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A STUDY OF FEATHERPRINTS BY SCANNING ELECTRON MICROSCOPY

by

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SUMMARY

The surface of the rachis, rami and rachidial barbules of feathers of 109 species, belonging to 56 families and 17 orders, is investigated by means of the scanning electron microscope. Photographic illustrations, dealing with 18 species, demonstrating the wide diversity of featherprints, including micropapillae, fibrillary striations, pits and cell boundaries are presented.

Key Words : feather surface — featherprints — ultrastructure.

INTRODUCTION

Faced with identification problems when only a few feathers or parts of feathers are available, the ultrastructure of the feather surface was investigated.

On the rachis, the rami and the rachidial barbules of all investigated species a great diversity of ultrastructures was discovered. We call them featherprints. It became evident that these structures are interesting clues for purposes of identification.

The great diversity of structures found created first of all the need for a detailed enumeration and illustration with hypotheses about their possible function.

MATERIAL AND METHODS

Feathers were obtained from live birds, recently dead specimens and from museum collections. Whenever possible feathers from both sexes and also from juveniles and adults were collected.

Feathers from 14 different parts of the skin were used for intraspecific studies. These feathers include : tailfeathers, upper and under tail-coverts, primaries, upper

and under wing-coverts, feathers of the rump, the back, the nape, the crown, the throat, the breast, the belly and the flank.

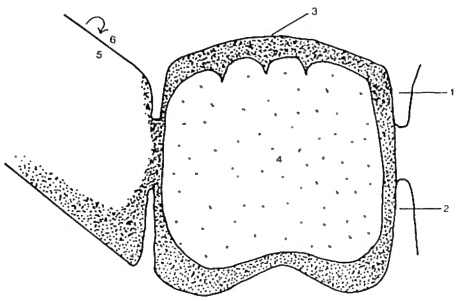


Fig. 1. — Cross section through a feather with obverso-lateral surface of the rachis (1), reverso-lateral surface of the rachis (2), obverse surface of the rachis (3), transverse section of the rachis (4), proximal surface of a ramus (5), distal surface of a ramus (6).

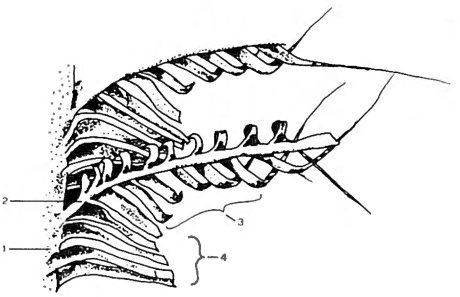


Fig. 2. — Position of the rachidial barbules with rachis (1), barb (2), barbules (3), rachidial barbules (4) (LUCAS and STETTENHEIM, 1972).

Nine different sites of a feather were examined with magnifications up to 20,000 × : I = reverso-lateral surface of the rachis below the rami ; II = reverso-lateral surface of the rachis between the rami ; III = proximal surface of a ramus below the barbules ; IV = distal surface of a ramus below the barbules ; V = reverse surface of the base of the rachidial barbules ; VI = obverso-lateral surface of the rachis between the rami ; VII = proximal surface of a ramus above the barbules ; VIII = distal surface of a ramus above the barbules ; IX = obverse surface of the rachis.

The nomenclature of feather parts corresponds to LUCAS and STETTENHEIM (1972) and the terminology of feather orientation to DYCK (1971a) (cfr. Fig. 1 and 2).

Only the ninth primary was used for interspecific comparisons because the featherprints turned out to be intraspecifically stable (PERREMANS, 1990).

A scanning electron microscope (SEM 515, Philips) was used, allowing continuous magnifications from 20 × up to 160,000 × at a resolution of 5 nm and a focal depth of 20 µm.

Prior to investigation the feathers were washed and degreased. Small pieces of rachis (± 1 cm) with cut-off barbs were used. The relevant parts were attached to specimen stubs by means of two-sided cellotape and coated with gold (30 nm) in a « High Vacuum Gold Sputter-Coater » (Balzers Union).

Feathers of 109 species belonging to 56 families and 17 orders were examined.

RESULTS

A great diversity of feather surface structures and markings was observed, appearing in most species in a unique combination.

Micropapillae were present in 45 species on the nine examined feather sites. They appeared in various shapes : short as in the Long-tailed Cormorant (*Phalacrocorax africanus* (GMELIN, 1789)) (Pl. 1, A), long as in the Shoebill (*Balaeniceps rex* GOULD, 1850)(Pl. 1, B) ; in various densities : a high density as in the Pink-backed Pelican (*Pelecanus rufescens* GMELIN, 1789) (Pl. 1, C), a low density as in the Grey Crowned Crane (*Balearica regulorum* (BENNETT, 1834)) (Pl. 1, D) and in various configurations as in the Swift (*Apus apus* (LINNAEUS, 1758)) (Pl. 1, E).

