Structure and Light Reflection of Green Feathers of Fruit Doves (*Ptilinopus spp.*) and an Imperial Pigeon (*Ducula concinna*)

By JAN DYCK

Biologiske Skrifter **30**

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Abstract

The structure producing a green feather colour in the fruit dove *Ptilinopus rivoli* is described in detail. Colour is produced by the interference of light reflected from layers of melanin granules in barbule cells, as is commonly the case in feathers. Such colours are usually iridescent, but this is not the case in *Ptilinopus* doves, due to a unique arrangement of the melanin layers. These are curved so that they fit into approximately hemispherical swellings (reflectors) in the obverse parts of the cells. The colour-producing structure of a *Ducula* pigeon is described as an example of the usual iridescent barbule, and the different light reflection properties of the *Ptilinopus* and the *Ducula* plumage are confirmed experimentally with goniophotometric measurements.

Variation in reflector structure within the *Ptilinopus* genus is studied by the inclusion of six additional species.

By microspectrophotometry reflectance spectra of single reflectors have been obtained. Quantitative relations between some parameters of the spectra (f.i. maximum reflectance and λ_{max}) and some parameters of reflector structure have been obtained.

It is suggested that the decisive factor in the evolution of the reflector has been the evolution of a small diameter of the melanin granule. The selective pressure leading to the evolution of the reflectors is assumed to have been camouflage.

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Contents

Introduction

The numerous species of fruit doves of the genus *Ptilinopus* (*sensu* Goodwin 1967) mostly have plumage of a predominantly green colour. This green colour differs from that usually seen in the plumage of the Columbiformes in being a rich grass-green. There is no olive tint as in *Treron* species or metallic luster as in *Ducula* species, for example.

Bancroft *et al.* (1923) pointed out that the green colour of *Ptilinopus* feathers is produced in the barbules. This is different from most other green non-iridescent feather colours which are produced in the rami (e. g. in parrots).

Schmidt (1952) deduced from dark-field observations of intact *Ptilinopus* feathers that the colours are produced by the interference of light by small melanin granules and he also described the peculiar shape of the barbule cells. He held this shape to be responsible for the lack of the iridescence which otherwise characterises plumage colours produced by interference in barbule cells.

This paper describes the ultrastructure of the colour-producing barbule cells of seven *Ptilinopus* species. In addition the reflected light is described and correlations between cell structure and composition of reflected light are established. For comparison the green back colour of *Ducula concinna* is treated as well.

The discussion includes some aspects of ecology, classification and phylogeny.

Material and Methods

Feathers were plucked from specimens of the following species in the collection of the Zoological Museum, University of Copenhagen:

Ptilinopus c. cincta Ny Kat. 57.392 (feathers from lower back and rump)

Ptilinopus jambu, male, Ny Kat. 57.384 (feathers from back)

Ptilinopus superbus, male, Ny Kat. 57.368 (feathers from back)

Ptilinopus rivoli prasinorrhous, male, CN 318 (feathers from back)

Ptilinopus viridis lewisii, female, Ny Kat. 57.381 (feathers from back)

Ptilinopus victor, female or male imm. Ny Kat. 57.349 (feathers from back)

Ptilinopus luteovirens, male, Ny Kat. 57.523 (feathers from back)

Ducula concinna, male, Ny Kat. 57.342 (feathers from back)

Feathers were cleaned by ultrasonic treatment while immersed in absolute alcohol. Barbule cells were studied in reflected light using dark-field objectives (Zeiss Epiplan HD) fitted to the microspectrophotometer. The shape of the barbule cells was studied further with a scanning electron microscope (SEM: 'Stereoscan 600') after coating the cleaned feather parts with gold. The ultrastructure of the barbule cells was studied with the transmission electron microscope (TEM: Zeiss EM 9 S–2). Ultrathin sections were prepared with a diamond knife from cleaned feather parts embedded directly in 'Epon 812' and stained with uranyl acetate and lead citrate. Size of melanin granules was determined from copies with a final magnification of 50.000, lengths being measured to the nearest whole mm.

In order to quantify the lack of iridescence of the green plumage, a simple goniophotometer, produced at the institute, was used. The bird was placed horizontally below a thin plate with a hole in it, so that a circular area of the back (diameter 30 mm) was visible. The surroundings of the hole were covered with black mat cloth. The circular area was illuminated with unfiltered light from af 6 V, 15 W microscope lamp placed about 30 cm from the bird. With a photodetector (Spot Galvanometer, GVM 22c, "Radiometer", Copenhagen) the light flux reflected from the back was recorded (distance bird – photodetector: c. 35 cm). Both light source and detector could be moved along an arc of a circle (a half bicycle rim), so that the direction of the incident light beam could be varied between 20° and 160° and the reflection of light measured with 5° intervals in the same angular region. 90° corresponded to a direction perpendicular to the plane defined by the back of the bird.

The colours of the barbule cells were determined by reflection spectroscopy. Cleaned barbules were spread on a plasticine surface and the reflectance measured from cells presenting reflecting surfaces lying horizontally. A Zeiss microspectrophotometer O1 was used fitted with objectives for perpendicular incidence. Diameter of field of measurement was 3.2 µm and illuminator field stop .15 was used. For further details, see Dyck (1978).

Nomenclature of feather parts follows Lucas & Stettenheim (1972). For terms of orientation, see Dyck (1971).

Descriptions

1. Feather structure

1.1. *Ptilinopus rivoli*

The structure of *Pt. rivoli* feathers is described first. The other species' structures are dealth with only in those aspects where they differ from *Pt. rivoli*.

1.1.1. *Light and scanning electron microscopical observations*. Viewed in reflected light at a low magnification the green colour of a back feather is easily located to the barbules, the basal portion of which is seen to be a row of green, shining dots (or rings, depending on the focusing) (Plate 5:23). The terminal portion of the barbule is homogenously yellow, with a rounded barbule tip.

The feather vanes are green distally and brownish grey proximally, the former zone comprising 20–25% of the length. Distal and proximal barbules in the green zone are identical, each consisting basally of 7–9 green reflecting cells and terminally of about five yellow cells. The green reflecting cells are about 20 μm long each and the total length of the yellow part is 80–100 μm.

No barbicels are present on the barbules attaching terminally on the ramus. The first hooklets are found on barbules placed more basally on the ramus, on the border between the yellow and green cells. Still more basally, however, where the number of hooklets is three or more, there are also reflectors on barbule cells positioned terminally to the hooklets. Terminally to these reflectors there follows a yellow portion and the tip of the pennulum consists of a few unpigmented thread-like cells. Barbules placed even more basally on the ramus lack the yellow pigment; the corresponding portion is melanin pigmented. The obverse (dorsal) surface of the ramus is dark.

With the scanning electron microscope (SEM) it is seen that each lamella-shaped barbule bears 7–9 rounded structures on its obverse edge, evidently corresponding to the green reflecting cells. Viewed from above, the rounded part of each green cell appears as an ellipsoid with its long axis in the direction of the barbule (Plate 1:2). The furrow between two neighbouring cells runs not exactly perpendicularly to the direction of the barbule, so that the ellipsoids become somewhat skew (Plate 1:2). Since the production of a green colour takes place in these ellipsoid-shaped structures, they will be referred to in the following as *reflectors*. On the side of the barbule facing the base of the ramus the reflectors and lamella-shaped parts of the barbules are continuous (Plate 1:3). The surfaces of the lamella-shaped part shows a coarse fibrillary striation in a reverse-obverse direction, contrasting with a much finer, longitudinal striation on the reflectors (Plate 1:3). A view of the terminal (anterior) surface of the barbule (Plate 1:4) shows that the reflectors are not complete ellipsoids, but are strongly incurvate on their reverse surfaces. The concave, reverse surface of the reflector is flush with the lamella-shaped part of the barbule, so that the reflector comes to project freely (Plate 1:4). The cell boundaries are seen as reverse-obverse oriented ridges on the lamella-shaped part and this also shows a depression on each cell (Plate 1:4), a depression which corresponds to the remnant of the nucleus.

The lamella-shaped part of the barbule is somewhat curved and the reverse edge is slightly undulating (Plate 1:4).

The height of the barbule including the reflector is 20–30 μm. Width × height × length of the reflectors are (8–)10–13 × 6.5–10 × 20 μm^3.

1.1.2. *Transmission electron microscopical observations*. A transverse section of a barbule cell (Plate 1:5) ilustrates well the division of the cell into an obverse reflector with numerous layers of melanin granules,

and a reverse lamella-shaped part with only scattered melanin granules. Approximately in the middle of the latter part the dense remnant of the nucleus is found and adjacent to this the terminal (anterior) surface shows a depression.

Plate 2:7 shows that the fifteen or so melanin granule layers are curved and placed so that they exactly follow the outline of the reflector. The melanin granule layers terminate on the terminal (anterior) edge of the reflector and there are no melanin granule layers on the underside of the reflector. On the basal (posterior) surface of the barbule the melanin granule layers extend a considerable distance towards the reverse edge. The number of melanin granule layers decreases with increasing distance from the reflector. In the centre of the reflector tightly packed melanin granules, not arranged in layers, are present. A longitudinal section of a reflector (Plate 2:8) shows that the melanin granules are rod-shaped and oriented longitudinally. Again it is observed that the layers closely follow the outline of the reflector.

The mean number of melanin granule layers was determined to 15.7 as follows: The approximate position of the centre of the circle corresponding to the obverse outline of the reflector was determined on a transverse section. Radiating lines were drawn from the centre to the reflector surface at 30° intervals and the number of layers counted along those lines along which no obvious reduction in the number of layers had taken place. The number of layers is not always well defined due to irregularities of the layering near the bottom. It has been attempted to include only free layers, not the central mass of tightly packed granules, in accordance with the model of Huxley (Fig. 4 in Huxley (1968)). For each species, counts were made on three different cells; means and standard deviations in Table 1 are with respect to different cells.

The mean center-to-center distance between the melanin granule layers is 165 nm (Table 2), a value based on five measurements on each of three different reflectors. The pictures suggest that this distance is constant, in any one section, from the outermost to the innermost layers.

The surface on the reflector is covered by a dense epicuticle beneath which is a keratin layer of similar thickness to the keratin layers between the melanin granule layers. On a transverse section the melanin granules are seen to be surrounded by a thin, irregular layer of a less dense material (Plate 1:6). In some granules of the outermost layer this material is continuous with dense lines connecting with the epicuticle. In many places similar lines connects two melanin granules situated beneath each other. A pattern of keratin fibrils, each fibril approximate-

TABLE 1. Number of melanin granule layers in reflectors of seven *Ptilinopus* and one *Ducula* species. For method of counting, see text.

Species	Mean	S. Dev. (n=3)
P. cincta	3.9	1.0
P. jambu	16.3	0.2
P. superbus	11.9	0.8
P. rivoli	15.8	1.5
P. viridis	14.9	1.6
P. victor	19.9	1.0
P. luteovirens	17.8	1.9
D. concinna	6.8	0.4

TABLE 2. Center-to-center distance between melanin granule layers of reflectors of seven *Ptilinopus* and one *Ducula* species. For method of measuring, see text. Means and standard deviations are with respect to different cells.

Species	Distance (nm)	
	Mean	S. Dev. (n=3)
P. cincta	195.8	7.0
P. jambu	161.5	1.5
P. superbus	181.7	9.3
P. rivoli	164.7	10.7
P. viridis	169.3	14.7
P. victor	176.7	13.7
P. luteovirens	180.8	6.4
D. concinna	161.2	3.6

ly hexagonal in cross-section (being demarcated by 2+2 melanin granules and two lines) is thereby created (Plate 1:6).

Irregularities in the orientation of the melanin granule layers are mainly observed among the innermost layers, close to the clumps of melanin granules in the central part of the reflector (Plate 2:7, Plate 1:6). No exceptions to a longitudinal orientation of the melanin granules have been observed.

The melanin granules are frequently flattened in outline where they touch each other (Plate 1:6). In the melanin granule clumps in the center, dense packing is often observed (Plate 1:6) and the outline of the granules is changed to a hexagonal one in correspondence herewith.

Although the outline of melanin granules sectioned longitudinally is slightly irregular, the most characteristic feature is the relatively constant width (Plate 3:9,10). The ends are rounded to a varying degree. There is a gap, measuring about 5 nm, separating the ends of two neighbouring granules. The gap may be oriented perpendicularly or obliquely with respect to the main direction of the granules (Plate 3:9,10). Some of the melanin granules are somewhat bent; this is less prominent in a vertical longitudinal section (Plate 3:9) than in a horizontal longitudinal section (Plate 3:10). The latter figure shows that melanin granules in the same layer often have outlines which fit closely together.

The rod-shaped melanin granules measure 82 × 780 nm (Table 3). Means obtained from different cells are found to vary somewhat (Table 3). Within a single cell standard variations with respect to diameter and length of the melanin granules are about 10 and 100 nm, respectively.

