. Thin sections were cut on a LKB ultramicrotome, and viewed unstained in a JEOL JEM-100 CX II Transmission Electron Microscope.

We have assigned species to six categories (see Table 1), distinguished on the basis of melanin granule structure and arrangement. The thickness of the outer keratin layer of the barbule (Durrer and Villiger

1970a) was less reliable because it varied in different sections. Where we examined species figured in Durrer and Villiger (1970a), we obtained identical results with the exception of *Grafisia torquata* (see below). Our six structural types are as follows:

Type A.—Melanin granules are circular in cross section and solid. Within the barbule they are scattered, but there is a distinct outer band (Fig. 1a).

Type B.—Melanin granules appear as thin, solid platelets, with either a stratified surface layer (Fig. 1b) or a distinct single outer layer (Fig. 1c).

Type C.—Melanin granules are circular, hollow, and scattered within the barbule (Fig. 1d).

Type D.—Melanin granules are circular, hollow, and arranged in layers near the surface (Fig. 2a).

Type E.—Melanin granules are oblong, hollow, with a single outer row placed end-to-end around the perimeter of the barbule, and others scattered in the interior (Fig. 2b). The granules may be short and thick, or slender and elongated. The dull ventral plumage of *Lamprotornis corruscus* shows the typical arrangement, but the granules are apparently solid, not hollow (Fig. 2c).

Type F.—The melanin granules are oblong, hollow, and arranged in several rows on the dorsal surface of the feather, with only a single row on the ventral surface (Fig. 2d).

Durrer and Villiger (1970a) found that all non-African starlings had solid, circular melanin granules, corresponding to their types A and C (type A in our study). This may represent the primitive condition. A cladogram of our structural types (Fig. 3) closely resembles Fig. 2 of Durrer and Villiger (1970a), except that they did not record a category equivalent to our type C. If shared derived characters are taken to be the best indicators of relationship between different species, this scheme implies that if species share type A, this character by itself provides no information concerning their relationships to each other.

All modern treatments of the starling family have followed Amadon's (1962) arrangement of the genera and species. The only major modifications of this system have been proposed by Wolters (1976). Their different views will be considered briefly in the light of the evidence from the melanin granules.

The largest genus of African starlings is *Lamprotornis,* which may include *Coccycolius* (Amadon 1943,

TABLE 1. The Afrotropical Sturnidae.

Species[a]	Melanin granule type
Cinnyricinclus femoralis	A
C. leucogaster	D
C. sharpii	A
Coccycolius iris	F
Cosmopsarus regius	E
C. unicolor	C
Grafisia torquata	C
Lamprotornis acuticaudus	E
L. australis	E
L. caudatus	E
L. chalcurus	E
L. chalybaeus	E
L. chloropterus	E
L. corruscus	E
L. cupreocauda	B
L. mevesii	E
L. nitens	E
L. ornatus	E
L. purpureiceps	B
L. purpureus	E
L. purpuropterus	E
L. splendidus	E
Neocichla gutturalis	A
Onychognathus albirostris	A
O. blythii	A
O. frater	A
O. fulgidus	A
O. morio	A
O. nabouroup	A
O. salvadorii	A
O. tenuirostris	A
O. tristramii[b]	A
O. walleri	A
Poeoptera kenricki	B
P. lugubris	B
P. stuhlmanni	B
Speculipastor bicolor	A
Spreo albicapillus	C
S. bicolor	C
S. fischeri	C
S. hildebrandti	E
S. pulcher	E
S. shelleyi	E
S. superbus	E

[a] The nomenclature follows Hall and Moreau (1970).
[b] *Onychognathus tristramii* is not found in Africa, being restricted to the Arabian peninsula and Israel, but is included as it certainly belongs to the Afrotropical starlings.
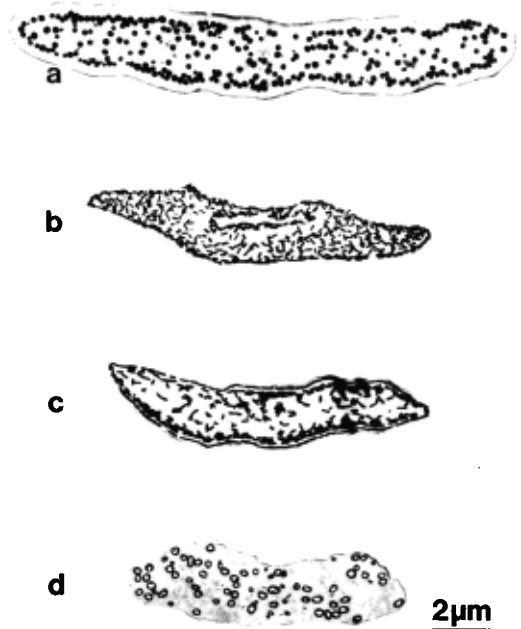
Fig. 1. Electron micrographs of transverse sections of starling feathers, showing different structural types: (a) type A, *Creatophora cinerea*; (b) type B, *Poeoptera kenricki*; (c) type B, *Lamprotornis purpureiceps*; (d) type C, *Spreo fischeri*.

