

MICROSCOPIC IDENTIFICATION OF FEATHERS AND FEATHER FRAGMENTS OF PALEARCTIC BIRDS

by

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ABSTRACT

Using light microscopy, a method has been developed for the identification of feathers and feather fragments collected after collisions between birds and aircraft. Characters of the downy barbules of feathers are described for 22 orders of birds. The use of a key in combination with the macroscopic method of comparing feathers with bird skins in a museum collection results in identification to order or family level in 97% of the analysed bird strikes. Application of the method to other fields of biological research including taxonomy is discussed.

RÉSUMÉ

Une méthode utilisant la microscopie optique a été mise à point pour l'identification des plumes et des fragments de plume collectés après des collisions entre oiseaux et avions. On décrit les caractères des barbules duveteuses des plumes pour 22 ordres d'oiseaux. L'utilisation d'une clé en même temps que la comparaison macroscopique des plumes avec des exemplaires de collections muséales, permet dans 97% des cas de collisions l'identification au niveau de l'ordre ou de la famille. On discute l'application de cette méthode à d'autres domaines de la recherche biologique, y compris la taxonomie.

INTRODUCTION

One of the first steps in solving the problem of collisions between birds and aircraft is establishing which bird species are most accident-prone. During many years, bird strike statistics were based on observations by pilots and ground personnel, and on the occurrence of dead birds found on airfields. Consequently, bird strike statistics were strongly biased by the presence of large and easily recognizable species (Buurma & Brom, 1979). These, however, do not necessarily constitute the highest risk. So if bird identification is extended beyond macroscopical examination, this would result in

a much better assessment of the problem and could suggest the most adequate preventive measures.

LaHam (1967) started the application of microscopic investigation of scrapings collected from engines, combined with the use of amino acid analysis of protein residues, and was able to diagnose bird strikes, so that defective engines rapidly could be separated into those due to either bird strikes or mechanical failures.

The microscopic structure of feathers was first studied by Chandler (1916). He described the structure of pennaceous feathers of North American birds, and found large differences between different taxa. He also examined the downy barbules of a few species and provided evidence that the structure of these barbules is of diagnostic and taxonomic value.

In the present study, the characters of the downy barbules of 350 palearctic species are described.* The results have been applied to the identification of feather fragments collected after collisions between birds and aircraft. About 1400 bird-aircraft incidents have been analysed, which allowed for a statistical evaluation of the groups of birds most often involved in bird strikes (Brom & Buurma, 1979, 1981; Buurma & Brom, 1980, 1981; Buurma, 1983; Brom, 1984; Buurma et al., 1984; for literature synopsis see Brom, 1986).

Feather identification is not only important in bird strike analysis, but it has shown to be useful in many areas of study: in forensic science as applied to criminology, food contaminations, and wildlife law enforcement

* A preliminary version of this paper was sent to interested colleagues in many countries (Brom, 1980).

(Davies, 1970; Deedrick & Mullery, 1981; Olsen, 1981; Robertson et al., 1984), in archeological work (Hargrave, 1965; Messinger, 1965; Bennike & Dyck, 1986), and in ecological studies on feeding habits of carnivorous animals (Day, 1966; Altenburg et al., 1982; Astier, 1982; Gilbert & Nancekivell, 1982).

MATERIAL AND METHODS

Material

The examined feathers were taken from freshly dead birds and from specimens in the skin collection of the Zoölogisch Museum Amsterdam (ZMA). No differences in feather structures proved to exist when fresh feathers were compared with feathers from bird skins that had been preserved for many years.

Methods

The characters examined in this study are found at the downy base (*pars plumea*) of the contour feathers of a bird (fig. 1). When making preparations, only this part is taken: the downy barbs are cut off close to the shaft of the feather and are sandwiched between an object glass and a cover slip, which are glued together along the edges. This technique is simple and not time-consuming. After initial experiments with embedding substances, mounting the feathers dry under the cover slip turned out to be most appropriate. More contrast is obtained than with the employment of embedding substances which have unsuitable refractive indices.

Dirty or greasy feathers are washed in warm water to which a mild soap or detergent has been added. Then they are rinsed several times in clear water to remove the soap and dried with a hair dryer. Dirty or twisted feathers can usually be restored to their original shape by this procedure. Different feathers require somewhat different techniques of drying. Feathers with long and lax barbules (such as those of owls and other birds of prey) are more difficult to blow out as their tips tend to become tangled, whereas feathers from birds like waterfowl fluff up readily.

The feather structures were studied by light microscopy using magnifications between 50 and 500 ×.

DESCRIPTION OF CHARACTERS

A feather is composed of three elements: the axis, the barbs, and the barbules. The proximal part of a feather, the calamus, is fixed in the skin of the bird. From the distal part, called the shaft or rachis, barbs are branching off on both

sides to form the outer and inner vanes. From these barbs, barbules are branching off to form the outer and inner vanules. The basal part of the vanes is more (in body feathers) or less (in flight feathers) downy in character.

The downy barbules consist of a base and a pennulum, and it is here that we find the features on which many taxa of birds, sometimes down to species level, can be distinguished. The following characters are used in identification:

1. The borders of the cells forming the pennulae are often swollen or show prongs. In this way, the barbules are divided into nodes and internodes, clearly visible at lower magnifications. Nodes vary in shape from round to heart-shaped to elongated and may be more or less strongly pigmented. Prongs vary in length and curvature. Collectively nodes and prongs are called nodal structures.
2. Nodal structures may be uniformly distributed along the entire length of the barbule or found only at its base or tip.
3. The basal cells by which the barbules are attached to the barbs may show villi (outgrowths).
4. The length of the barbules as well as the number of nodal structures per mm are distinctive for certain groups. Whenever possible, the nodal structures have been counted (at magnification of 50 ×) and their number per mm of barbule is given.

The intraspecific variability of these characters was examined before differences between higher taxa of birds were described.

- a. Topical variation: Of five species (Black-headed Gull *Larus ridibundus*, Lapwing *Vanellus vanellus*, Oystercatcher *Haematopus ostralegus*, Chaffinch *Fringilla coelebs*, and Skylark *Alauda arvensis*) an extensive series of feather preparations (taken from 26 different feathers from each specimen) was examined in order to determine the variation within an individual plumage. Considerable differences proved to exist in degree of pigmentation, number of nodal structures per mm of barbule, and length of the barbules. The

following feather regions have been found to cover the whole range of variation within one bird: breast, belly, under tail coverts, upper tail coverts, mantle, and upper wing coverts. In case of a bird strike it is usually not known from which part of the bird a feather originates. So, in the tables only ranges are given (instead of averages) for number of nodes per mm and for length of barbule. In all species a feather was studied from each of the six regions mentioned above. From each feather at least 5 barbules were measured and counted for nodal structures, so the given ranges result from about 30 measurements and counts for each species.

- b. Individual variation: Feathers from two individuals of the same species have been compared to establish the degree of individual variation. This was done for Black-headed Gull *Larus ridibundus*, Goosander *Mergus merganser*, Swift *Apus apus*, and Secretary Bird *Sagittarius serpentarius*. No intraspecific variation was found.
- c. Sexual variation: In two species (Lapwing *Vanellus vanellus* and Red-footed Falcon *Falco vespertinus*) feathers from both sexes have been compared. Even in the highly dimorphic Red-footed Falcon no differences were found.
- d. Variation with age and time of the year: Barbules from juvenile and adult plumage were compared for Goshawk *Accipiter gentilis*, Black-headed Gull *Larus ridibundus*, Meadow Pipit *Anthus pratensis*, and Greenfinch *Carduelis chloris*. Nestlings and fledglings differ from older birds because the downy barbules, if present, are simple and not fully developed. In a fully developed juvenile plumage, however, the size and structure of the downy barbules is indistinguishable from the adult.
- No variation with the time of the year was found. As the examined barbules are the most basal ones of the feather, located close to the skin, they are not as much subject to wear as is the plumage in general.

DESCRIPTION OF ORDERS

The description of bird species follows the taxonomic sequence as given by Voous (1973, 1977).

In addition to a description of the structure of their downy barbules, information on the weights of the different species has been included, as weight is a key factor in the analysis of bird strikes (Buurma, 1984). This information was mainly taken from Cramp & Simmons (1977, 1980, 1983), Brough (1983), and Cramp (1985), and from collection files in the Zoölogisch Museum Amsterdam.

1. GAVIIFORMES (fig. 2; table I)

This order consists of a single family (Gaviidae). All species have been examined. Range of weights 800-6400 g.

Description. — The barbules are extremely short (0.5-1.1 mm). At low magnification they appear filamentous, not pigmented. They possess prongs, most conspicuously at their tips. A subdivision of the barbules is perceptible, but no enlarged nodes are present. No villi at the basal cells.

TABLE I

Body weight (in g) and length of barbules (in mm) in Gaviiformes.

Species		body weight	barbule length
<i>Gavia stellata</i>	Red-throated Diver	800-2460	0.5-0.9
<i>G. arctica</i>	Black-throated Diver	1200-3792	0.5-1.0
<i>G. immer</i>	Great Northern Diver	2200-4480	0.7-1.1
<i>G. adamsii</i>	White-billed Diver	3700-6400	0.8-1.1

2. PODICIPEDIFORMES (fig. 3; table II)

This order consists of a single family (Podicipedidae). Five species have been examined. Range of weights 91-1490 g.

Description. — The barbules are on average longer (0.7-1.7 mm) than in Gaviiformes.



Fig. 1. Position of the downy barbules that are described in this paper: 1 = shaft or rachis, 2 = calamus, 3 = vane, 4 = downy part of feather (pars plumea), 5 = barb, 6 = barbule.

Fig. 2. Black-throated Diver *Gavia arctica*; breast feather (105 ×).

Fig. 3. Black-necked Grebe *Podiceps nigricollis*; belly feather (165 ×).

Fig. 4. Cory's Shearwater *Calonectris diomedea*; mantle feather (105 ×).

Fig. 5. Leach's Storm Petrel *Oceanodroma leucorhoa*; mantle feather (105 ×).

Fig. 6. Great Cormorant *Phalacrocorax carbo*; upper tail covert (105 ×).