The accuracies of the values of Table 3 are realistic only with respect to species differences. The size of a single granule could be determined to an accuracy of 10 nm.

1.2. *Ptilinopus cincta*

This species is atypical with respect to the green colour which generally characterizes *Ptilinopus* doves. The bird is mainly black and white, the white areas mostly with a yellowish tint. There is an olive-green area posteriorly on the underside. At low magnification the barbules of the feathers of this region are homogeneously yellow without reflectors and have not been investigated more closely. Only on the lower back and upper rump is there a green area in which the barbules bear reflectors. The colour of this area, however, is not the typical

TABLE 3. Size of rod-shaped melanin granules in reflectors of seven *Ptilinopus* and one *Ducula* species. A number of granules were measured in two or three cells of each species. Means and standard deviations are with respect to different cells.

Species	Diameter (nm)		Number of granules measured	Length (nm)		Number of granules measured
	Mean	S. Dev. (n=3)		Mean	S. Dev. (n=3)	
P. cincta	124.4	7.9	90	816	58	36
P. jambu	84.6	2.4	91	818	23	54
P. superbus	112.4	1.0	92	717	–	22
P. rivoli	82.0	2.3	85	780	59	62
P. viridis	87.4	2.3	90	877	–	23
P. victor	74.4	6.0	95	780	–	38
P. luteovirens	75.8	10.6	92	767	17	29
D. concinna	105.6	1.5	85	886	37	30

rich grass-green, but is greyish green with a purplish lustre.

The barbules vary in colour along the barbs and this variation again is different for different barbs, so here only a single barb is described (barb r 5; for numbering of barbs, se Dyck 1971). This barb can be roughly divided into three zones; the terminal zone has reflectors reflecting purple light. Most barbules end with the most terminal reflector, but some bear a yellow terminal piece. In the central zone the reflectors are green and the barbules all bear a yellow terminal piece, the end of which is slightly forked or squarish. In the basal zone the reflectors are golden green; the barbules are long and equipped with barbicels. The terminal parts appear light grey. Following the ramus basally, the first distal barbules bearing hooklets (1–2) have these positioned on the border between the yellow pigmented and the reflector-bearing part of the barbule. When more hooklets are present more basally on the ramus, some reflector-bearing cells are positioned terminally to the hooklets.

SEM-observation shows that the reflectors are much narrower (Plate 3:11) than those of *Pt. rivoli* (Plate 1:1). Otherwise the barbule structure appears to be similar in the two species. Plate 3:13 is a TEM transverse section of a reflector (purple or green colour). The reflector has the same basic structure as the *rivoli* reflector, but the number of melanin granule layers is only about four (Table 1) and the curvature of the layers is more irregular.

The melanin granules are considerably thicker ($p<.001$; two-tailed t-test) but of the same length as the *rivoli* granules (Table 3). Since it could not be determined whether the colours of the reflectors from which the melanin granule diameter was determined where purple or green, and since melanin granule diameter is probably larger in purple than in green reflectors, the larger diameter of the *cincta* melanin granules may be partly due to measurements made on purple reflector granules. I consider it very improbable, however, that the difference between *cincta* and *rivoli* can be explained solely by this.

1.3. *Ptilinopus jambu*

Characteristic of the reflectors of this species is a certain lack of regularity in the curvature of the melanin granule layers. On a transverse section of the reflector (Plate 3:14) the melanized part appears to consist of segments within each of which the melanin granule layers are straight. Thus the overall curvature of a melanin granule layer is partly the result of a stepwise change of orientation rather than a continuous change of orientation as in the *rivoli* reflector (Plate 2:7). Such a segmentation is also indicated in sections of the *rivoli* reflector as well as in the reflectors of other species, but in none of them to the extent observed in *jambu* sections.

To some extent the outline of the reflector follows the segmentation (Plate 3:14). The segmentation of the reflectors was not observed with the SEM. The width of the *jambu* reflector is similar to that of *rivoli*. Plate 3:14 is not through the centre of a reflector; therefore it is not typical with respect to width and number of melanin granule layers.

1.4. *Ptilinopus superbus*

The back is a rich golden green colour with a coppery tinge (Goodwin 1967).

The number of green reflectors is slightly lower (6–7 per barbule) than in *rivoli*. Also the yellow terminal piece appears to be slightly shorter.

The *superbus*-reflector is narrower (Plate 3:12) than that of *rivoli*. In addition to many melanin granule layers on the obverse (upper) part of the reflector a few layers are also present on the reverse (lower) part of the reflector (Plate 3:15). Furthermore, melanin granule layers are in the reverse part of the cell, while there are no layers in the middle part (Plate 3:15). The number of reverse layers is lower than in the reflector, and there is no widening of the cell.

On a few of the barbules investigated with the SEM a facet was observed on the basal (posterior) surface of the reflector (Plate 3:12). The facet has a circular outline and its plane is roughly parallel to

the main axis of the barbule inclined at about 45° to the plane of the feather plate. On TEM-sections of reflectors no facet could be identified with certainty. Attempts to localize reflectors with facets by observing a whole feather in reflected light were not succesful, and so it is not known whether such reflectors are restricted to a certain part of a feather.

Compared to the *rivoli* melanin granule the *superbus* granule has a larger diameter ($p<.001$, two-tailed t-test), and a similar length (Table 3).

1.5. *Ptilinopus viridis*

The green colour is more yellowish than that of *rivoli*. The number of green reflectors is slightly lower (6–7 per barbule) than in *rivoli*. In transverse section the reflector is more rounded than that of *rivoli*. In *rivoli* the basal (posterior) surface of the reflector graduates smoothly into the lamella-shaped part (Plate 1:3, 2:7), but in *viridis* the basal reflector surface is distinctly rounded and there is a discontinuity where the surface of the reflector and of the lamella-shaped part meet (Plate 4:20). Furthermore, the melanin granule layers stop at this boundary in *viridis* (Plate 4:20), where in *rivoli* they continue into the lamella-shaped part (Plate 2:7).

1.6. *Ptilinopus victor*

In this species there is a distinct colour dimorphism, the male being a vivid fire orange (Goodwin 1967) and the female mostly dark green. Subadult males and juveniles are also predominantly green (Goodwin 1967). Microscopically the structure of the green feathers is similar to that already described for other *Ptilinopus* species. The number of green reflectors is higher (9–10 per barbule) than in *rivoli* and the length of the yellow part is only about half that of *rivoli* (Plate 4:16).

The reflectors tend to be triangular in transverse section (Plate 4:21) with one corner of the triangle corresponding to the most obverse part of the reflector. Some *rivoli* reflectors have the same shape while some *victor* reflectors do not, but the overall tendency appears to be as stated.

As in *viridis* the basal (posterior) surface of the reflector is rounded and discontinuous with the posterior surface of the lamella-shaped part of the cell. Likewise the melanin granule layers stop at this boundary and the lamella-shaped part is almost completely devoid of melanin granules.

1.7. *Ptilinopus luteovirens*

Like *victor* this species exhibits sexual dimorphism, the male mainly being striped yellow-green (Goodwin 1967). The back feathers of the investigated specimen (male) are pointed. The vanes adjacent to the shaft are pennaceous, while the lateral parts are of a loose hairy texture. The pennaceous portion is yellow-green distally, a colour which gradually changes to a plain green proximally. The lateral portions are also green. In the green parts of a feather the structure is similar to that described for other *Ptilinopus* species. The number of reflectors per barbule is only about five. The yellow-green colour arises where the yellow-pigmented terminal portion of the distal barbules is much elongated (Plate 4:17) so that they extend over the following ramus, thus covering the reflectors of the proximal and distal barbules on this ramus. In this way practically nothing but yellow-pigmented feather parts are visible from above, the green reflectors mainly contributing to overall colour insofar as the green light is transmitted by the yellow barbule parts. These yellow barbule parts are about 400 μm long and somewhat twisted (Plate 4:17). Basally the distal barbules bear about five reflectors. The proximal barbules bear about eight reflectors each, and also their terminal parts are elongated, but these are little pigmented if at all, and they are strongly pointed, almost thread-like in the greather part of their length.

The reflectors tend to be triangular (Plate 4:18). A feature not observed in the reflectors of the other species is a slight depression on the basal (posterior) surface of most reflectors (Plate 4:18). SEM-

observation from above shows the depression to be a longitudinal furrow.

There is a discontinuity between the reflector and the lamella-shaped part on the basal surface of the barbule and the melanin granule layers stop there. The lamella-shaped part is almost completely devoid of melanin granules.

1.8. *Ducula concinna*

The upper parts are iridescent green, a colour distinctly different from the non-iridescent green of most of the *Ptilinopus* species treated above.

As in the *Ptilinopus* species, the green colour is produced in the barbules, but viewed in reflected light only the obverse edges of these are seen as narrow green stripes with cell boundaries indicated (Plate 5:24). Barbules placed terminally on the rami consist of 11–12 green reflecting cells basally and about three unpigmented cells terminally. Proximal and distal barbules are similar, no barbicels being present. Each cell is about 20 μm long. Distal barbules attaching more basally to the ramus are longer and bear hooklets. Reflecting cells (about six) are present also terminally to the hooklet-bearing cells. SEM-observation reveals that no reflectors are present (Plate 4:19). The entire barbule is lamella-shaped and smooth except for shallow depressions corresponding to cell boundaries.

A transverse section of a barbule cell reveals layers of melanin granules along its periphery (Plate 4:22). The number of layers diminishes gradually from about seven in the obverse part of the cell to two or three in the reverse part in parallel with the decreasing width of the cell.

Compared to the *rivoli* melanin granule the *Ducula* granule has a larger diameter ($p<.001$, two-tailed t-test) and a similar length (Table 3).

1.9. *Intraspecific variation*

This was studied in *Pt. superbus* (four additional specimens).

The number of reflectors per barbule in the corresponding position of a feather was found to be c. 4, c. 4, c. 5 and 6–7, thus less than in *rivoli* and the *superbus* specimen first studied.

In three of the four specimens the reflector was decidedly narrow than in *rivoli,* in the fourth only slightly. All four specimens had a few melanin granule layers in the reverse part of the reflector as in the specimen first studied. Three of the four specimens had a few melanin granule layers in the reverse part of the reflector-bearing cells, while the fourth specimen had them indicated only.

Facets, like those observed in the specimen first studied (Plate 3:12), were not observed in any of the four specimens. Since, in the first specimen, the facets were observed on only some of the barbules, the possibility that the facets constitute an abnormality cannot be ruled out, but their regular structure speaks against this.

The number of melanin granule layers in a single reflector of each of the four specimens were 10.0, 11.0, 11.0 and 12.9, giving a mean of 11.2, which is similar to the value for the specimen originally studied (Table 1). Standard deviation is 1.2 which indicates that interindividual variation is not much larger than intraindividual variation (Table 1).

Mean melanin granule diameters in a single cell of each of the four specimens were 97.0, 107.9, 115.6 and 138.3 nm. This variation is much larger than in the specimen originally studied (Table 3), but the mean (114.7 nm) is similar to that of the original specimen (112.4 nm).

It is concluded that the traits, structural and mensural, observed in a single individual, in general are also present in other individuals, and thus are characteristic of the species. Exceptions are the facets, the presence and significance of which is an enigma, and the melanin granule diameter which shows a larger interindividual variation.

2. Reflection of light

2.1. *Angular distribution of reflected light*

One of the characteristic features of the *Ptilinopus* green is that the colour is relatively constant under

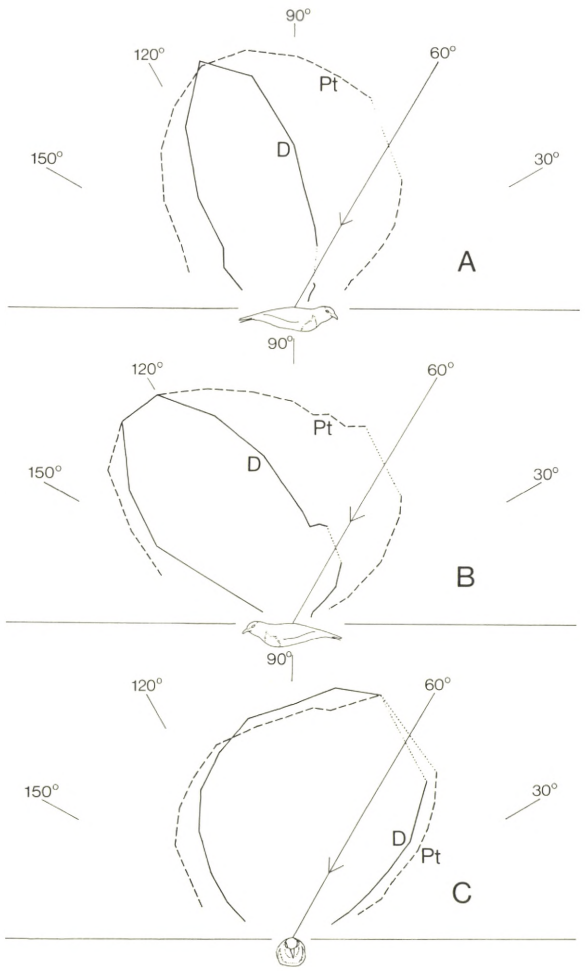

Fig. 1. Angular distribution of light reflected from the backs of *Pt. rivoli* (Pt) and *Ducula concinna* (D). The incident light beam is represented by an arrow. The intensities of reflected light are given as relative values, proportional to the distance from the illuminated spot on the birds' back to the point on the curve in a particular direction. The dotted parts of the curves denote the angular section, where reflected light intensities could not be measured due to the position of the lamp. A, B and C correspond to the different positions of the bird relative to the incident light beam, as illustrated.