1962). Amadon (1956) recognized *Coccycolius* as a separate genus, as did Hall and Moreau (1970) and Wolters (1976). Although feather type F can certainly be derived from type E, the two are strikingly different, and this would favor the retention of two genera. The other species of *Lamprotornis* share type E, with the exception of *L. cupreocauda* and *L. purpureiceps*. These two species constitute Wolters's (1976) subge-

nus *Hylopsar*, and are grouped as a superspecies by Hall and Moreau (1970). Here similar colors apparently are produced by a very different underlying structure. While these species share type B with the genus *Poeoptera*, there are differences in the details of the melanin granule arrangement, as well as other morphological differences.

The differences in structure in the granules from the dull ventral plumage of *Lamprotornis corruscus* evidently are related to changes in the development of the melanin granules. In *L. chloropterus* (Durrer and Villiger 1967) the melanin granules in developing feathers are initially solid but later become filled with proteinaceous material, which finally disappears and leaves an airspace inside the granule. It appears that this injection of protein has failed to occur in melanin granules from the ventral feather tracts of *L. corruscus*, but in other respects the normal arrangement has been preserved.

All species of *Onychognathus* share the primitive type A, but all also have rufous-colored primary remiges in both sexes. Amadon (1943) suggested a relationship to the genus *Poeoptera*, in which the females have rufous primaries but not the males. Wolters (1976) included *Poeoptera* in *Onychognathus*, although he placed the 13 species in 7 subgenera. However, the 3 species of *Poeoptera* show the dis-
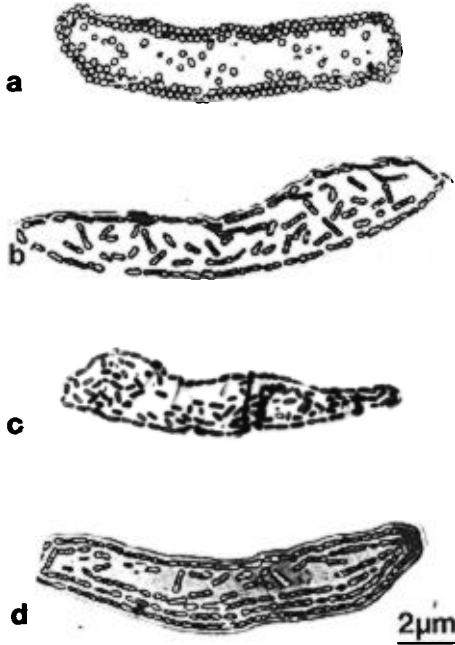
Fig. 2. Electron micrographs of transverse sections of starling feathers, showing different structural types: (a) type D, *Cinnyricinclus leucogaster*; (b) type E, *Lamprotornis chalybaeus*; (c) type E, *Lamprotornis corruscus*; (d) type F, *Coccycolius iris*.
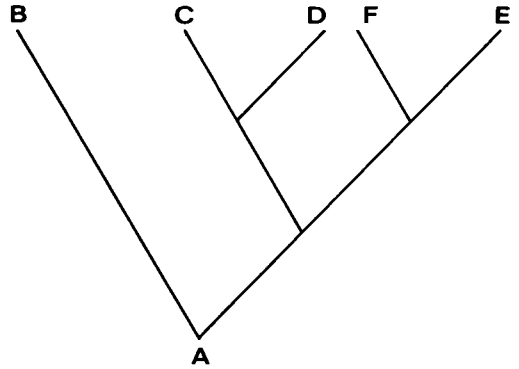

Fig. 3. A hypothetical sequence for the derivation of the different structural types. Round, solid, scattered melanin granules are taken to represent the primitive condition. Hollow granules, oblong or flattened granules, and stratified arrangements are all derived states.

tinctive type B melanin granule arrangement, and because the female of *Cinnyricinclus leucogaster* also has rufous primary feathers, this character should not be overemphasized as indicative of close relationship.