Prongs are always present at the tips and in this respect grebes may resemble Anseriformes, but triangular nodes are not present. Proximally, a subdivision of the barbules is perceptible, usually indicated by prongs present at only one side of the barbule, but nodes cannot be counted. No villi at the basal cells.

3. PROCELLARIIFORMES (figs. 4-5; table III)

Five species from two families (Procellariidae and Hydrobatidae) have been examined. Range of weights 18-1130 g.

Description. — The barbules are extremely short (0.5-1.1 mm), and a subdivision into

TABLE II

Body weight (in g) and length of barbules (in mm) in Podicipediformes.

Species		body weight	barbule length
<i>Tachybaptus ruficollis</i>	Little Grebe	91-315	0.7-1.3
<i>Podiceps cristatus</i>	Great Crested Grebe	492-1490	0.7-1.5
<i>P. grisegena</i>	Red-necked Grebe	316-1270	0.7-1.4
<i>P. auritus</i>	Slavonian Grebe	300-500	0.7-1.6
<i>P. nigricollis</i>	Black-necked Grebe	213-450	0.7-1.7

slightly swollen nodes or well-developed prongs (21-29 per mm) and internodes is easily perceptible. Usually the nodes are not pigmented, except in *Oceanodroma leucorhoa* and often in *Hydrobates pelagicus*. No villi at the basal cells.

TABLE III

Body weight (in g), length of barbules (in mm), and number of nodal structures (per mm barbule) in Procellariiformes.

Species		body weight	barbule length	N of nodes
<i>Fulmarus glacialis</i>	Northern Fulmar	535-1000	0.7-1.1	25-29
<i>Calonectris diomedea</i>	Cory's Shearwater	500-1130	0.6-1.0	21-26
<i>Puffinus puffinus</i>	Manx Shearwater	310-565	0.6-1.0	22-27
<i>Hydrobates pelagicus</i>	Storm Petrel	18-40	0.5-1.1	24-29
<i>Oceanodroma leucorhoa</i>	Leach's Storm Petrel	29-57	0.5-1.0	23-27

4. PELECANIFORMES (figs. 6-7; table IV)

Six species from five families (Phaethontidae, Sulidae, Phalacrocoracidae, Pelecanidae, and Fregatidae) have been examined. Range of weights 427-13000 g.

Description. — The barbules are short (0.5-1.5 mm) and smoothly filamentous for most of their length. No villi at the basal cells. In pigmentation of the pennulae and in length of the prongs some variation exists within this order.

Pelecanidae and Fregatidae: The barbules are not pigmented and no swollen nodes are found. At the tips there are minute prongs which sometimes extend along the whole length of the barbule.

Phalacrocoracidae: The barbules are usually not pigmented; sometimes a diffuse pigmentation is visible which gives the impression of a subdivision of the barbules, but nodal structures could not be counted. At the tips there are always some minute prongs, which often are only perceptible at higher magnifications; occasionally the prongs extend along the entire length of the barbule.

Sulidae: The barbules are not pigmented, but they possess many very well-developed prongs along their entire length. These prongs reach a length of over 0.1 mm and they are always longer than the adjacent internodes. They are slender, filamentous, and frequently bifurcated, and they only slightly decrease in length towards the tips of the barbules.

Phaethontidae: The barbules are not pigmented and possess short prongs along their entire length (21-25 per mm).

TABLE IV

Body weight (in g) and length of barbules (in mm) in Pelecaniformes.

Species		body weight	barbule length
<i>Phaethon aethereus</i>	Red-billed Tropicbird	427-730	0.6-1.0
<i>Sula bassana</i>	Northern Gannet	1630-3610	0.5-1.0
<i>Phalacrocorax carbo</i>	Great Cormorant	1500-4900	0.7-1.2
<i>P. aristotelis</i>	Shag	1470-2154	0.6-1.2
<i>Pelecanus conspicillatus</i>	Australian Pelican	4000-13000	0.7-1.3
<i>Fregata magnificens</i>	Magnificent Frigatebird	1061-1750	0.9-1.5

5. CICONIIFORMES (figs. 8-10; table V)

Thirteen species from three families (Ardeidae, Ciconiidae, and Threskiornithidae) have been examined. Range of weights 64-5000 g.

Description. — The barbules vary in length from 0.8 to 3.0 mm. Some differences exist between the families examined, in the length of the barbules, degree of pigmentation, presence of prongs, and number of nodal structures per mm. No villi at the basal cells.

Ciconiidae: The barbules are rather long (1.2-2.5 mm), slender, filamentous and not pigmented. Usually there are small, inconspicuous prongs along the entire length of the barbule (11-14 per mm), which are fewer in number than in both other families.

Ardeidae: The barbules are rather long (1.1-3.0 mm), very slender, filamentous, with slightly enlarged nodal structures which can often be counted. In *Bubulcus*, *Ardeola*, *Egretta*, and *Nycticorax* the barbules are not pigmented, and some minute prongs can be found. In *Ardea*, *Botaurus*, and *Ixobrychus* the barbules may be uniformly (or almost uniformly) pigmented (pigment not collected into conspicuous spots) or not pigmented, with minute prongs usually present only distally.

TABLE V

Body weight (in g) and length of barbules (in mm) in Ciconiiformes.

Species		body weight	barbule length
<i>Botaurus stellaris</i>	Bittern	430-1940	1.3-2.0
<i>Ixobrychus minutus</i>	Little Bittern	64-170	1.6-2.1
<i>Nycticorax nycticorax</i>	Night Heron	339-1014	1.2-2.1
<i>Ardeola ralloides</i>	Squacco Heron	180-370	1.1-2.2
<i>Bubulcus ibis</i>	Cattle Egret	300-450	1.3-2.4
<i>Egretta garzetta</i>	Little Egret	280-614	1.1-1.9
<i>E. alba</i>	Great White Egret	760-1680	1.2-3.0
<i>Ardea cinerea</i>	Grey Heron	810-2300	1.2-2.5
<i>A. purpurea</i>	Purple Heron	515-1650	1.2-2.5
<i>Ciconia nigra</i>	Black Stork	2400-3000	1.2-2.1
<i>C. ciconia</i>	White Stork	2140-5000	1.3-2.5
<i>Plegadis falcinellus</i>	Glossy Ibis	365-850	0.8-1.2
<i>Platalea leucorodia</i>	Spoonbill	795-1960	0.9-1.3

Threskiornithidae: The barbules are shorter than in both other families (0.8-1.3 mm), stout and coarse, and they are not pigmented. Along their entire length the barbules possess well-developed prongs (19-23 per mm in *Platalea* and 21-26 in *Plegadis*), which are always shorter than the adjacent internodes. The nodal structures

are more numerous per mm than in both other families.

6. PHOENICOPTERIFORMES (fig. 11)

This order consists of a single family (Phoenicopteridae). Two species have been examined: Greater Flamingo *Phoenicopterus ruber* and Lesser Flamingo *P. minor*. Range of weights 1412-4400 g.

Description. — The barbules are very short (0.5-1.2 mm) and not pigmented. Along their entire length small sprongs are found (22-27 per mm), that are slightly longer than in Ciconiiformes. Only distally some slightly enlarged nodes may be present. No villi at the basal cells.

7. ANSERIFORMES (figs. 12-14; table VI)

Thirty-eight species of the family Anatidae have been examined. Range of weights 163-15000 g.

Description. — The barbules are rather short (0.5-2.0 mm, but usually less than 1.3 mm) and simple in structure. For the greater part of their length they are thread-like. The nodes are undeveloped except at the distal part of the barbule where a number of triangular (but visible as heart-shaped under the microscope) nodes are found, followed by a slender tip. The number of terminal nodes may differ considerably (from 1 to 10) in different genera, but no diagnostic value resides in this character as large differences can be found between feathers of a single bird. The nodes may sometimes be reduced and in that case a few terminal pairs of prongs are taking their place. Pigmentation of the barbules is confined to the nodes and varies in density from species to species. The internodes are long (longer in geese than in ducks) and often show a conspicuous bending or kinking, usually most pronounced in geese. No significant differences are found in the length of the barbules of the various species. However, three large groups can be distinguished when the part of the barbule is measured that shows nodal structures.

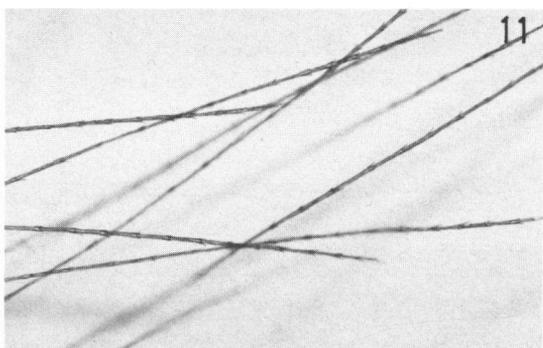
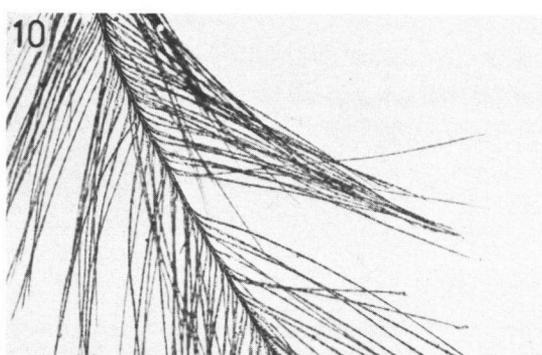
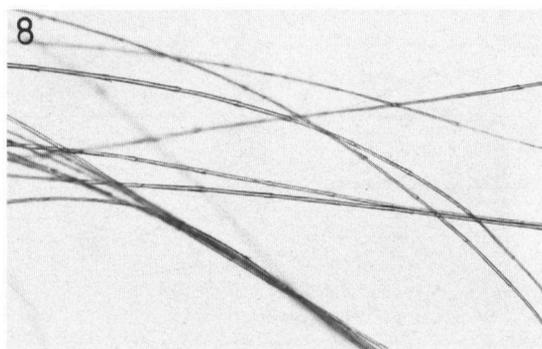


Fig. 7. Northern Gannet *Sula bassana*; throat feather (105 ×).