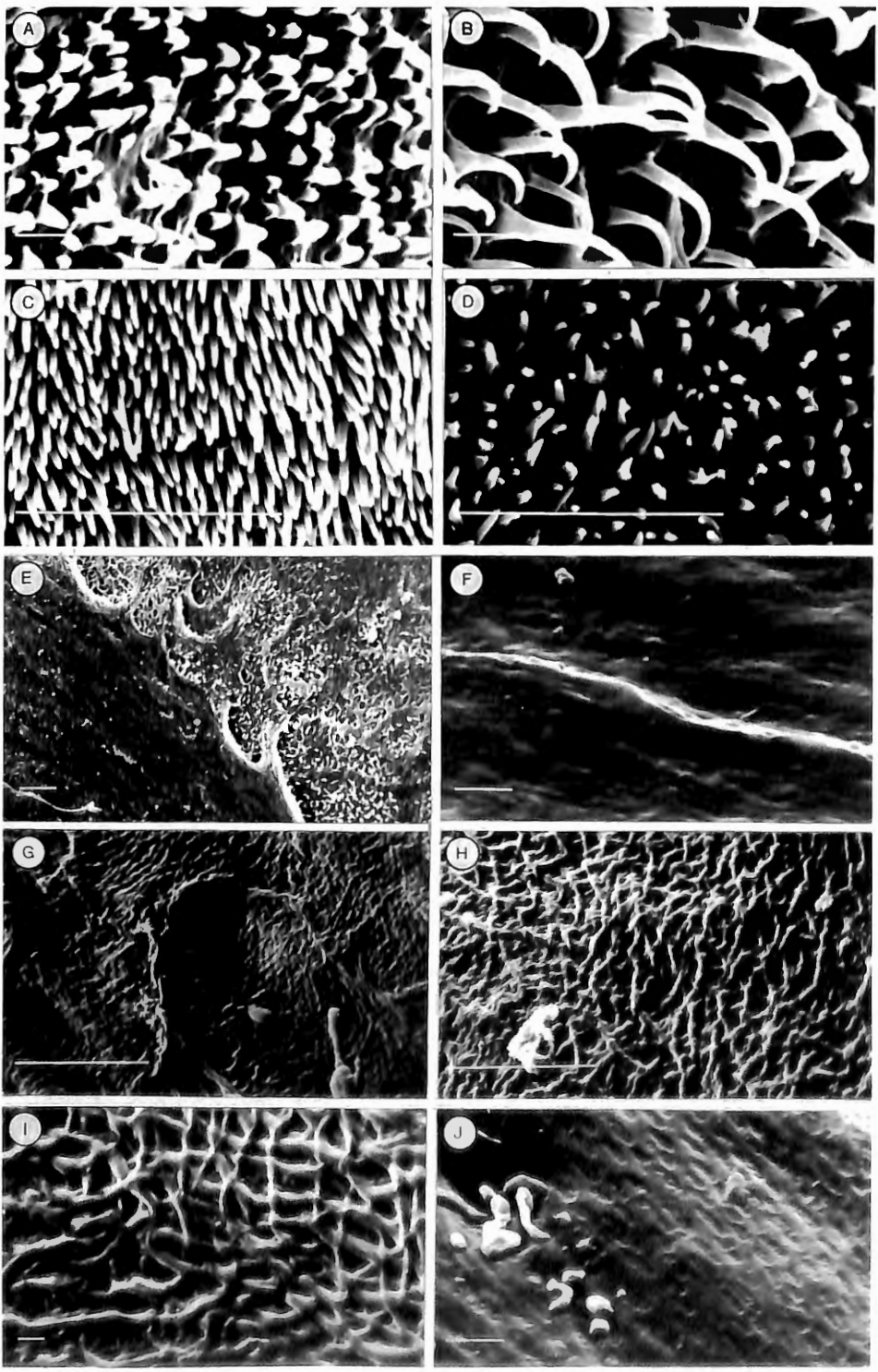
The surface of the rachis, the rami and the rachidial barbules varied also from relatively smooth to very roughly frayed as shown on Pl. 1, F to I : relatively smooth on the obverse surface of the rachis in the Great Tit (*Parus major* LINNAEUS, 1758) (F) ; finely frayed on the reverso-lateral surface of the rachis below the rami in the Robin (*Erithacus rubecula* (LINNAEUS, 1758)) (G) ; roughly frayed on the proximal surface of a ramus below the barbules in the Puffin (*Fratercula arctica* (LINNAEUS, 1758)) (H) ; very roughly frayed on the reverso-lateral surface of the rachis between the rami in the Moorhen (*Gallinula chloropus* (LINNAEUS, 1758)) (I). The surface could also be roughly frayed in the presence of a few micropapillae.