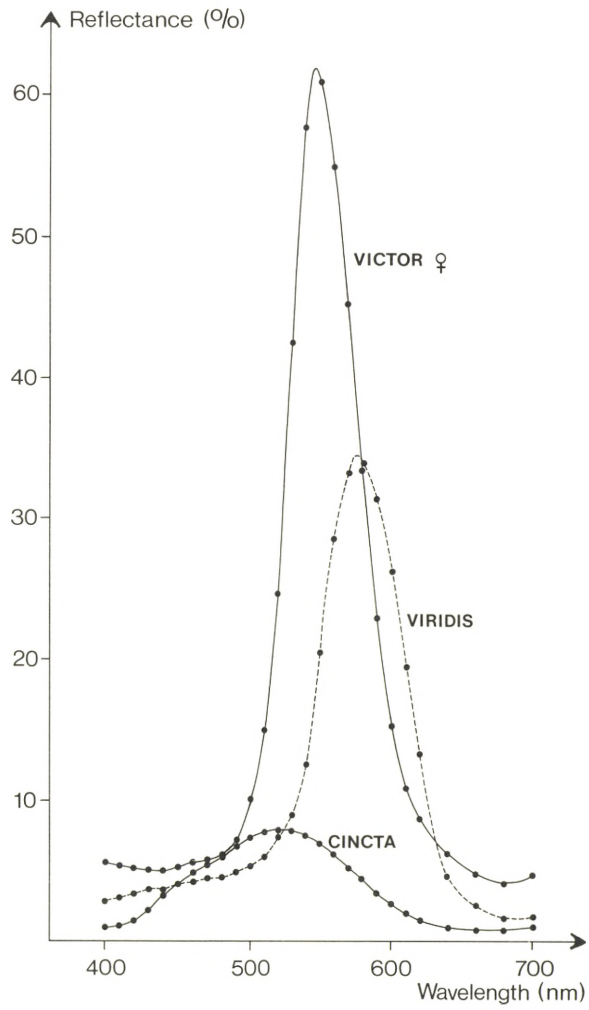

Fig. 2. Reflectance spectra of single reflectors of *Pt. cincta, viridis* and *victor.*

varying viewing conditions; the hue and the lightness change very little. This is in contrast to the iridescent green colour of *Ducula;* here both hue and lightness vary very considerably when the orientation of the plumage surface is changed relatively to the source of illumination or the eyes of the observer. Observations with the unaided eye were supplemented by measurements with the goniophotometer described above. This measures variations in the intensity of light reflected in

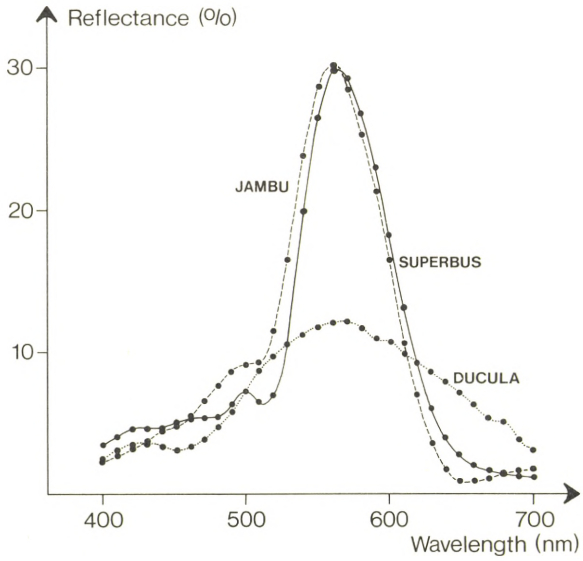

Fig. 3. Reflectance spectra of single reflectors of *Pt. jambu* and *superbus* and of a barbule cell of *Ducula concinna*.

different directions, but not the spectral composition of the light reflected.

Fig. 1 shows the results of measurements on *Pt. rivoli* and *Ducula*. When the birds are placed with their heads towards the lamp (A) most of the light reflected from the *Ducula* back is distributed over a rather small angle sector corresponding approximately to specular reflection, while the light reflected from the *Ptilinopus* back is distributed over a much larger angle sector, with a larger proportion being reflected in directions close to that of the incident light. If the birds are placed with their heads away from the lamp (B) peak reflections in both occur at larger angles than in (A). The difference between the species is similar to that of (A), but somewhat less pronounced. When the birds are placed with their body axis at a right angle to the plane defined by lamp and photodetector (C) both birds reflect most in the direction of the incident light and the difference between them is small.

The angular distributions from the backs of *superbus* and *viridis* under the conditions corresponding to Fig. 1A were also measured. The results were very similar to that obtained with *rivoli*.

If the incident beam of light strikes the back at an angle of 45° instead of 60° a difference between *rivoli* and *Ducula* is still present, but it is somewhat less pronounced than in Fig. 1A.

2.2. *Reflectance spectra of single cells*

A reflectance spectrum of each of three different cells of each species was recorded. The typical spectrum shows low reflectance in the short- and long-wave regions of the visible spectrum and a marked, symmetrical peak in the green part of the spectrum (Figs. 2, 3).

TABLE 4. Reflectance spectra of seven *Ptilinopus* and one *Ducula* species. Values of r_{max}, λ_{max} and width of the reflectance peak at $r_{\frac{max}{2}}$. Values for three spectra (no. 1, 2 & 3) of each species.

Species	r_{max} (%)			λ_{max} (nm)			Peak width (nm)		
	1	2	3	1	2	3	1	2	3
P. cincta	7.9	5.2	5.5	520	535	550	136	281	314
P. jambu	38.7	51.8	30.3	563	562	561	64	65	75
P. superbus	29.8	53.0	41.6	564	576	570	70	69	73
P. rivoli	50.9	50.3	56.7	560	547	565	70	73	64
P. viridis	51.4	47.8	34.8	564	560	574	62	74	74
P. victor	60.2	54.6	62.6	546	550	554	59	60	59
P. luteovirens	54.6	61.0	50.0	556	535	552	57	51	61
D. concinna	11.6	11.8	12.0	546	554	566	135	184	170

λ_{max} varies between 535 and 576 nm (Table 4), except for a single *cincta* spectrum with λ_{max} at 520 nm (Fig. 2). Maximum reflectance (r_{max}) varies between 5% (*cincta*) and 63% (*victor*) (Table 4). Most spectra of *cincta*, *superbus* and *Ducula* show steadily decreasing reflectance up to 700 nm (Fig. 3), while most spectra of *jambu*, *rivoli*, *viridis*, *victor* and *luteovirens* show a minimum in the region 660–690 nm (Fig. 3). Some spectra show one or several maxima in the region 400–520 nm (Figs. 2, 3). The following may be species specific; *rivoli:* one at 410–435 nm (four of six spectra), *superbus:* one at 500–520 nm (four of six spectra), *Ducula:* one at 410–430 nm (three of three spectra). Several *cincta* and *Ducula* spectra show additional minima and incurvations around 600 nm (Fig. 3). With the exception of *cincta* which shows an overall low reflectance (Fig. 2), r_{420} varies between approximately 3 and 7% with a median value close to 4%, and reflectance at the minimum in the red part of the spectrum (or r_{700}) varies between 0.6 and 5% with a median value at 2.4%. *jambu* appears to reflect relatively less in the red compared to the blue region than the other species (Fig. 3).

Except for *cincta* and *Ducula*, which show larger values, the band-width (the width of the reflectance peak at $r_{max}/2$) varies between 51 and 75 nm (Table 4). Fig. 4 shows the band-width divided by λ_{max} as a function of r_{max}. The points tend to form a hyperbola.

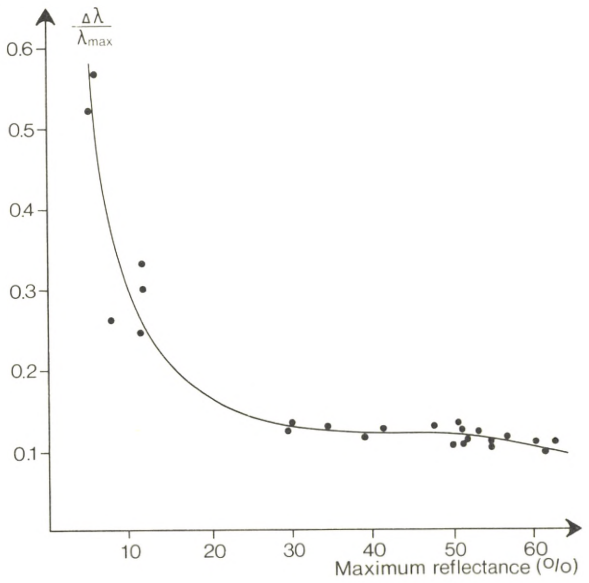

Fig. 4. Band-width divided by λ_{max} as a function of maximum reflectance.

Relations between Reflector Structure and Spectral Reflectance

In Fig. 5 the mean value of r_{max} (Table 4) has been plotted as a function of the mean value of the number of melanin granule layers (Table 1) for the eight species. A positive correlation between the two parameters is clearly indicated ($r=0.97$; $P<.0005$ (one-tailed)). *jambu*, however, shows a rather low reflectance for its number of melanin granule layers. The equation of the regression line is

$$r_{max}\ (\%) = 3.470 \times \text{number of layers} - 7.39.$$

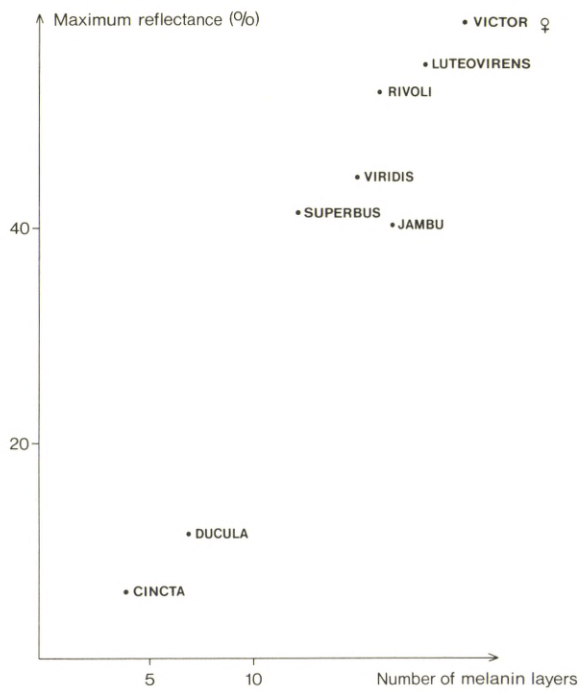

Fig. 5. Maximum reflectance as a function of number of melanin granule layers in seven species of *Ptilinopus* and in *Ducula concinna*.

This means that on the average each additional melanin granule layer increased r_{max} by 3.5%. The corresponding value for the uppermost points on Fig. 5 (five species, *jambu* excluded) is 2.4%. Taking into consideration the relatively low r_{max} of *Ducula* and *cincta* this indicates that the increment in r_{max} per additional melanin granule layer is particularly high between approximately six and twelve layers, corresponding to a sigmoid curve (Fig. 7).

It is obvious that there is a negative correlation between the bandwidth divided by λ_{max}, and the number of melanin granule layers (Table 1 and Fig. 4). This holds also if *cincta* and *Ducula* are excluded. The relation is:

$$\frac{\triangle\lambda}{\lambda_{max}} = -\ 0.00266 \times \text{number of layers} + 0.160$$
$$(r=-.077;\ N=6;\ P<.025\ \text{(one-tailed)})$$

The melanin granule diameters of the eight species fall into two groups. Those of *cincta, superbus* and *Ducula* are larger than 100 nm, while the remaining five species have diameters between 74 and 88 nm (Table 3). For the latter species there is a positive correlation ($p<.01$, two-tailed) between λ_{max} and melanin granule diameter (Fig. 6 a). For the same five species there is no correlation ($p.>.10$, two-tailed) between λ_{max} and center-to-center distance between melanin granule layers (Table 2), but there is a negative correlation ($p<.05$, two-tailed) between λ_{max} and the thickness of the keratin layer between the melanin granule layers (d_{ker}, defined as center-to-center distance minus melanin granule diameter, Plate 1:6) (Fig. 6 b).