Fig. 8. White Stork *Ciconia ciconia*; under tail covert (105 ×).

Fig. 9. Bittern *Botaurus stellaris*; under wing covert (42 ×).

Fig. 10. Spoonbill *Platalea leucorodia*; upper wing covert (42 ×).

Fig. 11. Greater Flamingo *Phoenicopterus ruber*; breast feather (105 ×).

Fig. 12. Pochard *Aythya ferina*; belly feather (105 ×). Heart-shaped nodes at the tips of the barbules.

The barbules of ducks show nodal arrangement for 10-35% of their length, those of geese for 30-70%, and those of swans for 55-85%. Only the Shelducks (genus *Tadorna*) form an intermediate group with 23-44%. No villi at the basal cells.

8. ACCIPITRIFORMES (figs. 15-16; table VII)

This order of birds of prey consists of two families (Accipitridae and Pandionidae). Seventeen species have been examined. Range of weights 103-7500 g.

TABLE VI

Body weight (in g) and length of barbules (in mm)
in Anseriformes.

Species		body weight	barbule length
<i>Cygnus olor</i>	Mute Swan	5500-15000	0.8-1.1
<i>C. columbianus</i>	Bewick's Swan	3300-9600	0.7-1.1
<i>C. cygnus</i>	Whooper Swan	7000-14000	0.7-1.1
<i>Anser fabalis</i>	Bean Goose	1500-4300	0.7-1.2
<i>A. brachyrhynchus</i>	Pink-footed Goose	1410-3350	0.7-1.4
<i>A. albifrons</i>	White-fronted Goose	1150-3340	0.6-1.4
<i>A. erythropus</i>	Lesser White-fronted Goose	1310-2500	0.7-1.1
<i>A. anser</i>	Greylag Goose	1980-4560	0.6-1.1
<i>A. indicus</i>	Bar-headed Goose	2000-3200	0.7-1.3
<i>Branta canadensis</i>	Canada Goose	1100-7570	0.8-1.3
<i>B. leucopsis</i>	Barnacle Goose	1020-2650	0.9-2.0
<i>B. bernicla</i>	Brent Goose	850-2220	0.6-1.1
<i>B. ruficollis</i>	Red-breasted Goose	1000-1625	0.7-1.5
<i>Tadorna ferruginea</i>	Ruddy Shelduck	925-1600	0.6-1.5
<i>T. tadorna</i>	Shelduck	500-1650	0.6-1.3
<i>Aix galericulata</i>	Mandarin Duck	428-725	0.8-1.7
<i>Anas penelope</i>	Wigeon	400-1090	0.6-1.8
<i>A. strepera</i>	Gadwall	470-1300	0.5-1.2
<i>A. crecca</i>	Teal	163-500	0.7-1.7
<i>A. platyrhynchos</i>	Mallard	500-1800	0.7-2.0
<i>A. acuta</i>	Pintail	400-1444	0.7-1.1
<i>A. querquedula</i>	Garganey	250-600	0.6-1.1
<i>A. discors</i>	Blue-winged Teal	188-590	0.7-1.4
<i>A. clypeata</i>	Shoveler	300-1100	0.6-1.1
<i>Netta rufina</i>	Red-crested Pochard	694-1550	0.6-1.6
<i>Aythya ferina</i>	Pochard	467-1300	0.7-1.2
<i>A. nyroca</i>	Ferruginous Duck	400-740	0.6-1.1
<i>A. fuligula</i>	Tufted Duck	335-1400	0.6-1.0
<i>A. marila</i>	Scaup	690-1372	0.6-1.1
<i>Somateria mollissima</i>	Eider	1150-2900	0.5-0.9
<i>Clangula hyemalis</i>	Long-tailed Duck	453-955	0.5-0.8
<i>Melanitta nigra</i>	Common Scoter	600-1610	0.5-1.3
<i>M. fusca</i>	Velvet Scoter	850-2104	0.5-0.8
<i>Bucephala clangula</i>	Goldeneye	496-1400	0.7-1.2
<i>Mergus albellus</i>	Smew	500-950	0.5-0.9
<i>M. serrator</i>	Red-breasted Merganser	644-1360	0.5-1.2
<i>M. merganser</i>	Goosander	860-2160	0.8-1.6
<i>Oxyura leucocephala</i>	White-headed Duck	400-900	0.7-1.1

Description. — The barbules are very long and slender (1.0-5.8 mm), and not pigmented (only in the Bateleur *Terathopius ecaudatus* heavily pigmented barbules are found). A subdivision of the barbules is often hardly perceptible, as the nodes are only very slightly enlarged (10-20 per mm). They possess short prongs, which are asymmetrical in most cases. These prongs occur sometimes along the entire length

of the barbule, sometimes at the tips only, but usually only at the bases. Counting the nodes or prongs is usually difficult and sometimes impossible at magnifications up to 200×. No villi at the basal cells.

TABLE VII

Body weight (in g) and length of barbules (in mm) in Accipitriformes.

Species		body weight	barbule length
<i>Pernis apivorus</i>	Honey Buzzard	360-1490	2.5-5.8
<i>Milvus migrans</i>	Black Kite	500-1186	2.0-3.6
<i>M. milvus</i>	Red Kite	757-1600	1.8-3.0
<i>Haliaeetus albicilla</i>	White-tailed Eagle	3019-7500	1.8-4.1
<i>Terathopius ecaudatus</i>	Bateleur	1820-2950	1.8-2.1
<i>Circus aeruginosus</i>	Marsh Harrier	320-1370	2.3-3.7
<i>C. cyaneus</i>	Hen Harrier	200-740	2.4-4.0
<i>C. macrourus</i>	Pallid Harrier	235-604	2.3-3.4
<i>C. pygargus</i>	Montagu's Harrier	227-445	2.3-3.1
<i>Melierax metabates</i>	Dark Chanting Goshawk	488-852	1.5-2.2
<i>Accipiter gentilis</i>	Goshawk	517-2054	1.9-4.8
<i>A. nisus</i>	Sparrowhawk	103-346	1.8-3.8
<i>Buteo buteo</i>	Buzzard	427-1364	1.8-4.1
<i>B. lagopus</i>	Rough-legged Buzzard	600-1660	1.9-3.4
<i>Aquila rapax</i>	Steppe Eagle	1572-4850	2.4-3.8
<i>A. chrysaetos</i>	Golden Eagle	2840-6665	2.0-3.5
<i>Pandion haliaetus</i>	Osprey	1120-2050	1.0-1.7

9. FALCONIFORMES (figs. 17-18; table VIII)

Nine species of the family Falconidae have been examined. Range of weights 90-2100 g.

Description. — The barbules are rather long (1.1-3.4 mm) and always clearly divided along their entire length into slightly enlarged and heavily pigmented nodes, and very slender and wavy internodes. In this they are completely different from the Accipitriformes. The number of nodes can always be counted and varies from 11 to 24. Larger birds tend to possess longer barbules with fewer nodes per mm than smaller birds, but the differences are too small to be diagnostic. No prongs are found in this group

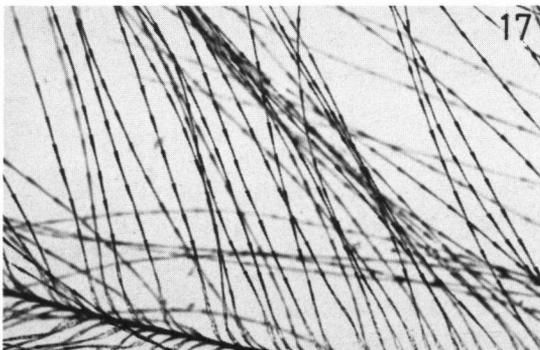
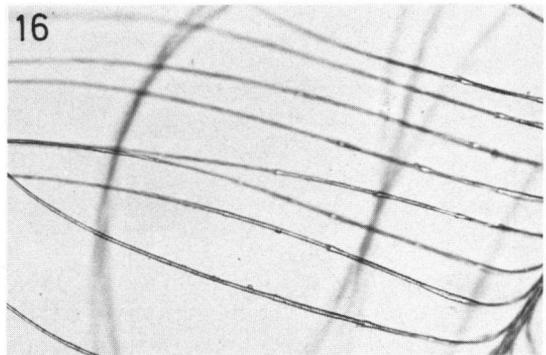
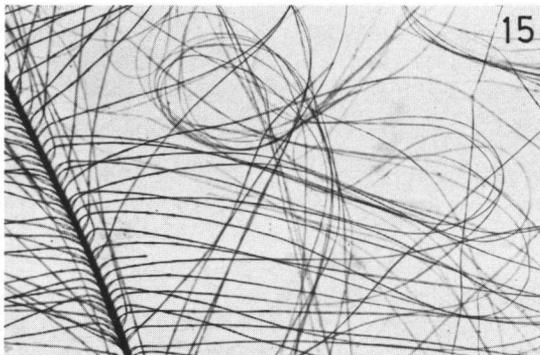
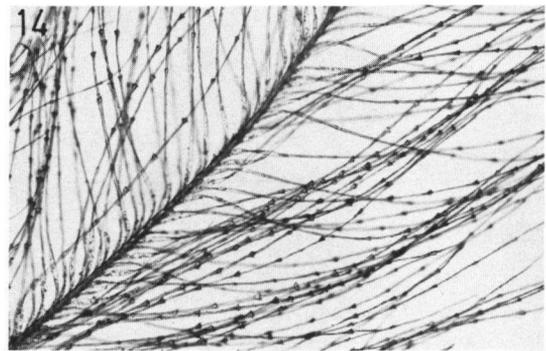
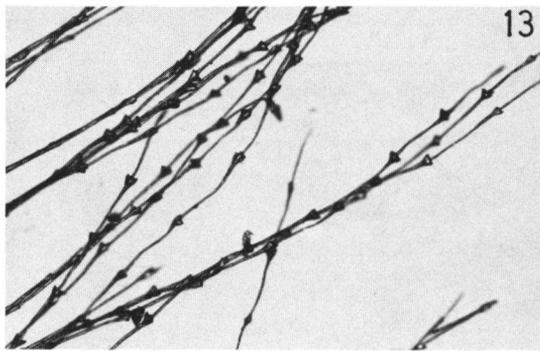


Fig. 13. Barnacle Goose *Branta leucopsis*; back feather (105 ×). Barbules show characteristic kinking.