The three species of *Cinnyricinclus* are associated primarily on the basis of their similar immature plumages. Hall and Moreau (1970) commented that *C. femoralis* and *C. sharpii* are certainly closely related, but they may be rather distant from *C. leucogaster*. Wolters (1976) placed them in three monotypic genera. The melanin granule arrangement clearly separates *C. leucogaster* (type D) from the other two species, which share the type A arrangement. Thus, the present study provides no further information on the closest relatives of *C. femoralis* or *C. sharpii*.

Durrer and Villiger (1970a) examined feathers only from *Spreo superbus* and found the melanin granule structure to be typical of the genus *Lamprotornis*. We confirmed this, and found the same pattern in *S. hildebrandti*, *S. pulcher*, and *S. shelleyi*. Amadon (1956) admitted that the genus *Spreo* was a somewhat artificial group but urged its retention for convenience. Wolters (1976) used monotypic genera for *S. bicolor* and *S. albicapillus*, placing the other species in Roberts's (1922) genus *Lamprospreo*. Clancey (1958) and

Brooke (1971) have independently proposed that *Spreo* should be restricted to the species *S. bicolor*, *S. fischeri*, and *S. albicapillus*, while the other species should be included in *Lamprotornis*. Our data support such an arrangement.

Recently, Sibley and Ahlquist (1984) presented a diagram of relationships among the Sturnidae, based on DNA-DNA hybridization measurements. They examined material from *Spreo bicolor* and *Lamprotornis nitens* and concluded that these two genera are closely related. Their results also indicate a clear separation between the African starling genera *Lamprotornis*, *Spreo*, *Onychognathus*, *Cinnyricinclus* and the Oriental and Palaearctic genera. However, *Creatophora* is closely associated with *Sturnus* and *Acridotheres*, which is in full agreement with earlier views (Amadon 1943, 1956; Hall and Moreau 1970; Wolters 1976) and is also supported by studies of the jaw musculature (Beecher 1978).

Cosmopsarus regius falls into type E, while *C. unicolor* shares type C with some members of *Spreo* and *Grafisia torquata*. This is surprising as the close relationship of the two species of *Cosmopsarus* has never been questioned. Amadon (1943) included both species of *Cosmopsarus* in an enlarged genus *Spreo*, together with *Grafisia* and *Speculipastor*, but later changed his views.

The monotypic genera *Creatophora*, *Neocichla*, and *Speculipastor* all show the primitive type A arrangement. However, for *Grafisia torquata* our specimens showed hollow granules of type C, not solid type A structures as figured in Durrer and Villiger (1970a). This does not appear to be an artifact due to different methods, and according to the acknowledgments in their paper they obtained feathers of this species from the same source as we did (BMNH). We can only conclude that in one case feather material has been misidentified. Reichenow (1909) originally described

this species as *Spreo torquata*, but for the present its relationships remain obscure.

A systematic revision of the African starlings is long overdue. Our results suggest that the composition of the genera *Cinnyricinclus, Cosmopsarus, Lamprotornis,* and *Spreo* should be reexamined.

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Clutch Size, Daylength, and Seasonality of Resources: Comments on Ashmole's Hypothesis

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Clutch size tends to increase with latitude both within and among bird species. For nidicolous birds, Lack (1947) suggested this might be due to the longer daylength at higher latitudes that allowed parents to collect more food and feed larger broods. Ashmole (1961) proposed an alternative hypothesis: that clutch size depends on the relationship between resource level and population density during the breeding season. If populations are limited by nonbreeding season resources, clutch size will increase as the seasonality of resources increases, regardless of average resource level. Ricklefs (1980) called this Ashmole's hypothesis. I am prompted by the recent renewal of interest in this topic (Ricklefs 1980; Koenig 1984a, b; Møller 1984) to offer some comments on the mathematical representation and predictions of Ashmole's hypothesis.

Ricklefs (1980) introduced the notion that fluctuation in food resources available to bird populations can be represented by the seasonal pattern of actual evapotranspiration (AE). He expressed Ashmole's hypothesis in terms of summer and winter AE as

$$\text{clutch size } (C) = aS/W, \tag{1}$$

where a is an arbitrary constant, S is summer (breeding season) AE, and W is winter (nonbreeding season) AE. In this formulation, clutch size is directly proportional to seasonality of resources (i.e. the ratio of summer to winter AE) and does not depend on the absolute level of resources.