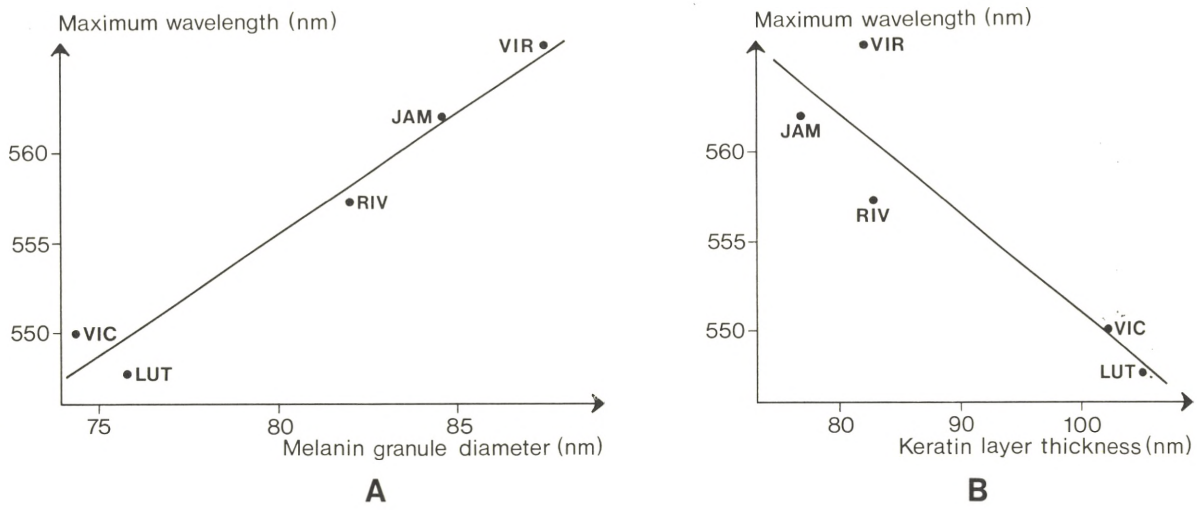

Fig. 6. The relationships between λ_{max} and (A) melanin granule diameter and (B) keratin layer thickness in five *Ptilinopus* species. The equations of the regression lines are (A) $\lambda_{max} = 1.357 \cdot d_{mel} + 446.9$ nm and (B) $\lambda_{max} = -0.550 \cdot d_{ker} + 606.0$ nm. Values of λ_{max} are means taken from Table 4.

Discussion

1. Feather structure

Structurally coloured barbules from different species show a variety of modifications of the typical barbule (review: Lucas & Stettenheim 1972). The cells in the modified part of the barbule may become broadened and flattened, and frequently the barbules show torsion, so that the modified cells lie in the plane of the vane.

Ducula and *Ptilinopus* barbules do not show torsion. Of the lamella-shaped barbules only the obverse edges are seen under normal viewing conditions, thus corresponding to that orientation of barbules which Auber (1957) referred to as the "generalized" condition. Durrer (1977) introduced the term "edge iridescence" ("Kantenschiller"). I find this a useful term, which applies well to the *Ducula* condition. I see no reason to restrict its use to modifications of the base, as Durrer does. It further seems to be Durrer's opinion that "Kantenschiller" is associated only with faint iridescence. This does not fit with *Ducula,* which shows intense iridescence, nor with *Trogon violaceus,* in wich the intensely iridescent barbules are similarly oriented (personal observation).

Structurally coloured barbules from different species vary with respect to the part of the barbule that produces colour. Lucas & Stettenheim (1972) list five categories. In *Ducula* it is the base and the basal portion of the pennulum which produce colour, corresponding to their category three. In *Ptilinopus* this arrangement is also observed in barbules attaching to the basal part of the ramus, while in barbules attaching more terminally only the base is reflecting. I assume, following Auber (1957), that the basal condition represents the original one which is then the same as in *Ducula.*

The shape of the *Ptilinopus* reflector seems first to have been described by Schmidt (1952), who in *Ptilinopus magnificus* (*Megaloprepia poliura*) characterized them as hemispherical enlargements of the cells along the upper edge of the lamella-shaped barbules. He observed similarly shaped reflectors in three other *Ptilinopus* species investigated (*monacha, pelewensis* and *perousii*) and also in *Carpophaga* (species?).

Reflectors related to the *Ptilinopus* type are present in a bird-of-paradise *Diphyllodes magnificus* male (Dorst et al. 1974) (belly and breast feathers, in median breast feathers only in a terminal zone). Observations in reflected light reveal that proximal as well as distal barbules consist of green reflecting cells with an outline, when seen from above, similar to that of *Pt. rivoli* reflectors, although not as regularly oval and appr. 1.5 times longer. The hue is rather constant when the plumage is viewed under varying conditions, but the colour is much darker than the *Ptilinopus* colour, which undoubtedly can be related to a much lower number of reflectors per unit of area in the *Diphyllodes* plumage (personal observation). Dorst (1974) ascribes the lack of iridescence to the barbules being narrow and stretching in different directions above the plane of the feather. The orientation of the barbules is undoubtedly the cause of the velvety appearance of these plumage parts and probably together with the shape of the cells causes the constancy of hue and lack of iridescence.

Durrer (1977) gives an excellent survey of the ultrastructure of iridescent feathers. He distinguishes 19 different types varying with respect to type of melanin granule and arrangement of the melanin granules within the barbules. The structure found in *Ptilinopus* conforms to his "StS" type (layers of small, compact, rod-shaped melanin granules separated by keratin layers). Besides in *Ptilinopus spp.* this type has been found in the following columbiform species: *Chalcophaps indica,*

Phaps chalcoptera, Caloenas nicobaria and *Ducula concinna* (Dyck 1976, Durrer 1977). The type is also present in *Tauraco corythaix* and *Chrysococcyx cupreus* (Cuculiformes) (Durrer 1977) and in *Parotia sefilata* (Paradisaeidae) (Durrer 1977, Dorst et al. 1974). In other birds-of-paradise a somewhat similar type is found, in which the keratin layers are separated by double layers of melanin granules, closely apposed (Dorst et al. 1974, Durrer 1977).

The number of melanin granule layers varies in these species (excepting *Ptilinopus*) between 3–4 (*Phaps, Tauraco*) and appr. 25 (*Parotia*). The diameter of the melanin granules varies between 77 (*Chrysococcyx*) and 123 nm (*Phaps, Tauraco*) in agreement with the variation within the *Ptilinopus spp.* (Table 3). The keratin layers tend to be somewhat thinner (42 to 91 nm) than in the *Ptilinopus spp.* The *Ptilinopus* melanin granules appear to be slightly longer (7–900 nm than those of *Chrysococcyx* (6–700 nm) (Durrer & Villiger 1970). There is good agreement between measurements by Durrer (1977) and myself on the structure of *Ducula concinna:* The diameter of the melanin granules is found to be 112, respectively 106 nm and the thickness of the keratin layer is found to be 58, respectively 56 nm.

2. Optical properties and feather structure

The *Ptilinopus* reflector with its alternating layers of melanin and keratin clearly depends on thin-film interference for colour production. For a given number of layers reflectance is maximal if the optical thickness of each layer is 1/4 λ_{max} (*in vacuo*) and Land (1972) terms this an "ideal" system. If the refractive indices of keratin and melanin are taken as 1.55 and 2.0, respectively (Durrer & Villiger 1962) and λ_{max} as 560 nm (Table 4, *Pt. rivoli*), we find that in an "ideal" system d_{ker} = 90 nm and d_{mel} = 70 nm. As defined previously (p. 16) for *Pt. rivoli* d_{ker} = 83 nm and putting d_{mel} equal to melanin granule diameter we obtain d_{mel} = 82 nm (Table 3), both values in reasonably good agreement with the "ideal" values.

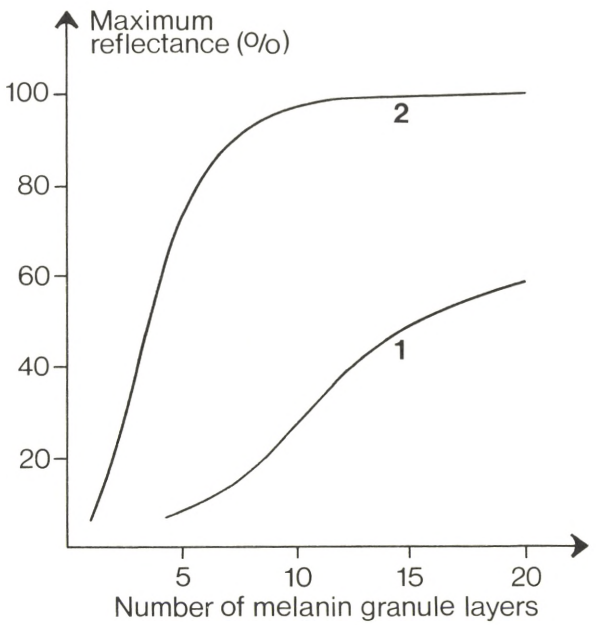

Fig. 7. The relationship between maximum reflectance and number of melanin granule layers as measured (1) and as calculated, assuming an "ideal" keratin-melanin system with no light absorption (2).

Fig. 7 compares r_{max} as function of the number of melanin granule layers as measured in *Ptilinopus* reflectors with an "ideal" keratin-melanin system. With less than about ten layers, r_{max} is much less than in the "ideal" system. But with twenty layers r_{max} is about 60% of the theoretical maximum and the shape of the curve suggests that with still more layers r_{max} will continue to increase until it eventually levels off at 65–70%.

Reasons for r_{max} being lower than in an "ideal" system are (1) Absorption of light by melanin (in transmitted light melanized feather parts are brownish). (2) Irregularities in the layering of the melanin granules. (3) Shape and thickness of layers. The precise effect on light reflection of substituting $\lambda/4$ – film with a layer of rods with diameter $\lambda/4$ is to my knowledge unknown (see also Land 1972). The present findings indicate that the effect is not large. Defining thickness layers in *Ptilinopus* reflectors as above, the melanin layers are thicker and keratin

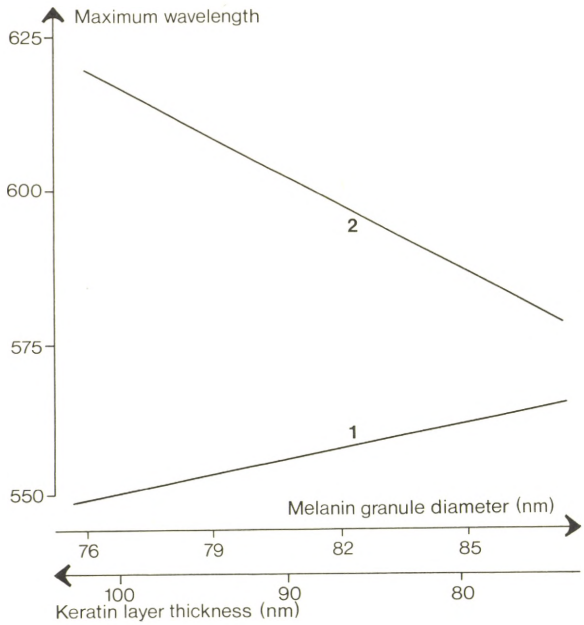

Fig. 8. The relationship between λ_{max}, melanin granule diameter and keratin layer thickness as measured (1) and according to theory (2).

layers thinner than in the "ideal" system. Theoretical considerations (Land 1972) show that the effect of this on r_{max} is small.

The reflectance of *Pt. jambu* is lower than predicted by its number of melanin granule layers (Fig. 5). Taking into account the small number of measurements on which means are based this may be purely random, but another, less complete, series of reflectance measurements gave a similar result. A comparatively low reflectance could be related to the fact that the melanin granule layers on a transverse section appear as discontinuous straight lines (Plate 3:14) instead of as smooth curves in the other species.

Chalcophaps indica with nine melanin granule layers has a r_{max} of 23% (Dyck 1976). This fits neatly with the *Ptilinopus* results (Fig. 7).

I feel that r_{max} is only rather slightly influenced by the fact that the reflector layers are curved, not plane, taking into account the small field of measurement used.

Species differences in λ_{max}: The five species having melanin granules with small diameter (*jambu, rivoli, viridis, victor* and *luteovirens*) are treated first.

In an "ideal" system an increase in λ_{max} is obtained by increasing the thicknesses of both high-index and low-index layers. The *Ptilinopus*-system does not fit with this since an increase in λ_{max} is correlated with an increase in melanin granule diameter but with a decrease in keratin layer thickness (Fig. 6).

In a "non-ideal" system λ_{max} is given by twice the sum of the optical thickness of the high- and low-index layers (Land 1972). This holds strictly only for an infinite number of layers (Vogt 1980). With 15–20 melanin granule layers (Table 1) the error by making this approximation is small. Fig. 8 investigates whether λ_{max} of the *Ptilinopus*-system follows this equation. Clearly it does not. Obviously the decrease in keratin layer thickness more than outweighs the increase in melanin granule diameter and we should observe a decrease in λ_{max} in the series of species which actually show an increase.