Fig. 14. Whooper Swan *Cygnus cygnus*; neck feather (105 ×).

Fig. 15. Goshawk *Accipiter gentilis*; upper wing covert (42 ×).

Fig. 16. Buzzard *Buteo buteo*; breast feather (130 ×).

Fig. 17. Hobby *Falco subbuteo*; breast feather (85 ×).

Fig. 18. Red-footed Falcon *Falco vespertinus*; breast feather (85 ×).

(at magnifications up to 200 ×). No villi at the basal cells.

10. GALLIFORMES (figs. 19-20; table IX)

Thirteen species from two families (Tetraonidae and Phasianidae) have been examined. Range of weights 52-6500 g.

Description. — The barbules are very long (1.6-5.5 mm) and they are always clearly divided along their entire length into pigmented nodes and filamentous internodes. At their proximal part the barbules possess poorly developed nodes, which, however, soon increase in width and develop a typical ring-like shape. Frequently, some of these rings become

TABLE VIII

Body weight (in g), length of barbules (in mm), and number of nodes (per mm barbule) in Falconiformes.

Species		body weight	barbule length	N of nodes
<i>Falco naumanni</i>	Lesser Kestrel	90-208	1.2-2.1	13-22
<i>F. tinnunculus</i>	Kestrel	113-314	1.2-2.6	13-24
<i>F. sparverius</i>	American Kestrel	95-130	1.1-2.5	13-23
<i>F. vespertinus</i>	Red-footed Falcon	130-197	1.4-2.4	13-23
<i>F. columbarius</i>	Merlin	125-300	1.4-2.6	14-23
<i>F. subbuteo</i>	Hobby	131-340	1.3-2.7	14-21
<i>F. eleonora</i>	Eleonora's Falcon	270-510	1.4-2.6	13-18
<i>F. rusticolus</i>	Gyr Falcon	800-2100	1.5-3.4	11-17
<i>F. peregrinus</i>	Peregrine	330-1333	1.8-3.0	12-19

detached and slide along the slender internodes like rings on a wire, breaking up into groups of 2-10 (multiple nodes; fig. 20). Toward the tips of the barbules, the ring-like structure is again lost, and the nodes become simply swollen. Larger birds tend to have longer barbules and fewer nodes per mm. Multiple nodes are not always present in great numbers and may be difficult to find. No villi at the basal cells.

TABLE IX

Body weight (in g), length of barbules (in mm), and number of nodes (per mm barbule) in Galliformes (multiple nodes not included).

Species		body weight	barbule length	N of nodes
<i>Bonasa bonasia</i>	Hazel Grouse	278-500	1.8-3.2	20-28
<i>Lagopus lagopus</i>	Willow/Red Grouse	400-908	1.7-3.3	20-29
<i>L. mutus</i>	Ptarmigan	243-610	2.0-3.9	14-26
<i>Tetrao tetrix</i>	Black Grouse	615-1750	2.8-3.8	13-24
<i>T. urogallus</i>	Capercaillie	1370-6500	2.2-5.5	15-26
<i>Callipepla californica</i>	California Quail	130-207	1.7-3.0	20-34
<i>Alectoris chukar</i>	Chukar	365-595	2.3-3.6	18-27
<i>A. rufa</i>	Red-legged Partridge	240-547	1.9-3.0	23-31
<i>Francolinus francolinus</i>	Black Francolin	227-570	2.5-3.3	22-28
<i>Perdix perdix</i>	Partridge	310-480	2.1-4.0	22-30
<i>Coturnix coturnix</i>	Quail	52-155	1.8-2.6	25-35
<i>C. japonica</i>	Japanese Quail	—	1.6-2.4	25-35
<i>Phasianus colchicus</i>	Pheasant	500-2015	2.5-4.1	15-23

11. GRUIFORMES (figs. 21-23; table X)

Fifteen species from five families (Turnicidae, Rallidae, Aramididae, Gruidae, and Otidae) have been examined. Range of weights 28-18000 g.

Description. — The barbules vary from extremely short (0.4 mm) to extremely long (5.9 mm). Large differences exist between the families that were studied. In none of them villi are present at the basal cells.

Turnicidae: The barbules are short (0.6-1.3 mm) and subdivided along their entire length by pigmented, but hardly enlarged nodes (23-29 per mm, difficult to count).

Rallidae: The barbules are rather short (0.4-1.7 mm) and subdivided into heavily pigmented nodes (15-32 per mm) and short internodes. The pigment is mainly present in the nodes and the distal part of the internodes. The minute prongs at the nodes and the proximal part of the internodes are more or less unpigmented. Towards the base of the barbules usually 2-4 nodes are enlarged, whereas further along the barbule and in the tip region they are only slightly swollen and often difficult to

TABLE X

Body weight (in g), length of barbules (in mm), and number of nodes (per mm barbule) in Gruiformes.

Species		body weight	barbule length	N of nodes
<i>Turnix sylvatica</i>	Andalusian Hemipode	29-70	0.6-1.3	23-29
<i>Rallus aquaticus</i>	Water Rail	74-190	0.6-1.1	26-32
<i>Porzana porzana</i>	Spotted Crane	47-147	0.5-1.3	22-28
<i>P. parva</i>	Little Crane	30-72	0.5-1.2	25-30
<i>P. pusilla</i>	Baillon's Crane	28-60	0.5-1.2	26-30
<i>Crex crex</i>	Corn Crane	95-210	0.5-1.4	22-29
<i>Gallinula chloropus</i>	Moorhen	140-493	0.7-1.5	19-29
<i>Porphyrio porphyrio</i>	Purple Coot	325-1000	0.6-1.7	15-19
<i>Gallinula cinerea</i>	Watercock	200-510	0.4-1.3	21-26
<i>Fulica atra</i>	Coot	300-1460	0.6-1.4	18-24
<i>Grus grus</i>	Common Crane	3000-7000	1.0-2.2	—
<i>Anthropoides virgo</i>	Demoiselle Crane	1985-3060	0.8-2.2	—
<i>Tetrax tetrax</i>	Little Bustard	525-1000	1.7-3.8	—
<i>Chlamydotis undulata</i>	Houbara	1100-1375	1.9-4.9	—
<i>Otis tarda</i>	Great Bustard	3200-18000	2.0-5.9	—

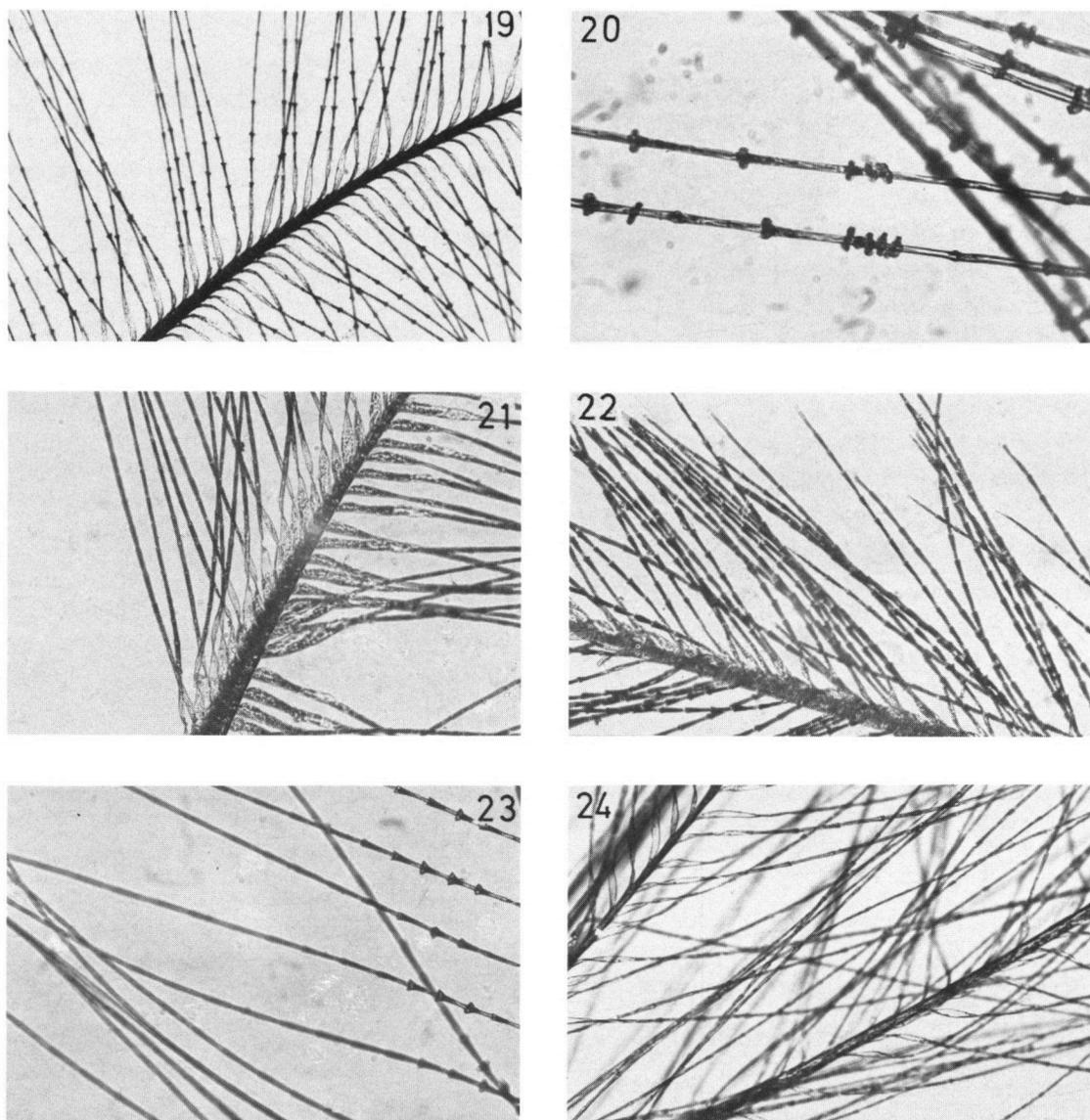


Fig. 19. Black Grouse *Tetrao tetrix*; breast feather (85 ×).