Another type of texture of the rachis included pits. Very small pits were found on the obverse surface of the rachis in the Woodpigeon (*Columba palumbus* LINNAEUS, 1758) (Pl. 1, J), deep pits on the same surface in the Puffin (*Fratercula arctica*) (Pl. 2, A), deep pits containing a core also on this surface in the Lesser Flamingo (*Phoenicopterus minor* GEOFFROY SAINT-HILAIRE, 1798) (Pl. 2, B), great deep pits on the reverso-lateral surface of the rachis below the rami in the Green Woodpecker (*Picus viridis* LINNAEUS, 1758) (Pl. 2, C) and a honey comb structure on the obverse surface of the rachis in the Vulturine Fish Eagle (*Gypohierax angolensis* (GMELIN, 1788)) (Pl. 2, D).

On all sites the surface showed cell boundaries. Five different types were distinguished (Pl. 2, E to I). They were found as fine, deep laying lines (type 1) on the proximal surface of a ramus below the barbules in the Gannet (*Sula bassana* (LINNAEUS, 1758)) (E), as fine, rising lines (type 2) on the distal surface of a ramus below the barbules in the Green-backed Heron (*Butorides striatus* (LINNAEUS, 1758)) (F), as thick, rising lines (type 3) on the reverso-lateral surface of the rachis below the rami in the Snipe (*Gallinago gallinago* (LINNAEUS, 1758)) (G), as incomplete cell boundaries (type 4) on the reverso-lateral surface of the rachis in the Collared Dove (*Streptopelia decaocto* (FRIVALDSZKY, 1838)) (H) and as very thick lines (type 5) on the reverso-lateral surface of the rachis below the rami in the Mallard (*Anas platyrhynchos* LINNAEUS, 1758) (I). The cell boundaries supposedly correspond to the cell borders of the original surface cells.

Cell walls could be protruding or flat. Protruding cell walls (Pl. 2, J) were found on the obverse surface of the rachis in the Gannet (*Sula bassana*). In a lot of

PLATE 1



specimens an oval depression, possibly corresponding to the original position of the nucleus of the cell, was found.

The structures on the lateral surface of the rachis and on the proximal and distal surface of the rami were in most cases more pronounced on the reverse part of the feather, although in some species they appeared with the same intensity on the obverse part. Usually the same structure was found at the proximal and distal surface of a ramus — close to the attachment of the ramus with the rachis — as on the corresponding lateral rachis surface. These structures became nearly always less and less distinct away from the attachment although in some species the rami showed no fading of the structures along the remaining barb piece. In still other species the structures on the rami surfaces differed from those observed on the lateral surface of the rachis.

The reverse surface of the base of the rachidial barbules may be frayed or may carry micropapillae. Such micropapillae have up to now only been found in the Rock Dove (feral form, *Columba livia* GMELIN, 1789), the Woodpigeon (*Columba palumbus*) and the Collared Dove (*Streptopelia decaocto*).