That this discrepancy arises because unrealistic values for the refractive indices have been used is unlikely. Bancroft *et al.* (1923) and Schmidt (1949) determined the refractive index of feather keratin to 1.54 and 1.55, respectively. In view of the homogeneity of feather keratins (Brush, in press) it is unlikely that the value for *Ptilinopus*-keratin deviates markedly from the 1.55 used. The only attempt to measure n_{mel} known to me is that of Schmidt (1949), who for melanin granules of iridescent *Columba* feathers found it to be larger than that of diiodomethane (1.74). Calculations show that in order to have an increase in λ_{max} with increasing melanin granule diameter with slope corresponding to that measured (fig. 8), n_{mel} must be 4.5, a value quite unrealistic for a partly transparent substance. Furthermore λ_{max} with this value for n_{mel} becomes ~ 1000 nm. Therefore, although the value for n_{mel} is rather uncertain, I find it safe to conclude that a multilayer of rods cannot be equated with the

simpler multilayer reflector with plane interfaces, when the purpose is to determine λ_{max} precisely from the dimensions and refractive indices. λ_{max} is more closely correlated with melanin granule diameter than with keratin layer thickness. Probably this is due to the rod-shape of the melanin granules. A further complicating factor is the absorption of light by the melanin pigment.

The determination of hue appears to be similar in the speculum feathers of ducks, where the colour-producing system (Rutschke 1966) is similar to that of *Ptilinopus*. Melanin granule diameter is larger and keratin layer thickness smaller in green compared to bluegreen feathers. In coppery red feathers compared to green feathers, melanin granule diameter is increased further still, but here also the keratin layers become thicker.

The above considerations are based on the assumption that the refractive index of melanin is the same in all the five *Ptilinopus* species with small melanin granules.

The three remaining species (*cincta, superbus* and *Ducula*) have melanin granules with larger diameters and keratin layers with smaller thickness than the five species (*jambu, rivoli, viridis, victor* and *luteovirens*) (Tables 2, 3). If the correlation between λ_{max} and melanin granule diameter valid for the five species (Fig. 6) is used for these three species, we find that λ_{max} for these should be approximately 600 nm, which it is not (Table 4). The simplest way of explaining the discrepancy is probably to assume that the melanins of *cincta, superbus* and *Ducula* have refractive indices which are lower than that of the melanin of the five species.

Durrer (1977) calculates λ_{max} of *Ducula* by using the formula for a "non-ideal" $\lambda/4$ multilayer with plane interfaces (which gives 630 nm). He assumes that there is also a λ_{max} at 450 nm, representing a second order maximum due to interference of rays reflected from the upper and lower surface of each melanin granule layer. The *Ducula* spectra show a weak maximum at 410–430 nm (Fig. 3); possibly its presence can be explained in conformity with Durrer's suggestion. But the shape of the *Ducula* spectrum with one major peak suggests to me that the colour of the barbule is almost completely determined by the thickness of the repeating sequence of melanin granules + keratin. The weak maxima at 500–520 nm in *superbus* and at 410–435 nm in *rivoli* may, as in *Ducula*, be determined by the dimensions of the melanin granules.

Bandwidth: The bandwidth of the *Ptilinopus* spectra is narrower than that of an "ideal" system, i.e. the colours are purer. Bandwidth divided by λ_{max} for an "ideal" system consisting of fifteen plates of refractive index 2.0 separated by layers of refractive index 1.55 is calculated to .193, while that of the *Ptilinopus* species with more than ten melanin granule layers is between .10 and .13 (Fig. 4).

The discrepancy may be due to the fact that the *Ptilinopus* system is "non-ideal", since such systems produce purer colours than do "ideal" ones (Land 1972). The examples given by Land (Fig. 7), however, seem to show that this factor can explain only a small part of the discrepancy.

It is more probable that the discrepancy is due to the melanin layer consisting of rods instead of plates. Consider the reflection of light from a plate, respectively a rod (cylinder), with λ_{max} at 560 nm and refractive index 1.56. The bandwidth of light reflected (at perpendicular incidence) from a single plate can be calculated as 820 nm. A cylinder scatters light in different directions. Here only light scattered directly backwards is considered. The graphs given by Farone et al. (1963) for infinite cylinders are used. The diameter of the cylinder in question is 151.5 nm and the bandwidth 410 nm, when the electric vector of the incident radiation is parallel to the cylinder axis. When this vector is perpendicular to the cylinder axis λ_{max} is shifted to 500 nm and bandwidth becomes 360 nm. When the incident light is unpolarized the back-scattered light (containing both orientations of the electric vector) will therefore have a somewhat larger bandwidth than if the incident light is plane polarized. It is estimated that the bandwidth ratio cylinder: plate lies somewhere between 1/2 and 2/3, which compares well with the bandwidth ratio *Ptilinopus:*

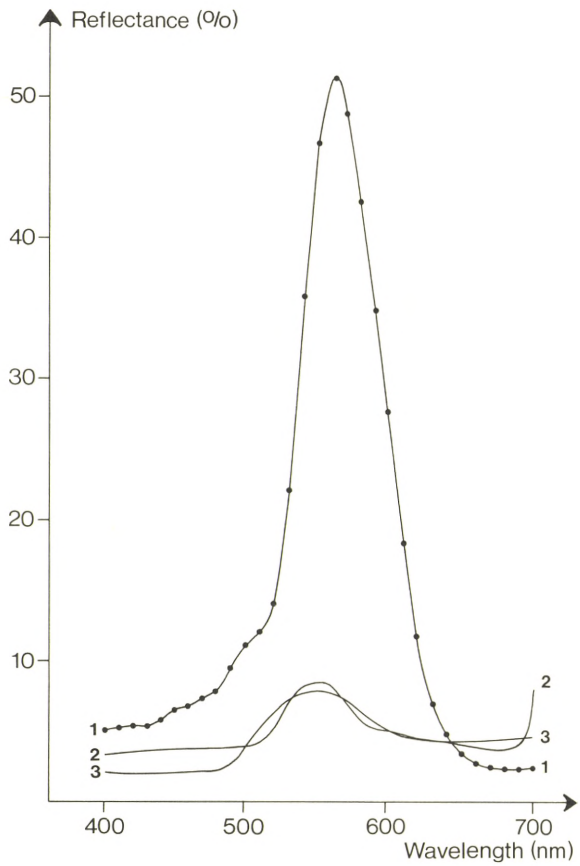

Fig. 9. Reflectance spectra of, respectively, a single reflector (1) and the dorsal, green plumage (3) of *Ptilinopus rivoli* and a green *Tilia* leaf (2).

"ideal system" (0.5–0.7). It therefore seems that the shape of the melanin granules is the decisive factor in determining bandwidth and thereby purity of the reflected light; the role of the absorption of light by melanin on bandwidth, however, is unknown.

3. Ecological aspects

Ptilinopus doves are forest birds, spending much time among the foliage (Austin 1961) and feeding on berries and fruits (Crome 1975, Goodwin 1967). It is obvious to assume that the function of the green plumage is to make the doves inconspicuous among the foliage, and this assumption has repeatedly been made (Cain 1954, Orenstein & Bruce 1976, Schmidt 1952). Some observers specifically mention how difficult it can be to detect doves sitting in the trees (Austin 1961, Cain & Galbraith 1956, Gilliard & Lecroy 1967, Rand 1941–42, Wood 1924).

Characteristic of the reflectance spectrum in the visible region of a green leaf are a distinct maximum in the green part (at 555 nm) and a distinct minimum in the far red (at 680 nm) (Moss & Loomis 1952 and Fig. 9). These leaf spectrum characteristics match well with those of *Ptilinopus* reflector spectra, with peak reflectances clustered around 560 nm and minima in the region 660–690 nm (Table 4).

However, the overall shape of the reflector spectrum is not a good fit with a leaf spectrum (Fig. 9), since the green peak is much more marked in the reflector spectrum, corresponding to a more saturated green colour. But in the intact plumage the relative intensity of the green reflector light is much reduced, since the feather surfarce consists not only of reflectors but also of furrows between reflectors and interspaces between barbules, which, being in shadow, appear dark, and finally of dark rami and yellow pigmented terminal barbule parts (comp. Plate 5:23). Therefore the reflectance spectrum of the plumage as measured with a conventional reflection spectrophotometer (DK 2A, Beckman) has a peak in the green region which is much less marked (Fig. 9), and the overall shape of the spectrum has a reasonable resemblance to that of a green leaf of similar lightness (Fig. 9). This figure refers to *Pt. rivoli*, and similar results have been obtained with other *Ptilinopus* species (Dyck 1966, unpublished measurements).

It thus seems clear that the reflectors and the yellow barbule tips make it possible to produce feathers with a green colour which is a good match of leaf green. However, the resemblance of the reflectance spectra is not the whole story. The *Ducula* reflectors also have peak reflectance at the same wavelength as leaves (Table 4), yet the subjective impression is that the colour of the *Ducula*

plumage is not a good match of leaf green. Due to the iridescence of the plumage, its hue and lightness vary with the illumination and viewing conditions.

The varying hue of the *Ducula* plumage can readily be observed, but has not been confirmed experimentally, although the varying lightness has (Fig. 1). Fig. 1 A clearly shows how the lightness of a *Ptilinopus* plumage is rather constant over a wide range of viewing angles, while the lightness of the *Ducula* plumage varies strongly with the viewing angle. Since the *Ptilinopus* plumage also has a constant hue under varying illumination and viewing conditions, this means that the colour of the plumage is a good match of leaf green, more or less independently of the angle under which the bird is seen and the distribution of light and shadow. Wereas *Ducula,* if it can be said to match leaf green at all, does so only under a very restricted range of illumination and viewing conditions.

This difference between *Ptilinopus* and *Ducula* can be explained through the difference in the shape of the barbule cells. Consider light which strikes the plane of the feather at an angle of 60° and parallel to the long axis of the barbules. The obverse surface of a *Ducula* barbule is smooth and only slightly curved lengthwise (Fig. 10a), and the light rays are reflected approximately in the same direction. In *Ptilinopus* the lengthwise outline of the obverse edge of the barbule is shaped quite differently due to the reflectors, and there is much more scatter of the reflected light rays in different directions (Fig. 10b). In *Ducula* feathers the barbules are set to the rami at an angle of 15–20° (Plate 5:24). Since most rami of the feathers are more or less parallel to the vertebral column (the body axis) the barbules are also oriented more lengthwise on the body than transversely. One would therefore expect that if the incident light is in the plane of the body axis then the back plumage will reflect it more or less like a mirror. This is in agreement with the goniophotometric measurements (Fig. 1A, B).

If on the other hand the incident light is in a plane, transverse to the surface of the back and the body axis, most light rays will strike the barbules at

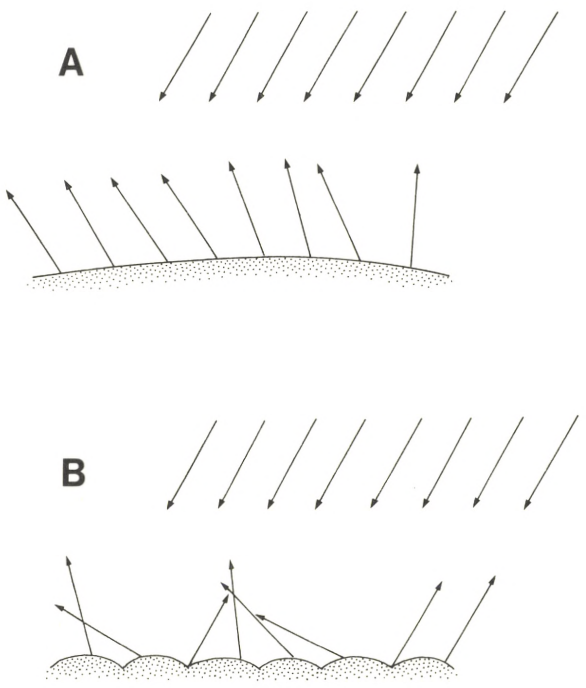

Fig. 10. The reflection of lightrays striking lengthwise on the obverse surface of a barbule; A: *Ducula,* B: *Ptilinopus.*

a right angle. Since, in that plane, the obverse part of a *Ducula* barbule is rounded (Plate 4:22), although not to the extent of a typical *Ptilinopus* reflector, one would therefore expect the reflected light to be scattered over a wide range of angles as it is from the *Ptilinopus* surface. Fig 1C confirms this.

In *Ptilinopus* we would expect the reflected light to be strongly scattered regardless of whether the incident light is parallel or transverse to the body axis because of the rounded shape of the reflectors. Fig. 1A, B, C confirms this. In addition to this, the barbules are set on the rami at an angle of circa 40° (Plate 5:23), whereby the reflectors of the proximal and distal barbules become oriented approximately at a right angle to each other. Through these two features the reflected light becomes almost completely diffuse and the characteristic constancy of the colour under varying viewing conditions is achieved.