Fig. 20. Black Grouse *Tetrao tetrix*; breast feather (325 ×). Barbules with multiple nodes

Fig. 21. Andalusian Hemipode *Turnix sylvatica*; breast feather (105 ×).

Fig. 22. Spotted Crake *Porzana porzana*; under tail covert (105 ×).

Fig. 23. Watercock *Gallicrex cinerea*; breast feather (105 ×).

Fig. 24. Oystercatcher *Haematopus ostralegus*; thigh feather (130 ×).

count. This reduction in the size of the nodes takes place quite abruptly over a distance of 1-3 internodes and is always more pronounced in one of both vanules. Larger birds tend to have fewer nodes per mm than smaller birds.

Gruidae: The barbules are of medium length (0.8-2.2 mm), not pigmented, and have the

form of almost unmodified threads, which, however, at higher magnification (200 ×) show minute prongs at the nodes; two of a pair of prongs are usually of unequal size. The small nodes and prongs cannot be counted.

Otididae: The barbules are extremely long (1.7-5.9 mm), not pigmented, and only

inconspicuously subdivided by nodes (but not by prongs). Only towards the bases some very slightly enlarged (but unpigmented) nodes are visible, which are too few in number to be counted.

12. CHARADRIIFORMES (figs. 24-33; table XI)

Sixty-eight species from nine families (Haematopodidae, Recurvirostridae, Glareolidae, Charadriidae, Scolopacidae, Stercorariidae, Laridae, Sternidae, and Alcidae) have been examined. Range of weights 14-2700 g.

Description. — The length of the barbules varies between 0.4 and 3.4 mm. Large differences exist between the nine families in the length of the barbules, degree of pigmentation, presence of prongs, and number of nodal structures per mm. No villi are present at the basal cells.

Haematopodidae: The barbules vary from 0.7 to 1.7 mm and are subdivided by nodes (17-23 per mm) which are not pigmented (thus, completely different from Lapwing). Towards the tips of the barbules, the nodes gradually become smaller and less conspicuous, and distally they often show short prongs.

Recurvirostridae: The barbules vary from 0.6 to 1.5 mm and are always subdivided by usually unpigmented nodes (but sometimes pigmented and situated at the bases of the barbules) which may possess minute prongs.

Glareolidae: The barbules vary from 0.5 to 1.3 mm and they are always subdivided by pigmented nodes (19-27 per mm).

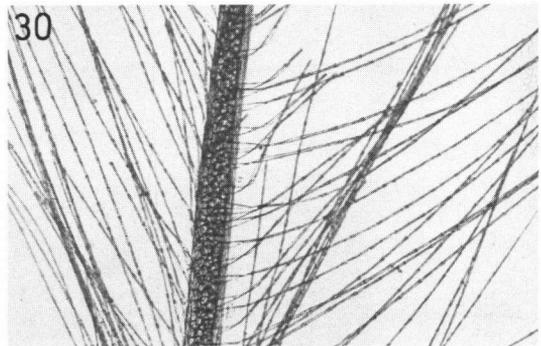
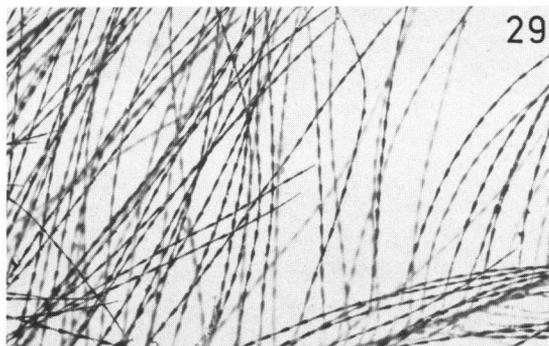
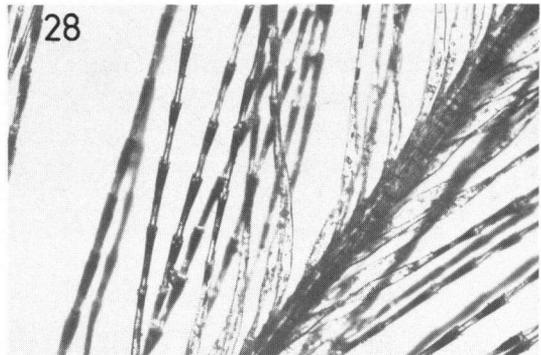
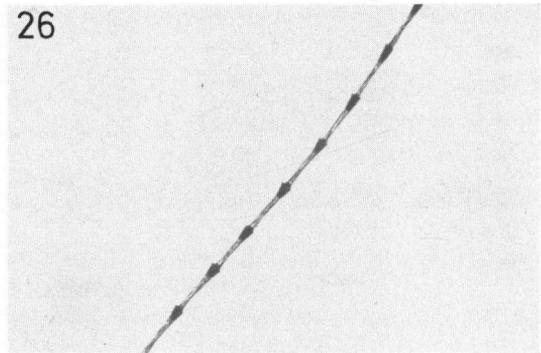
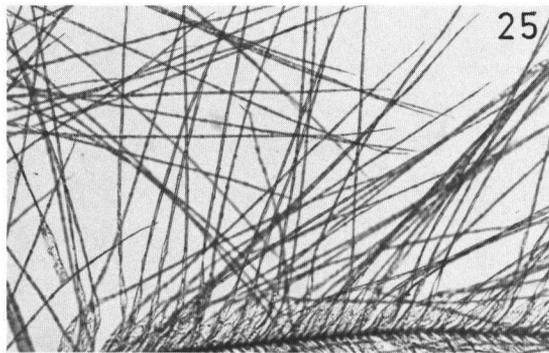
TABLE XI

Body weight (in g), length of barbules (in mm), and number of nodal structures (per mm barbule) in Charadriiformes.

Species		body weight	barbule length	N of nodes
<i>Haematopus ostralegus</i>	Oystercatcher	284-745	0.7-1.7	17-23
<i>Himantopus himantopus</i>	Black-winged Stilt	132-289	0.6-1.5	17-26
<i>Recurvirostra avosetta</i>	Avocet	231-435	0.6-1.4	17-24
<i>Glareola pratincola</i>	Pratincole	60-95	0.5-1.3	19-27
<i>G. nordmanni</i>	Black-winged Pratincole	87-105	0.6-1.2	20-27
<i>Charadrius dubius</i>	Little Ringed Plover	26-54	0.5-1.2	23-29

TABLE XI (continuation)

Species		body weight	barbule length	N of nodes
<i>C. hiaticula</i>	Ringed Plover	27-81	0.6-1.5	20-26
<i>C. vociferus</i>	Killdeer	65-90	0.9-1.5	22-27
<i>C. alexandrinus</i>	Kentish Plover	32-69	0.5-1.3	23-32
<i>C. mongolus</i>	Lesser Sand Plover	39-126	0.8-1.3	22-27
<i>C. leschenaultii</i>	Greater Sand Plover	60-120	0.7-1.3	21-29
<i>C. asiaticus</i>	Caspian Plover	60-91	0.7-1.3	22-34
<i>Eudromias morinellus</i>	Dotterel	86-142	0.8-2.2	19-30
<i>Pluvialis apricaria</i>	Golden Plover	88-239	0.6-1.7	19-26
<i>P. squatarola</i>	Grey Plover	105-335	0.6-1.9	18-24
<i>Hoplopterus spinosus</i>	Spur-winged Lapwing	127-170	0.9-1.3	18-22
<i>Chettusia gregaria</i>	Sociable Lapwing	180-260	0.7-1.7	16-21
<i>C. leucura</i>	White-tailed Lapwing	99-198	0.7-1.4	22-27
<i>Vanellus vanellus</i>	Lapwing	112-330	0.4-1.5	24-35
<i>Calidris canutus</i>	Knot	82-230	0.5-1.4	26-35
<i>C. alba</i>	Sanderling	41-88	0.5-1.2	25-32
<i>C. minuta</i>	Little Stint	14-44	0.5-1.2	24-34
<i>C. temminckii</i>	Temminck's Stint	15-35	0.6-1.6	23-33
<i>C. ferruginea</i>	Curlew Sandpiper	32-100	0.5-1.2	26-35
<i>C. alpina</i>	Dunlin	26-74	0.5-1.4	29-39
<i>Philomachus pugnax</i>	Ruff	67-254	0.5-1.4	25-33
<i>Lymnocyrtus minimus</i>	Jack Snipe	43-92	0.5-1.3	30-37
<i>Gallinago gallinago</i>	Common Snipe	76-227	0.5-1.4	24-33
<i>G. media</i>	Great Snipe	140-265	0.6-1.5	19-30
<i>Scolopax rusticola</i>	Woodcock	198-520	1.1-3.4	14-18
<i>Limosa limosa</i>	Black-tailed Godwit	160-500	0.5-1.3	26-35
<i>L. lapponica</i>	Bar-tailed Godwit	147-373	0.5-1.6	23-29
<i>Numenius phaeopus</i>	Whimbrel	227-660	0.5-1.0	27-34
<i>N. arquata</i>	Curlew	410-1280	0.5-1.1	25-31
<i>Tringa erythropus</i>	Spotted Redshank	97-205	0.5-1.2	25-31
<i>T. totanus</i>	Redshank	78-166	0.6-1.4	25-33
<i>T. stagnatilis</i>	Marsh Sandpiper	36-120	0.5-1.5	26-34
<i>T. nebularia</i>	Greenshank	134-283	0.5-1.3	22-28
<i>T. ochropus</i>	Green Sandpiper	50-112	0.6-1.4	25-31
<i>T. glareola</i>	Wood Sandpiper	34-89	0.6-1.2	26-35
<i>Actitis hypoleucos</i>	Common Sandpiper	28-73	0.6-1.6	24-30
<i>Arenaria interpres</i>	Turnstone	73-195	0.5-1.2	26-32
<i>Phalaropus lobatus</i>	Red-necked Phalarope	25-48	0.5-1.1	25-34
<i>P. fulcarius</i>	Grey Phalarope	30-77	0.5-1.1	25-33
<i>Stercorarius pomarinus</i>	Pomarine Skua	469-917	0.6-1.1	18-27
<i>S. parasiticus</i>	Arctic Skua	297-644	0.6-1.1	18-27
<i>S. longicaudus</i>	Long-tailed Skua	195-444	0.6-1.2	20-27
<i>S. skua</i>	Great Skua	600-2040	0.5-1.0	20-26
<i>Larus minutus</i>	Little Gull	80-150	0.5-1.0	19-24
<i>L. ridibundus</i>	Black-headed Gull	116-390	0.5-1.3	16-22
<i>L. canus</i>	Common Gull	300-586	0.5-1.3	16-22
<i>L. fuscus</i>	Lesser Black-backed Gull	534-1180	0.6-1.2	17-22
<i>L. argentatus</i>	Herring Gull	600-1800	0.7-1.2	16-21
<i>L. hyperboreus</i>	Glaucous Gull	1151-2700	0.5-1.2	18-22
<i>L. marinus</i>	Great Black-backed Gull	996-2275	0.7-1.4	15-20
<i>Rissa tridactyla</i>	Kittiwake	210-610	0.5-1.2	18-23
<i>Gelochelidon nilotica</i>	Gull-billed Tern	154-290	0.6-1.1	19-25
<i>Sterna sandvicensis</i>	Sandwich Tern	174-330	0.6-1.1	20-25
<i>S. hirundo</i>	Common Tern	76-175	0.6-1.1	18-26
<i>S. paradisaea</i>	Arctic Tern	87-142	0.6-1.1	19-24
<i>S. albifrons</i>	Little Tern	31-60	0.5-1.0	22-29
<i>Chlidonias hybrida</i>	Whiskered Tern	61-94	0.6-1.2	19-24
<i>C. nigra</i>	Black Tern	51-77	0.7-1.2	20-24
<i>Uria aalge</i>	Guillemot	612-1200	0.4-0.8	—
<i>U. lomvia</i>	Brünnich's Guillemot	604-1200	0.4-0.9	—
<i>Alca torda</i>	Razorbill	450-920	0.4-0.9	—
<i>Cepphus grylle</i>	Black Guillemot	312-615	0.6-1.1	—
<i>Fratrercula arctica</i>	Puffin	290-586	0.4-1.0	—