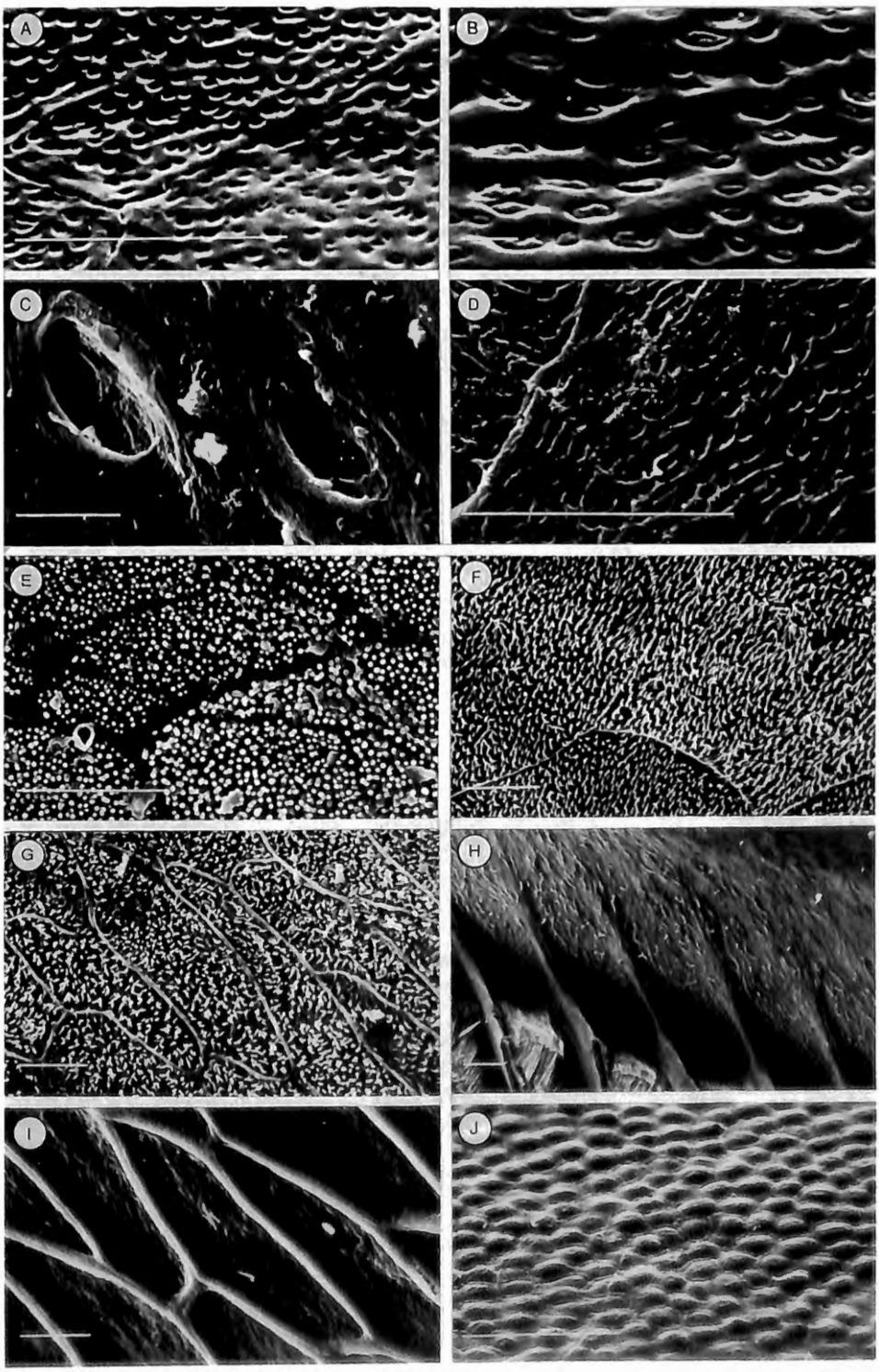
DISCUSSION

Rachis and rami of the developing feather are composed of two layers of cells : a thick inner core of spongy polygonal medulla cells and a thinner outer layer of compact amorphous cortex cells (STRONG, 1902, OLSON, 1970, LUCAS and STETTENHEIM, 1972, BLEIWEISS, 1987).

PLATE 1

Micropapillae in various shapes : A. Long-tailed Cormorant (*Phalacrocorax africanus*) : short micropapillae on the reverso-lateral surface of the rachis below the rami (bar = 1 µm). B. Shoebill (*Balaeniceps rex*) : long micropapillae on the reverso-lateral surface of the rachis between the rami (bar = 1 µm). **Micropapillae in various densities :** C. Pink-backed Pelican (*Pelecanus rufescens*) : micropapillae in a high density on the reverso-lateral surface of the rachis between the rami (bar = 10 µm). D. Grey Crowned Crane (*Balearica regulorum*) : micropapillae in a low density on the proximal surface of a ramus below the barbules (bar = 10 µm). **Micropapillae in various configurations :** E. Swift (*Apus apus*) : the reverso-lateral surface of the rachis below the rami (bar = 10 µm). **Frayed : relatively smooth :** F. Great Tit (*Parus major*) : the obverse surface of the rachis (bar = 1 µm). **Frayed : finely frayed :** G. Robin (*Erithacus rubecula*) : the reverso-lateral surface of the rachis below the rami (bar = 10 µm). **Frayed : roughly frayed :** H. Puffin (*Fratercula arctica*) : the proximal surface of a ramus below the barbules (bar = 10 µm). **Frayed : very roughly frayed :** I. Moorhen (*Gallinula chloropus*) : the reverso-lateral surface of the rachis between the rami (bar = 1 µm). **Pitted : very small pits :** J. Woodpigeon (*Columba palumbus*) : the obverse surface of the rachis (bar = 1 µm).