The variation of the light-reflecting properties of the *Ducula* plumage with the direction of the incident light raises the interesting possibility that the pigeon may appear conspicuous in one orientation and cryptic in another orientation of its body axis relative to the direction to the sun.

The cryptic function of the green *Ptilinopus* plumage possibly does not apply to *Pt. cincta*, since the colour here is greyish green with a purplish lustre. Furthermore it is only the lower back and upper rump that are green, and this area is almost completely hidden from view when the bird sits with its wings folded.

The fact that the barbs of this region tend to have reflectors which reflect purple light distally, while the green reflectors are found more proximally indicates that the species is in the process of changing the colour of this region from green to purple, accepting the hypothesis of Auber (1957) that changes in colour and morphology along a barb sometimes represent the evolutionary history of the species, the terminal configuration representing the most recent evolutionary step. Further indications that the species formerly had more of its plumage of the typical green *Ptilinopus* colour are that the barbules of the black back feathers have cells, which, when studied with the light microscope, have a shape very similar to that of the green reflectors, and that the juvenile plumage has much more green. Very tentatively it can be suggested that the plumage has shifted from a mainly cryptic, green colour to a more conspicuous, aposematic colouration.

It appears likely that more aspects of *Ptilinopus* plumage colouration than just the green part render them inconspicuous. Thus the white crescent on the breast of *Pt. rivoli* presumably breaks up the outline of the bird so that two patches of green resembling separate leaves result. The bluish-violet spots on the wing coverts of *Pt. superbus* may resemble fungoid spots on leaves, and so forth. Orenstein and Bruce (1976) have suggested that even the vivid orange colour of the male *Pt. victor* may to some extent have a cryptic function by making the body resemble one of the large dead leaves scattered through the forest canopy, while the dull green head blends into the foliage.

4. Reflector evolution

As mentioned above (p. 18), reflectors of the *Ptilinopus* type are known only from this group of birds, apart from a single species of bird-of-paradise, in which a related type appears to exist. The shape and orientation of the *Ducula* barbules correspond to the "generalized" configuration widely found in non-iridescent body contour feathers. I therefore assume that in *Ducula* we have a relatively simple type of iridescent barbule and in *Ptilinopus* a specialized one, and shall now discuss how the latter may have evolved from the former.

This evolution may be divided into several components:

a. The number of melanin granule layers increases. This change is most marked in *luteovirens* and *victor*. The function of this change is to increase peak reflectance and reduce band-width, thus increasing the purity of the produced colour.
b. The melanin granules become smaller in diameter. This change has taken place in all species except *cincta* and *superbus*. In accordance with Durrer (1977) I assume that small granules more readily arrange themselves in regular layers than do larger granules.
c. A change in cell shape occurs, with most of the keratin material being displaced towards the central, obverse part of the cell, so that the shape approximates to that of a sphere riding on a thin lamella. This change is most marked in *viridis*, least in *cincta* and *superbus*. The *jambu* reflector is special; its overall shape is advanced, but its segmentation probably makes it less efficient than the smoothly curved ones. The functional basis of the reflector shape is discussed above (p. 23).
d. The melanin granules disappear from the reverse lamella-shaped part of the cell. This change appear to have taken place in *cincta*,

viridis, luteovirens and *victor*. Its function may be to economize on melanin granule production.

e. The melanin granule layers disappear in the reverse part of the cell. This change appears to have taken place in all species expect *superbus*. Its function may be to allow the diffuse reflection to be maximized.

The supposed evolutionary changes are summarized in Table 5, ranked according to increasing number of melanin granule layers. Changes d and e are obviously coupled, but for changes a, b and c there is no reason a priori to expect any coupling. However, Table 5 strongly suggests some sort of connection, and this raises the question of whether one of the changes triggers the others. A possible candidate for such a change is that from a larger to a smaller melanin granule diameter (b).

It can be argued that it is easier to form strongly curved melanin granule layers when the granules become smaller (Durrer 1977). This would fit with the fact that *cincta* and *superbus* with little evolved reflectors have relatively large melanin granules as has *Ducula*.

The diameter of the melanin granules probably also influences the number of melanin granule layers that can be accomodated in a *Ptilinopus* reflector: Transverse sections of reflectors show (Plates 2:7, 4:20,21) that the curving is most regular in the outer layers. In the inner layers there is a tendency for a layer to appear as a number of linear segments. It seems obvious that a relatively large number of "segmented" layers is incompatible with good optical function for a reflector with curved layers. If it is correct that small granules more easily can be ordered in curved layers than can large ones, it seems logical that small granules make possible a larger number of layers than do large ones.

Comparison of Plate 4:20 and 21 indicate how the small granules of *victor* result in a higher number of smoothly curved layers than the somewhat larger granules of *viridis*. A further indication that small granules are necessary for many layers is that the sequence of species according to decreasing granule diameter, is almost identical with the sequence according to increasing number of layers (comp. Tables 3 & 5).

Thus there is some evidence that a reduction in melanin granule diameter has been a decisive factor in evolution of the highly curved melanin granule layers.

The diameters of the melanin granules of the *Ptilinopus* species are low compared to other species

TABLE 5. Advanced (A) and primitive (P) traits of reflectors in seven *Ptilinopus* species. The species are ranked according to the number of melanin granule layers in the reflector. For further explanation, see p.24.

Species	a Number of melanin granule layers	b Melanin granule diameter	c Reflector shape	d Melanin granules in reverse part of reflector cell	e Melanin granule layers in reverse part of reflector cell
cincta	4 P	P	P	A	A
superbus	12	P	P	P	P
viridis	15	A	A	A	A
rivoli	16	A	A	P	A
jambu	16	A	(A)	P	A
luteovirens	18	A	A	A	A
victor	20 A	A	A	A	A

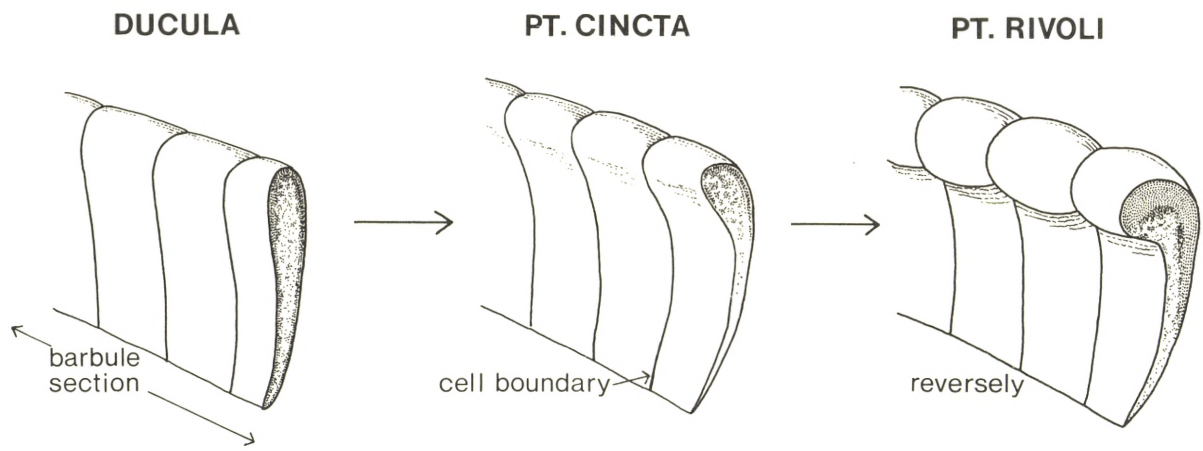

Fig. 11. The possible evolution of the typical *Ptilinopus*-reflector (as exemplified by *Pt. rivoli*) through stages resembling barbule cells of *Ducula concinna* and *Pt. cincta*.

having granules of this shape in structurally coloured barbules. The lowest value recorded by Durrer (1977) is 77 nm in *Chrysococcyx cupreus;* this species also has the layers rather strongly curved (Durrer & Villiger 1970).

Fig. 11 shows how *Ducula, cincta* and *rivoli* can be placed in an evolutionary series in accordance with the specific changes discussed above. Obviously *victor* could be added after *rivoli* as a species with a more evolved reflector. I do not, however, want to imply that the species shown have in fact evolved from each other (the lack of melanin granules in the reverse part of the cell in *cincta* and its low number of melanin granule layers makes such an assumption difficult), but I find it probable that the typical *Ptilinopus* reflector has evolved from a black or dark brown barbule cell (with melanin granules randomly distributed) through stages similar to those of *Ducula concinna* and *Pt. cincta.*

5. Classification

5.1. *Delimitation of the genus Ptilinopus*

The delimitation of the genus *Ptilinopus* has been difficult. Manuel (1936) expressed the opinion that the group is artificial "for the reason that there are no trenchant structural characters peculiar to it". Peters (1938) found it difficult to define the genus, on the basis of structural characters, and came to the conclusion that colour is probably more important than structure in this group. Cain (1954) carefully discusses the question and after revising the group reaches a similar conclusion. From the results of Schmidt (1952) and this investigation it seems that the genus can be defined as pigeons (doves) in which green plumage colours are due to the presence of hemispherical enlargements, reflecting green light, along the upper edge of the lamella-shaped barbules. This definition agrees with Peters and Cain in that it is based on the colour. It also removes the difficulty that Peters and Cain found themselves in because they found it necessary to distinguish between "structure" and colour. The characteristic *Ptilinopus*-green *does* represent a structural specialization, but at the cellular level. The reason that Peters and Cain distinguished between "structure" and colour undoubtedly was based on the – correct – fact that colour is also a subjective phenomenon. But they failed to recognize that specific colours very often are due to biochemical or structural specializations. It is noteworthy that despite this mental bloc these two workers decide

that colour was the important character in the classification of this group. This may illustrate the intuitive element in classificatory work. Short (1976), in a discussion of the use of external morphological characters in avian classification, expresses the view that colour itself, as opposed to colour pattern, is of rather limited value. Future studies may show that biochemical and structural specializations related to colour production are more common than hitherto suspected.

The presence of green reflectors in the plumage of all *Ptilinopus* species represented by specimens in the collections of the Zoological Museum in Copenhagen was confirmed by observation at 25 × magnification. The species were (sequence after Cain (1954)).

porphyrea	*richardsii*
cincta	*porphyraceus*
wallacii	*purpuratus*
aurantiifrons	*solomonensis*
perlatus	*rivoli*
superbus	*viridis*
perousii	*iozonus*
monacha	*hyogastra*
coronulatus	*melanospila*
pulchellus	*jambu*
regina	*victor*
greyii	*luteovirens*

In a few species (*perousii, regina, porphyrea*) some reflectors had a reddish tinge.

Schmidt (1952) described the reflectors in *Megaloprepia poliura* (as well as in *Pt. perousii, monacha* and *pelewensis*) and it seems therefore justified to include the two *Megaloprepia* species in *Ptilinopus* as done by Goodwin (1967).

5.2. *Arrangement within the genus*

Previous revisions are those of Cain (1954) and Goodwin (1967). The present discussion is based almost entirely on reflector structure. For definitions of primitive and advanced reflector characters, see section 4 of the discussion (with Table 5). Reflector structure is not suited for cladistic analysis.

cincta:

Together with *porphyrea* and *dohertyi* this species is assigned by Cain to the subgenus *Leucotreron,* which he lists first in his classification.

Goodwin also considers these three species to be rather primitive, but five species (among these *jambu* and *magnificus*) are considered even more primitive. (Goodwin depicts the presumed relationships within the genus by a phylogenetic tree; in referring to this I term early offshoots as primitive).

With respect to reflector structure *jambu* is clearly more advanced than *cincta* (Table 5). Schmidt's (1952) and my own observations on the shape of the reflectors of *magnificus* (referred to by Schmidt as *Megaloprepia poliura*) also indicate that they are more advanced than those of *cincta*. Assuming that Cain considered *Leucotreron* to be the most primitive subgenus when placing it first in his sequence, then there is agreement between the present findings and Cain's classification.

The colour pattern of the adult *cincta* with only a very small part of the plumage being green is unlikely to represent the primitive condition within the genus. As discussed p. 24 *cincta* may have shifted from a cryptic, predominantly green, to a more conspicuous colouration. *porphyrea* may be closer to the ancestral condition.

Cain remarks upon the similarity in colour pattern between the species belonging to *Leucotreron* and some *Ducula* species, and mentions the possibility that a complete revision may show that the subgenus *Leucotreron* should be separated generically from the subgenera *Ramphiculus* and *Ptilinopus*. Reflector structure clearly shows that *cincta* is more closely related to other *Ptilinopus spp.* than to *Ducula*.

superbus:

The six remaining species whose reflectors have been studied are all placed by Cain in his subgenus

Ptilinopus. These species differ clearly from *cincta* in their more elaborate reflector structure. On the other hand *superbus,* like *cincta,* shows primitive features in the relatively large diameter of its melanin granules and the relatively low number of layers, and judged from its reflector structure, is the most primitive of the six species.