- Fig. 25. Avocet *Recurvirostra avosetta*; breast feather (85 ×).
 Fig. 26. Pratincole *Glareola pratincola*; belly feather (205 ×).
 Fig. 27. Golden Plover *Pluvialis apricaria*; breast feather (85 ×).
 Fig. 28. Ringed Plover *Charadrius hiaticula*; belly feather (205 ×).
 Fig. 29. Dunlin *Calidris alpina*; breast feather (85 ×).
 Fig. 30. Long-tailed Skua *Stercorarius longicaudus*; mantle feather (85 ×).

Charadriidae: The barbules vary from 0.4 to 2.2 mm and they are always clearly subdivided by nodes (16-35 per mm), which may be pigmented as well as unpigmented. Prongs are not found within this family (at magnifications between 50 and 500 ×). Pigmented nodes are always found at the basal portion of the most

basal barbules. Considerable differences in the extent of pigmentation exist. In the Golden Plover *Pluvialis apricaria* some unpigmented nodes are found at the tips of the barbules only while the remaining nodes are all pigmented. In *Charadrius* usually only the nodes at the basal part of the most basal barbules are pigmented.

Scolopacidae: The barbules are rather short (0.5-1.6 mm; only in *Scolopax* they reach up to 3.4 mm). In some genera, such as *Scolopax*, *Gallinago*, *Lymnocyptes*, and *Phalaropus* the barbules are conspicuously subdivided by nodes (14-37 per mm) which are always pigmented. In the remaining species, pigmented as well as unpigmented nodes occur (22-39 per mm), which occasionally possess minute prongs. In *Numenius* the nodes are usually not pigmented, but pigmented ones may occur. In *Calidris*, *Tringa*, *Limosa*, *Arenaria*, and *Philomachus* the nodes are usually pigmented, but especially towards the tips of the barbules unpigmented nodes occur as well.

Stercorariidae: The barbules are very short (0.5-1.2 mm) and they are subdivided by unpigmented nodes or minute prongs (18-27 per mm).

Laridae: The barbules are short and along most of their length subdivided by unpigmented and rather inconspicuous nodes which often possess prongs. Always only the most basal barbules possess 3-8 enlarged and heavily pigmented nodes proximally.

Sternidae: This group closely resembles the gulls. The barbules vary from 0.5 to 1.2 mm and there are 18-29 nodal structures per mm.

Alcidae: The barbules are extremely short (0.4-1.1 mm) and they are faintly subdivided by indistinct nodes or well-developed prongs, which are most prominent distally. Often an inconspicuous and diffuse pigmentation is present.

13. PTEROCLIDIFORMES (fig. 34; table XII)

This order consists of a single family (Pteroclididae). Three species have been examined. Range of weights 200-650 g.

Description. — The barbules are very long (1.6-4.8 mm) and along their entire length divided into nodes (11-17 per mm) which often possess minute prongs, and internodes, both unpigmented. Only proximally 3-5 nodes are slightly enlarged and rather conspicuous, further along the barbules they are often hard to count. No villi at the basal cells.

TABLE XII

Body weight (in g), length of barbules (in mm), and number of nodal structures (per mm barbule) in Pteroclidiformes.

Species		body weight	barbule length	N of nodes
<i>Pterocles alchata</i>	Pin-tailed Sandgrouse	200-340	1.6-3.0	12-17
<i>P. orientalis</i>	Black-bellied Sandgrouse	410-650	1.6-4.8	12-17
<i>Syrhaptes paradoxus</i>	Pallas's Sandgrouse	254-340	1.7-4.2	11-15

14. COLUMBIFORMES (fig. 35; table XIII)

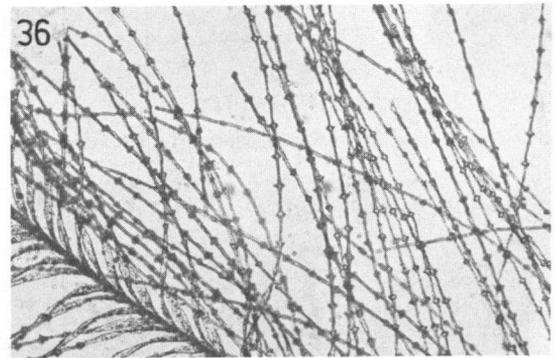
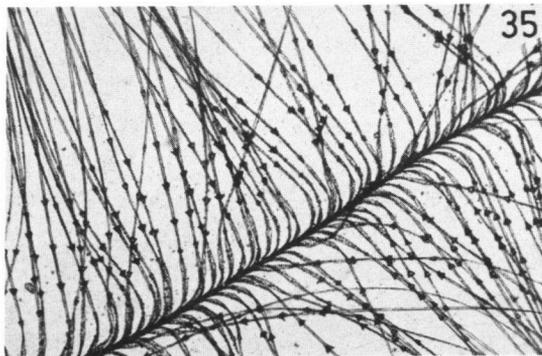
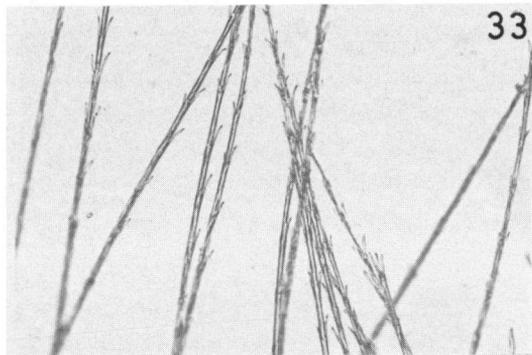
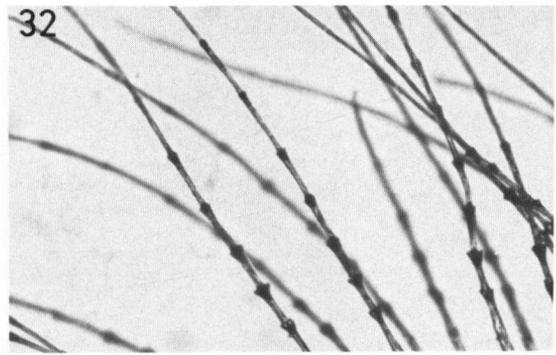
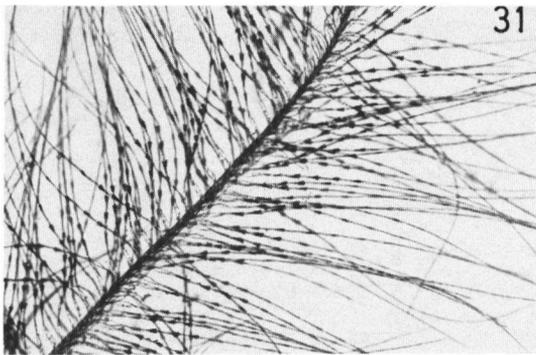
This order consists of a single family (Columbidae). Five species have been examined. Range of weights 74-739 g.

Description. — The barbules are very long (1.1-5.1 mm); on the basal part a number of very large, flattened, plate-like nodes are found: usually 3-8 of full size, then a number of smaller and less conspicuous ones, decreasing in size until they almost completely disappear, the whole distal portion of the barbule being smoothly filamentous or with very minute swollen nodes (occasionally with minute prongs). Only the most basal barbules of the feather possess expanded, quadrilobed nodes along their whole length (10-18 per mm). Pigmentation is slight and confined to the nodes. Among the species examined no diagnostic differences are found in the length of the barbules or the number of nodes per mm. No villi at the basal cells.

TABLE XIII

Body weight (in g), length of barbules (in mm), and number of nodes (per mm barbule) in Columbiformes.