PLATE 2



A very thin layer, called the epitrichium, covering the cortex of the rami was mentioned by HAECKER (1890). Similarly DYCK (1971a, 1979) described a thin, dense epicuticle covering the surface of the rami and barbules. The cortex of the rachis and rami is further subdivided in two layers (CLÉMENT, 1876, AUBER and APPLEYARD, 1951, RUTSCHKE, 1966, DYCK, 1971a,b) :

1. The outer layer or surface layer consists of flattened polygonal cells. These cells form a pattern similar to some of the cuticular scale patterns found on mammalian hairs (AUBER and APPLEYARD, 1951, 1955). OLSON (1970) could not distinguish cells in the surface layer of any of his specimens under a light microscope. DYCK (1971a, 1973) concluded that it is very unlikely that acellular barb cortexes exist based on observations with the electron microscope.

2. The inner layer or cortex proper (AUBER and APPLEYARD, 1951) consists of cells that are longer and less flattened than the surface layer cells. They are spindle-shaped and show some similarity to the cortical cells in mammalian hair.

As long ago as in 1918 GLADSTONE observed a network of polygons on the tegmen of a primary from the Pink-footed Goose (*Anser brachyrhynchus*). The magnifications he used were too small to distinguish fine details. AUBER and APPLEYARD (1951) confirmed these observations and found a network of polygons arranged with their long axes parallel to the length of the barb, on the ventral surface of the barbs of Guinea fowl (*Numida sp.*), « Silky » fowl (*Gallus sp.*) and Green Honeycreeper (*Chlorophanes spiza*). They also mentioned the appearance of coarse striations and fibrillary structures. They suggested these patterns were formed by the superimposition of the fibrillary striation within the surface cells upon the parallel fibrillary striations of the cortex proper. DYCK (1973) concluded that the surface cells show structures that are formed by the cells themselves. Based on our observations we agree with his conclusions.

PLATE 2

Pitted : deep pits : A. Puffin (*Fratercula arctica*) : the obverse surface of the rachis (bar = 1 µm). **Pitted : deep pits containing a core :** B. Lesser Flamingo (*Phoenicopterus minor*) : the obverse surface of the rachis (bar = 1 µm). **Pitted : great deep pits :** C. Green Woodpecker (*Picus viridis*) : the reverso-lateral surface of the rachis below the rami (bar = 1 µm). **Pitted : honey comb structure :** D. Vulturine Fish Eagle (*Gypohierax angolensis*) : the obverse surface of the rachis (bar = 10 µm). **Type of cell boundary : type 1 = fine, deep laying lines :** E. Gannet (*Sula bassana*) : the reverso-lateral surface of the rachis below the rami (bar = 10 µm). **Type of cell boundary : type 2 = fine, rising lines :** F. Green-backed Heron (*Butorides striatus*) : the distal surface of a ramus below the barbules (bar = 10 µm). **Type of cell boundary : type 3 = thick, rising lines :** G. Snipe (*Gallinago gallinago*) : the reverso-lateral surface of the rachis below the rami (bar = 10 µm). **Type of cell boundary : type 4 = incomplete cell boundaries :** H. Collared Dove (*Streptopelia decaocto*) : the reverso-lateral surface of the rachis (bar = 10 µm). **Type of cell boundary : type 5 = very thick lines :** I. Mallard (*Anas platyrhynchos*) : the reverso-lateral surface of the rachis below the rami (bar = 10 µm). **Cell surface : protruding cell walls :** J. Gannet (*Sula bassana*) : the obverse surface of the rachis (bar = 100 µm).

The longitudinal fibrillary striation probably can be explained by the longitudinal orientation of the fibrillary proteins constituting the cell interior of the surface layer cells. The question remains how micropapillae, pits and honey comb structures are formed.

For the villi-like outgrowths of the rachis, the rami and the rachidial barbules the term micropapillae has been adopted from LYSTER (1985, unpublished report). The reason for this is that the term villi is in use already for the outgrowths on the bases of the basalmost downy barbules (CHANDLER, 1916, BROM, 1986, 1990). These basal outgrowths are considered not to be homologous to ours.

The function of these surface structures is still unclear. Probably they do not play a role in the modification of feather gloss because they were mainly found on the reverse parts of the feather. They seem too small for insulation purposes. Since they were found on the primaries and tail feathers as well as on the body contour feathers no cooperation in the flight function is supposed. A possible function (DYCK, pers. comm.) could be that they contribute to the creation of friction between different feathers.

Further analysis will give more information on the exact value of this set of characters for determination purposes and for avian taxonomy.

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