Cain divides the subgenus *Ptilinopus* into six species-groups, of which the second – the *purpuratus* species-group is divided into two subgroups. The first of these comprises *superbus* and *perousii*. The latter resembles *superbus* in that its reflectors also are rather narrow (Schmidt 1952, own observations).

Goodwin places *superbus* as a rather advanced species, in fact the most advanced of the seven species. *perlatus,* which he places on the same branch, also has rather narrow reflectors, whereas *wallacei* (of the same branch) has not.

The systematic position of *superbus* as judged by reflector structure thus fits much better with Cain's than with Goodwin's classification.

rivoli and viridis:
Cain places these two species in the same species-group (the third of the six), but in two different subgroups, with *rivoli* in the most primitive. Goodwin places the two species on two different branches. Apart from one character nothing in reflector structure speaks against the two species being closely related (Table 5). The agreement with the classification of Cain thus seems to be better than with that of Goodwin.

jambu:
Cain finds it difficult to decide to which subgenus *jambu* belongs, and only with the greatest hesitation places it in the subgenus, in a species group containing only this species.

Goodwin considers it one of the most primitive species, even more primitive than *cincta.*

jambu has a rather advanced reflector and so the agreement with Cain's proposal is better than with that of Goodwin. The segmented nature of the melanin granule layers, however, lets the reflector of *jambu* differ from that of the other investigated species, and so there is also at the cellular level an indication of the isolated position of this species.

An isolated position of the species is indicated also by its reflectance spectrum, which shows an unusually high reflectance in the blue region compared to that of the red region and a relatively low value of peak reflectance taking the number of melanin granule layers into account (Fig. 5; this is based on only three measurements, so the low value could be the result of random variation. However, another less complete series of meassurements gave a similar result).

victor and luteovirens:
Cain and Goodwin agree that these two species are closely related forming, together with *layardi,* a superspecies. Cain ranks the three species as constituting the sixth of his six *Ptilinopus* species groups, while Goodwin considers them a primitive group, branching off at the same level as does the branch, to which *cincta* belongs.

The reflector of these two species are the most advanced of those studied, so clearly the agreement with Cain's classification is better than with that of Goodwin. The similarity of the reflectors of the two species is in agreement with the species belonging to the same superspecies.

The species belonging to this superspecies were formerly put into a separate genus, *Chrysoena.* Amadon (1943) pointed out that since the green plumage of the females is so similar to the plumage typical of *Ptilinopus* species, they should be included in *Ptilinopus*. Cain and Goodwin agree with this, and the reflector structures of *victor* and *luteovirens* clearly corroborate it.

Amadon (1943) ascribes the peculiarities of the male plumage of these species to further development of two tendencies common in various species of *Ptilinopus,* namely (1) towards diffuse and hair-like plumage, and (2) towards feathers with a thickened appearance due to closely appressed barbs. I agree that there is a tendency towards hair-

like feathers in eastern species, but measurements show that this is due to the barbs being more widely spaced. This is also the case in *luteovirens;* hence the thickened appearance of its body feathers cannot be due to appressed barbs. It is due to the longation of the barbules (p. 11).

The above discussion clearly shows that the variation in reflector structure among species fits much better with the classification proposed by Cain (1954) than with that by Goodwin (1967). The finding that information gained from a study at the cellular level fits well with a classification based on plumage patterns is satisfying.

6. Phylogeny

Goodwin (1967) proposes that the genera *Alectroenas, Ducula* and *Ptilinopus* are closely related with a common ancestor. The present findings support a close relationship between *Ducula* and *Ptilinopus* (p. 26). The olive-green tips of some under tail-coverts of *Alectroenas madagascariensis* owe their colour to green, iridescent barbules with yellowish tips. No reflectors are present. Although electron-microscopical studies have not been performed, it can reasonably be assumed that production of the green feather colour in *Alectroenas* is due to layers of melanin granules, as in *Ducula* and *Ptilinopus,* so that Goodwin's proposal (*op.cit.*) is supported.

In fruit pigeons of the genus *Treron* the olive-green colours are due to a combination of black and yellow feather parts (Frank 1939, Dyck 1978), while no structure producing green is present. The black melanin is found in the rami and the basal parts of the barbules, whereas the yellow pigment is present in the terminal parts of the latter. This distribution is the reverse of that found in olive-green feathers of piciform and passeriform species (Frank 1939, Dyck 1978), but agrees with that present in *Ptilinopus* (although the melanin granules here are arranged in layers so that black is altered to green). Furthermore, in the barbules of olive-green *Treron* feathers (*T. vernans* and *T. calva*) the melanin granules tend to be present only in the obverse parts of the cells, as in the *Ptilinopus* reflector cells, and in contrast to the olive-green feathers of piciform and passeriform species, where the melanin granules are rather evenly distributed throughout the barbule cells (unpublished observations). *cincta,* the most primitive of the *Ptilinopus* species studied with respect to reflector structure, has a yellowish olive lower belly. The colour is due to a combination of black rami and yellow barbules, analogous with the situation in *Treron* olive-green feathers. So with respect to the structures producing greenish plumage colours, *cincta* appears to be intermediate between *Treron* and typical *Ptilinopus* spp. There is thus some evidence that *Treron* may represent an offshoot of the line leading to *Ptilinopus,* as suggested by Goodwin (1967).

Colour-producing structures in barbules and analogous to layers of small rod-shaped melanin granules of *Ptilinopus* have been described in some other columbiform species: *Caloenas nicobaria* and *Phaps chalcoptera* (Durrer 1977; his StS-type) as well as *Chalcophaps indica* (Dyck 1976). All three species differ from *Ptilinopus,* however, in lacking terminal barbule parts without melanin granules and in that the colour-producing structure is restricted to the distal barbules.

Within the Columbiformes there are other types of colour-producing structures based on a entirely different feature, namely air-filled barbules. Species differ, however, in how they utilize the air for colour-production. In *Columba trocaz* (Schmidt & Ruska 1961), *C. livia,* and *Zenaida asiatica* (Durrer 1977) the colour is determined by the thickness of the outer keratin layer of the barbule cell (Dyck 1976, Durrer 1977). In *C. fasciata* the colour is produced by a compact layer of melanin granules in an air-filled space situated just within the outer keratin layer of the barbule cell (Durrer 1977). Finally in *Goura spp.* a bluish colour is produced by a network of keratin rods suspended in the air of the barbule cell (Häcker & Meyer 1902, pers. unpubl. obs.). That a similar arrangement is responsible for the blue colour of *Alectroenas spp.,* as stated by Häcker & Meyer (1902), I consider unlikely.

The rather incomplete data on colour-producing structures within Columbiformes thus suggest two main branches. Goodwin's scheme (1967) comprises three branches, and there is little agreement between his assignment of the genera to these branches and the information provided by the colour-producing structures.

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Plates

Key to Labelling:

B: Barbule
E: Epicuticle
F: Facet
KF: Keratin fibril
KL: Keratin layer
M: Melanin granule
N: Nucleus remnant
o: obverse part of barbule cell
r: reverse part of barbule cell
R: Ramus
Rf: Reflector

PLATE 1

Fig. 1. *Ptilinopus rivoli*. Barbules bearing reflectors on their obverse edge. SEM. Scale: 50 μm.

Fig. 2. *Pt. rivoli*. Barbules with reflectors; from above. SEM. Scale: 50 μm.

Fig. 3. *Pt. rivoli*. Part of barbule with reflectors; the side facing the base of the ramus. SEM. Scale: 10 μm.

Fig. 4. *Pt. rivoli*. Part of barbules with reflectors; the side facing the tip of the ramus, partly from above. SEM. Scale: 10 μm.

Fig. 5. *Pt. rivoli*. Transverse section through barbule cell with reflector. TEM. Scale: 2 μm.

Fig. 6. *Pt. rivoli*. Detail of transverse section through reflector. TEM. Scale: 0.2 μm.

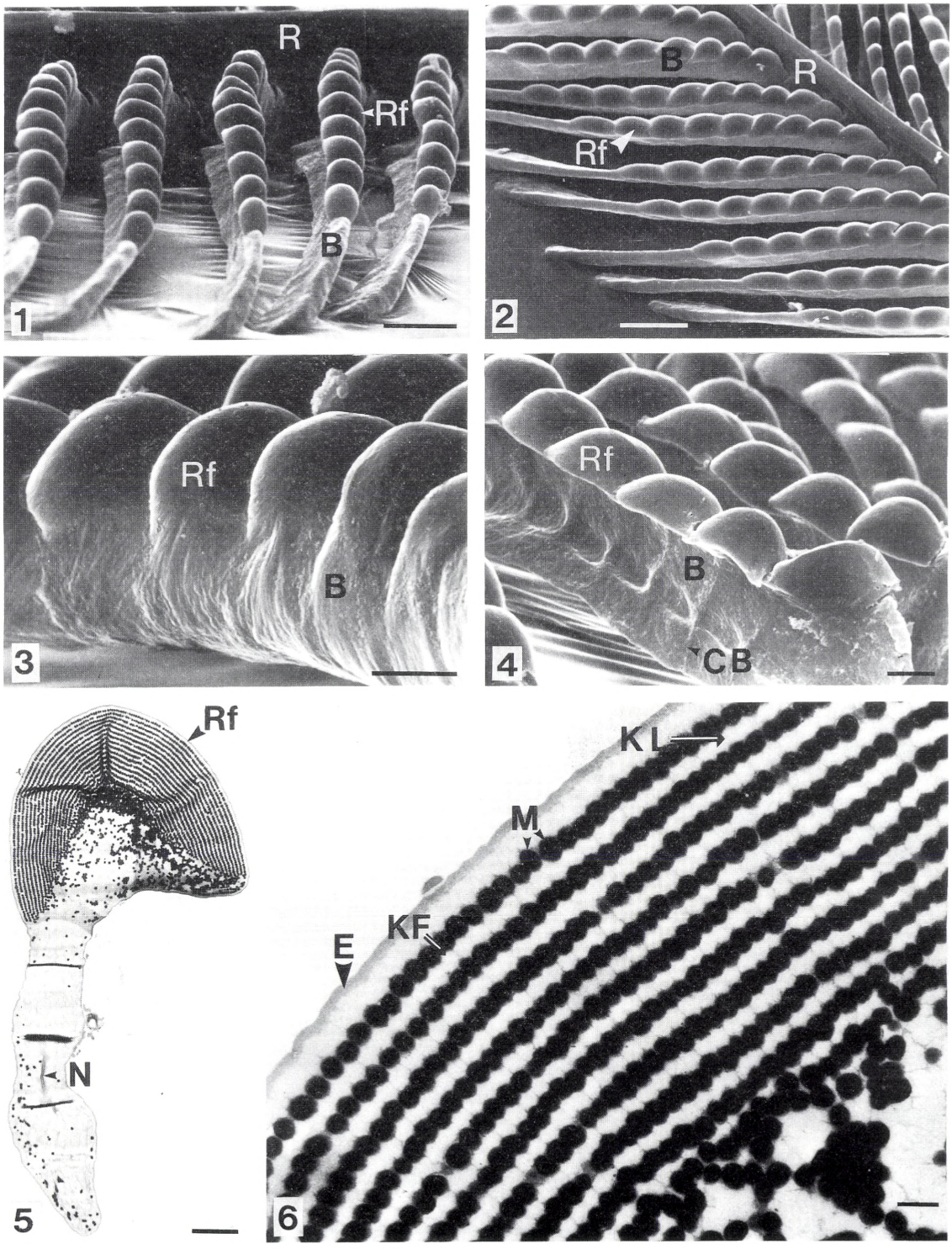
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PLATE 2

Fig. 7. *Pt. rivoli*. Transverse section through reflector. TEM. Scale: 1 μm.

Fig. 8. *Pt. rivoli*. Longitudinal section through reflector. TEM. Scale: 1 μm.