Species		body weight	barbule length	N of nodes
<i>Columba livia</i>	Rock Dove/ Feral Dove	194-570	1.2-4.4	11-16
<i>C. oenas</i>	Stock Dove	217-567	1.1-4.7	10-16
<i>C. palumbus</i>	Wood Pigeon	258-739	1.2-4.6	10-16
<i>Streptopelia decaocto</i>	Collared Dove	113-243	1.2-4.8	12-18
<i>S. turtur</i>	Turtle Dove	74-178	1.3-5.1	11-17



- Fig. 31. Little Gull *Larus minutus*; breast feather (85 ×).
 Fig. 32. Kittiwake *Rissa tridactyla*; belly feather (205 ×).
 Fig. 33. Razorbill *Alca torda*; breast feather (205 ×).
 Fig. 34. Pallas's Sandgrouse *Syrrhaptes paradoxus*; belly feather (205 ×).
 Fig. 35. Wood Pigeon *Columba palumbus*; mantle feather (85 ×).
 Fig. 36. Budgerigar *Melopsittacus undulatus*; belly feather (105 ×).

15. PSITTACIFORMES (fig. 36; table XIV)

Ten species from three families (Loriidae, Cacatuidae, and Psittacidae) have been examined. Range of weights 33-1286 g.

Description. — The barbules are long (0.8-3.5 mm) and possess globular or triangular

nodes (12-34 per mm) which are enlarged proximally but minute distally. Larger birds tend to possess fewer nodes per mm than smaller birds. Deeply pigmented nodes as well as unpigmented nodes can be found; in the first case the barbules may resemble those of the Passeriformes, but they are more slender and

wavy. The internodes sometimes show a bending or kinking. No villi at the basal cells.

TABLE XIV

Body weight (in g), length of barbules (in mm), and number of nodes (per mm barbule) in Psittaciformes.

Species		body weight	barbule length	N of nodes
<i>Melopsittacus undulatus</i>	Budgerigar	ca. 33	0.8-1.6	23-34
<i>Nymphicus hollandicus</i>	Cockatiel	72-113	1.4-2.8	13-21
<i>Cacatua sulphurea</i>	Sulphur-crested Cockatoo	320-358	1.4-3.5	14-23
<i>Psittacus erithacus</i>	Grey Parrot	200-300	1.3-2.6	17-25
<i>Lorius domicellus</i>	Purple-naped Lory	—	1.5-2.3	16-24
<i>Agapornis taranta</i>	Black-winged Lovebird	ca. 38	1.1-1.8	24-33
<i>Loriculus stigmatus</i>	Celebes Hanging Parrot	37-49	1.4-2.0	20-30
<i>Poicephalus rueppellii</i>	Rüppell's Parrot	—	1.5-2.3	17-28
<i>P. senegalus</i>	Senegal Parrot	—	1.2-2.5	19-27
<i>Ara ararauna</i>	Blue and Yellow Macaw	1157-1286	1.5-2.9	12-22

16. CUCULIFORMES (fig. 37)

Two species of the family Cuculidae have been examined. Range of weights 63-220 g.

Description. — The barbules are very long (1.4-3.2 mm in Great Spotted Cuckoo *Clamator glandarius* and 1.5-5.0 mm in Cuckoo *Cuculus canorus*) and very slender. They have globular nodes (8-18 per mm); those towards the base are large, whereas more distally they are minute. The internodes are extremely long and slender, and they sometimes show a slight kinking. No villi at the basal cells.

17. STRIGIFORMES (figs. 38-39; table XV)

This order consists of two families (Tytonidae and Strigidae) from which ten species have been examined. Range of weights 50-3260 g.

Description. — The barbules are very long (1.0-6.1 mm) and are divided by pigmented nodes along their entire length (8-30 per mm). The nodes show an abrupt reduction in size: 2-6 proximal nodes are enlarged, the remaining ones are small and longitudinally shaped. The degree of pigmentation varies from species to species. The Snowy Owl *Nyctea scandiaca* shows little pigmentation, whereas in the Tawny Owl

Strix aluco pigmentation is quite heavy. No villi at the basal cells.

TABLE XV

Body weight (in g), length of barbules (in mm), and number of nodes (per mm barbule) in Strigiformes.

Species		body weight	barbule length	N of nodes
<i>Tyto alba</i>	Barn Owl	206-660	1.5-3.7	8-15
<i>Otus scops</i>	Scops Owl	50-145	1.6-3.1	13-23
<i>Bubo bubo</i>	Eagle Owl	2000-3260	1.6-6.1	10-19
<i>Nyctea scandiaca</i>	Snowy Owl	710-2950	2.0-4.3	10-15
<i>Glaucidium passerinum</i>	Pygmy Owl	55-79	1.0-2.4	15-26
<i>Athene noctua</i>	Little Owl	85-271	1.2-2.9	15-24
<i>Strix aluco</i>	Tawny Owl	264-695	1.5-4.1	12-21
<i>Asio otus</i>	Long-eared Owl	151-378	1.7-5.2	10-17
<i>A. flammeus</i>	Short-eared Owl	229-500	2.0-4.2	10-17
<i>Aegolius funereus</i>	Tengmalm's Owl	109-197	1.2-2.8	14-30

18. CAPRIMULGIFORMES (fig. 40)

Three species of the family Caprimulgidae have been examined: Nightjar *Caprimulgus europaeus*, Red-necked Nightjar *C. ruficollis*, and Egyptian Nightjar *C. aegyptius*. Range of weights 45-100 g.

Description. — The barbules are of medium length (1.3-3.0 mm) and at low magnifications (50×) they appear as dark and heavily pigmented threads, resembling those of Apodiformes. At higher magnification (200×), the subdivision into nodes and internodes becomes perceptible, but even then only 2-5 basal nodes are visible. Thus, the number of nodes can only be estimated (14-16 per mm). No villi at the basal cells.

19. APODIFORMES (fig. 41)

Two species of the family Apodidae have been examined: Swift *Apus apus* and Alpine Swift *A. melba*. Range of weights 22-120 g.

Description. — The barbules are rather short (0.7-1.7 mm). At low magnification (50×) they appear as dark, heavily pigmented threads; at higher magnification (200×), a sub-

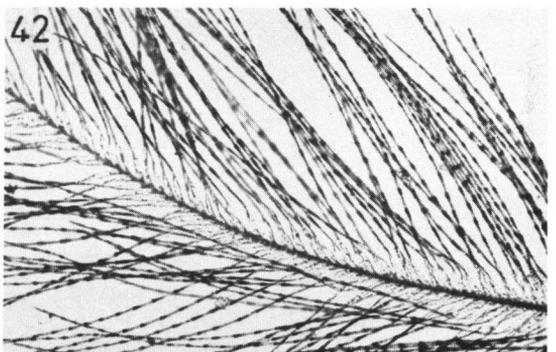
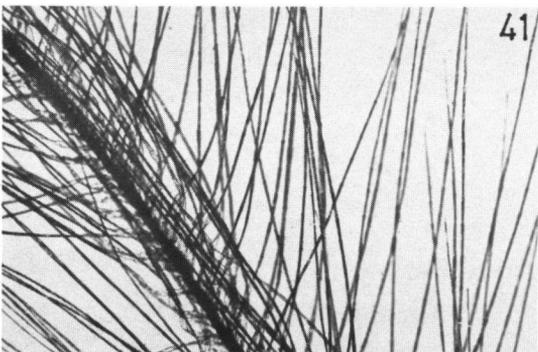
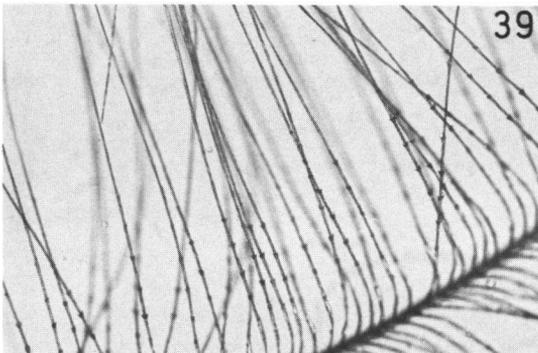
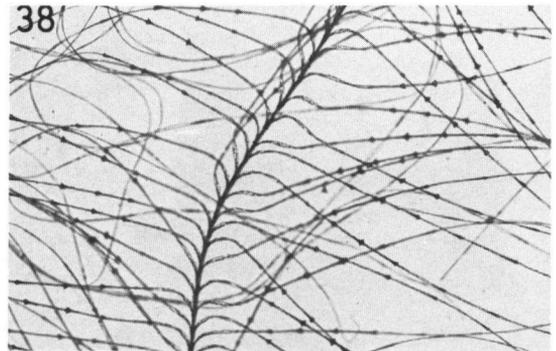


Fig. 37. Great Spotted Cuckoo *Clamator glandarius*; breast feather (105 ×)

Fig. 38. Barn Owl *Tyto alba*; neck feather (85 ×).

Fig. 39. Snowy Owl *Nyctea scandiaca*; upper wing covert (85 ×).

Fig. 40. Red-necked Nightjar *Caprimulgus ruficollis*; breast feather (85 ×).

Fig. 41. Swift *Apus apus*; breast feather (85 ×).

Fig. 42. Kingfisher *Alcedo atthis*; breast feather (85 ×).

division into nodes and internodes becomes visible. The nodes possess minute prongs, but nodes or prongs are very difficult to count. Both nodes and internodes are partly pigmented. No villi at the basal cells.

20. CORACIIFORMES (figs. 42-43; table XVI)

Four species from four families (Alcedinidae, Meropidae, Coraciidae, and Upupidae) have been examined. Range of weights 23-183 g.