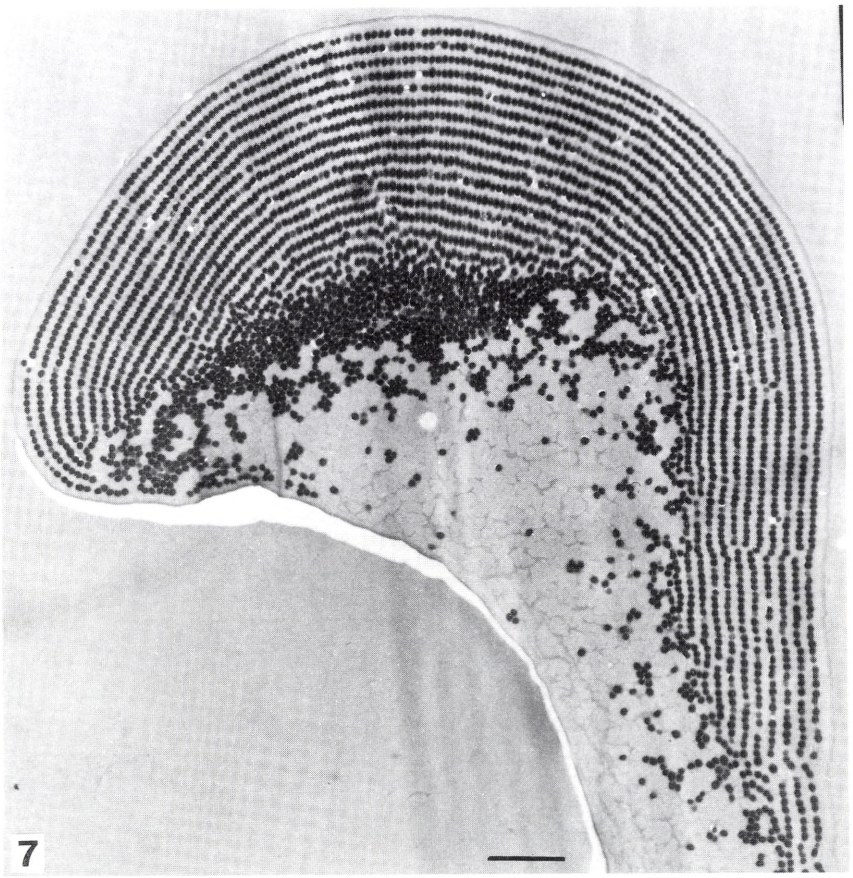
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PLATE 3

Fig. 9. *Pt. rivoli*. Detail of vertical, longitudinal section through reflector. Arrow 1: Perpendicularly oriented gap between melanin granules. Arrow 2: Obliquely oriented gap. TEM. Scale: 0.2 µm.

Fig. 10. *Pt. rivoli*. Detail of horizontal, longitudinal section through reflector. The outlines of the melanin granules fit closely together. TEM. Scale: 0.2 µm.

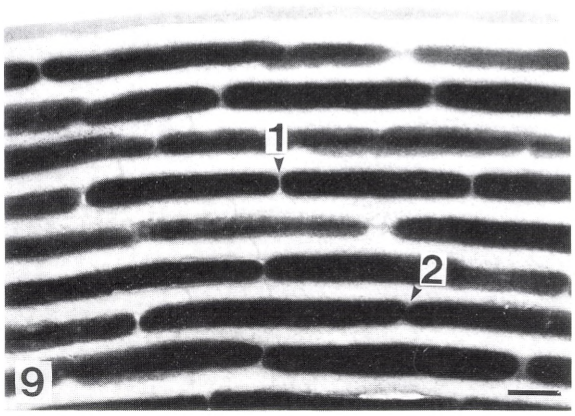
Fig. 11. *Pt. cincta*. Barbules with reflectors. SEM. Scale: 20 µm.

Fig. 12. *Pt. superbus*. Barbules with reflectors. SEM. Scale: 20 µm.

Fig. 13. *Pt. cincta*. Transverse section through reflector. TEM. Scale: 1 µm.

Fig. 14. *Pt. jambu*. Transverse section through reflector. Arrow indicates boundary between two segments. TEM. Scale: 1 µm.

Fig. 15. *Pt. superbus*. Transverse section through barbule cell with reflector. TEM. Scale: 2 µm.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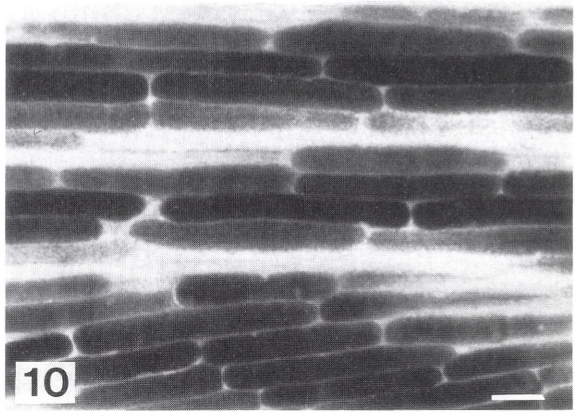
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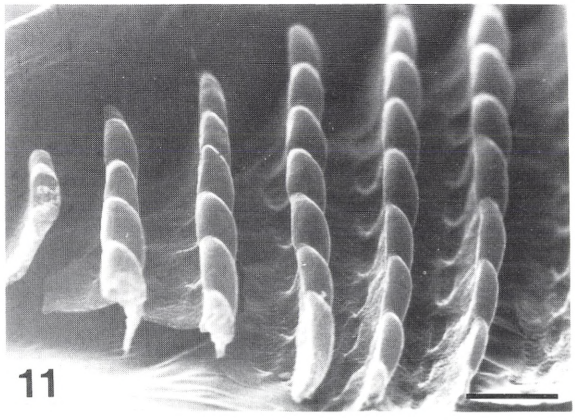
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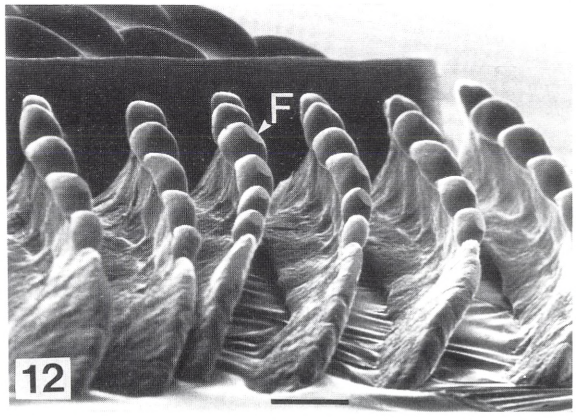
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PLATE 4

Fig. 16. *Pt. victor*. Barbules with reflectors. SEM. Scale: 20 μm.

Fig. 17. *Pt. luteovirens*. Barbules from above. Arrow: Yellow-pigmented portion of barbule. SEM. Scale: 100 μm.

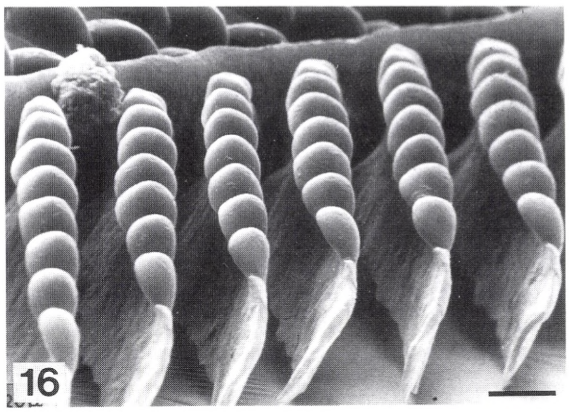
Fig. 18. *Pt. luteovirens*. Part of barbules with reflectors; the side facing the tip of the ramus, partly from above. Arrow: Depression on reflector surface. SEM. Scale: 5 μm.

Fig. 19. *Ducula concinna*. Barbules. SEM. Scale: 10 μm.

Fig. 20. *Pt. viridis*. Transverse section of reflector. Arrow: Boundary between reflector and lamella-shaped part of barbule. TEM. Scale: 2 μm.

Fig. 21. *Pt. victor*. Transverse section of reflector. TEM. Scale: 2 μm.

Fig. 22. *Ducula concinna*. Transverse section of barbule cell. TEM. Scale: 2 μm.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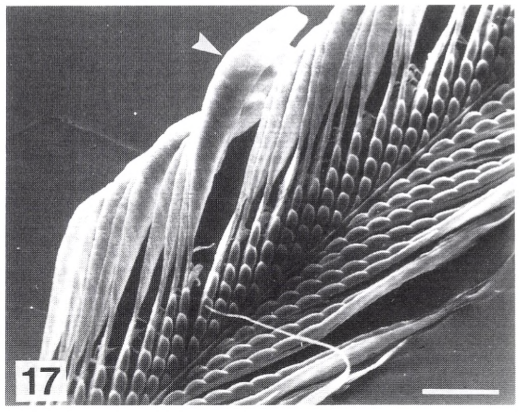
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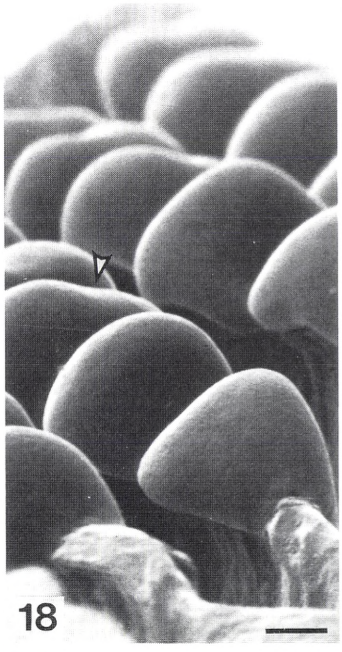
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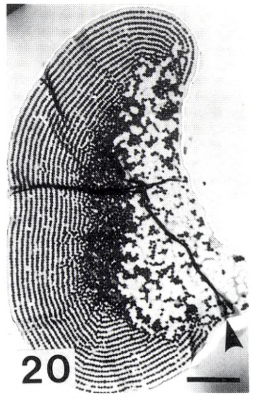
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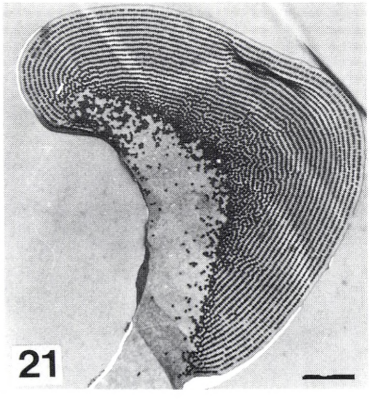
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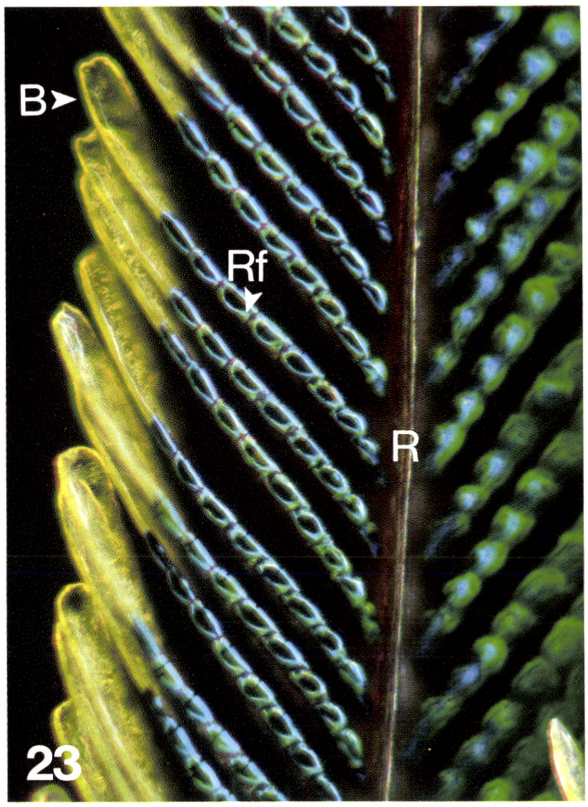
PLATE 5

Fig. 23. *Pt. rivoli*. Ramus with attached barbules (from above). Reflected light. Magnification: appr. × 265.

Fig. 24. *Ducula concinna*. Two rami with attached barbules (from above). Reflected light. Magnification as Fig. 23.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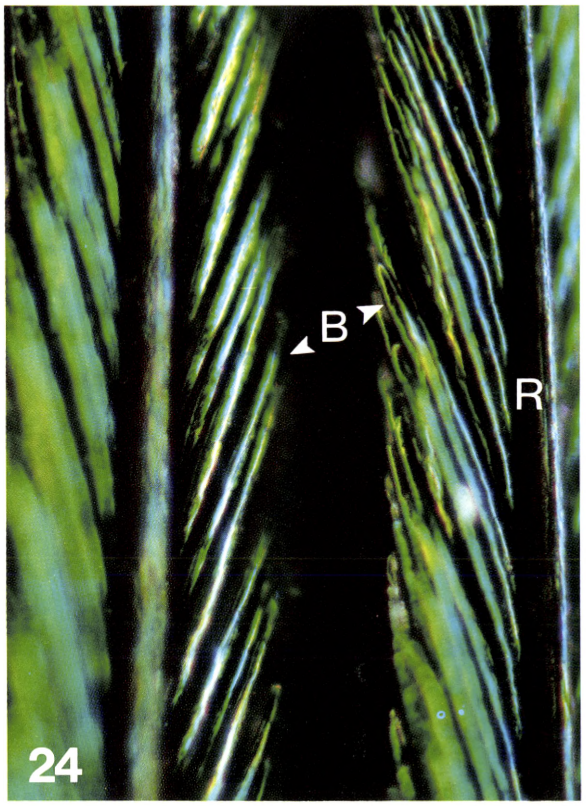
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