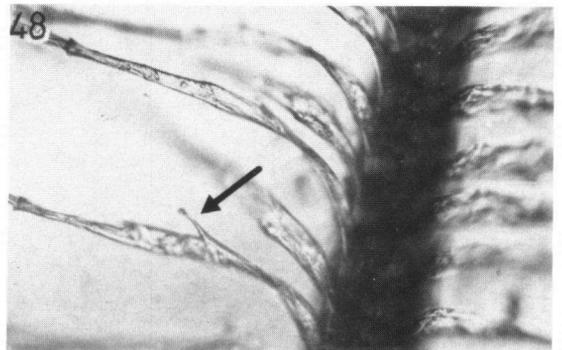
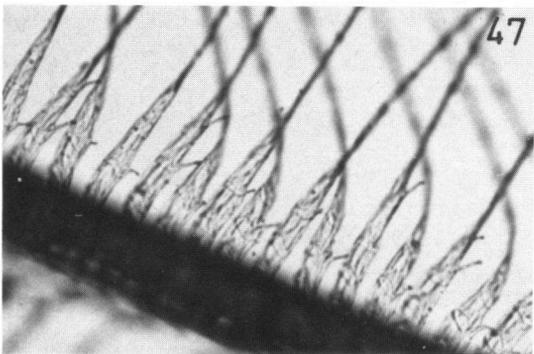
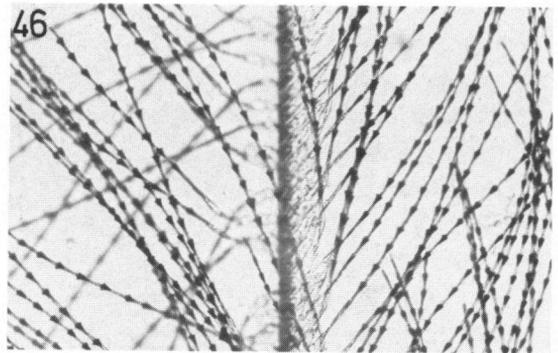
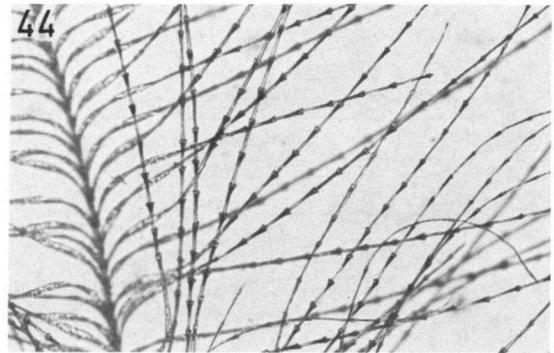
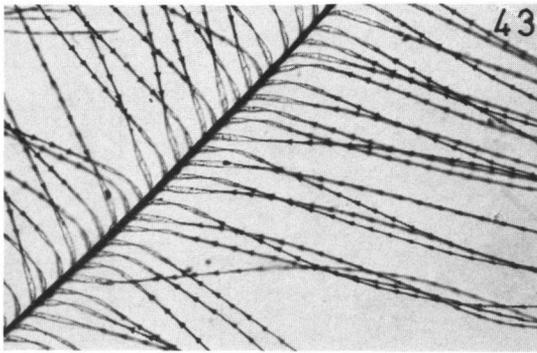


Fig. 43. Hoopoe *Upupa epops*; breast feather (85 ×).

Fig. 44. Black Woodpecker *Dryocopus martius*; belly feather (105 ×).

Fig. 45. Lesser Spotted Woodpecker *Dendrocopos minor*; breast feather (165 ×). Curved and scimitar-shaped villi at the basal cells.

Fig. 46. Skylark *Alauda arvensis*; breast feather (105 ×).

Fig. 47. Hooded Crow *Corvus corone cornix*; breast feather (205 ×). Villi at the basal cells.

Fig. 48. Hooded Crow *Corvus corone cornix*; breast feather (325 ×). Villus at basal cell (arrow).

Description. — The barbules are of medium length (0.8-2.9 mm) and they are clearly divided into pigmented nodes (14-32 per mm) and unpigmented internodes. The nodes slightly decrease in size towards the tips of the

barbules. Among the four species examined, a tendency seems to exist that larger birds possess fewer nodes per mm than smaller ones. No villi at the basal cells.

TABLE XVI

Body weight (in g), length of barbules (in mm), and number of nodes (per mm barbule) in Coraciiformes.

Species		body weight	barbule length	N of nodes
<i>Alcedo atthis</i>	Kingfisher	23-46	0.8-1.6	21-32
<i>Merops apiaster</i>	Bee-eater	37-60	0.9-1.4	21-26
<i>Coracias garrulus</i>	Roller	107-183	1.0-1.8	14-24
<i>Upupa epops</i>	Hoopoe	41-91	1.6-2.9	19-24

21. PICIFORMES (figs. 44-45; table XVII)

Eight species of the family Picidae have been examined. Range of weights 23-317 g.

Description. — The barbules are of medium length (0.6-2.5 mm) and along their entire length they are clearly divided into pigmented nodes (21-39 per mm) and unpigmented internodes. Only towards the tip the nodes slightly decrease in size. There is a tendency that larger birds possess fewer nodes per mm than smaller birds. At the basal cells curved or scimitar-shaped villi are present which usually are pointing in the direction of the barb. The length of these villi ranges from 0.02 to 0.22 mm.

TABLE XVII

Body weight (in g), length of barbules (in mm), and number of nodes (per mm barbule) in Piciformes.

Species		body weight	barbule length	N of nodes
<i>Jynx torquilla</i>	Wryneck	23-72	1.0-1.7	31-36
<i>Picus canus</i>	Grey-headed Woodpecker	98-162	0.9-1.5	29-36
<i>P. viridis</i>	Green Woodpecker	101-250	1.0-2.1	27-36
<i>Dryocopus martius</i>	Black Woodpecker	201-317	1.0-2.3	21-31
<i>Dendrocopos major</i>	Great Spotted Woodpecker	53-110	0.8-2.5	24-30
<i>D. medius</i>	Middle Spotted Woodpecker	54-85	1.0-1.9	27-36
<i>D. minor</i>	Lesser Spotted Woodpecker	14-25	0.6-1.2	33-39
<i>Picoides tridactylus</i>	Three-toed Woodpecker	51-80	0.8-1.7	24-35

22. PASSERIFORMES (figs. 46-48; table XVIII)

This order contains nearly half of the known species of birds. It is divided into several

suborders, of which in Europe only the largest (Oscines) is found. Some 100 species have been examined, belonging to 22 families. Range of weights 4-1560 g.

Description. — The barbules are of medium length (0.5-3.3 mm, but usually shorter than 2 mm). They are clearly subdivided into enlarged and pigmented nodes (16-55 per mm) and unpigmented internodes. The longest barbules are found in the families Turdidae (0.5-3.3 mm), Corvidae (0.6-2.7 mm), and Alaudidae (0.6-2.2 mm); in the remaining families they range from 0.5-1.6 mm. At the basal cells villi are present, which differ in shape from those found in Piciformes by being blunt, knobbed, or finger-like, instead of recurved or sharply pointed.

TABLE XVIII

Body weight (in g), length of barbules (in mm), and number of nodes (per mm barbule) in Passeriformes.

Species		body weight	barbule length	N of nodes
<i>Melanocorypha calandra</i>	Calandra Lark	55-63	0.8-1.7	30-35
<i>Galerida cristata</i>	Crested Lark	31-49	0.8-2.2	29-40
<i>Lullula arborea</i>	Wood Lark	20-40	0.7-1.7	28-42
<i>Alauda arvensis</i>	Skylark	23-54	0.7-1.6	28-40
<i>Eremophila alpestris</i>	Shore Lark	27-46	0.6-1.4	31-37
<i>Riparia riparia</i>	Sand Martin	9-19	0.6-1.1	28-36
<i>Hirundo rustica</i>	Swallow	11-28	0.6-1.2	27-35
<i>Delichon urbica</i>	House Martin	10-28	0.8-1.5	27-32
<i>Anthus campestris</i>	Tawny Pipit	16-27	0.5-1.3	26-35
<i>A. trivialis</i>	Tree Pipit	15-28	0.5-1.1	33-41
<i>A. pratensis</i>	Meadow Pipit	10-25	0.5-1.0	38-46
<i>A. spinoletta</i>	Water Pipit	16-31	0.6-1.1	31-42
<i>Motacilla flava</i>	Yellow Wagtail	11-26	0.7-1.4	29-38
<i>M. cinerea</i>	Grey Wagtail	14-25	0.6-1.3	29-38
<i>M. alba</i>	White Wagtail	15-30	0.5-1.0	36-42
<i>Bombycilla garrulus</i>	Waxwing	40-83	0.7-1.3	29-40
<i>Cinclus cinclus</i>	Dipper	49-100	0.6-1.3	26-34
<i>Troglodytes troglodytes</i>	Wren	4-14	0.6-1.4	38-53
<i>Prunella modularis</i>	Dunnock	13-26	0.8-1.7	34-43
<i>Erithacus rubecula</i>	Robin	10-25	0.7-1.5	30-44
<i>Luscinia megarhynchos</i>	Nightingale	12-27	0.6-1.3	30-43
<i>Phoenicurus ochruros</i>	Black Redstart	13-19	0.5-1.3	34-45
<i>Saxicola rubetra</i>	Whinchat	13-24	0.5-1.2	34-42
<i>S. torquata</i>	Stonechat	12-19	0.5-1.3	33-40
<i>Oenanthe oenanthe</i>	Wheatear	14-41	0.7-1.2	34-43
<i>Zoothera dauma</i>	White's Thrush	100-190	1.0-3.3	22-33
<i>Turdus torquatus</i>	Ring Ouzel	83-138	0.9-2.7	20-31
<i>T. merula</i>	Blackbird	73-135	1.0-1.9	30-41
<i>T. pilaris</i>	Fieldfare	52-146	0.6-2.2	24-34
<i>T. philomelos</i>	Song Thrush	51-107	1.0-2.6	24-35
<i>T. iliacus</i>	Redwing	38-88	0.8-1.7	27-34
<i>T. viscivorus</i>	Mistle Thrush	95-167	1.1-3.0	16-31
<i>Cettia cetti</i>	Cetti's Warbler	10-18	0.5-1.1	41-55

TABLE XVIII (continuation)

Species		body weight	barbule length	N of nodes
<i>Locustella naevia</i>	Grasshopper Warbler	11-16	0.6-1.3	35-44
<i>L. luscinioides</i>	Savi's Warbler	12-26	0.7-1.6	28-35
<i>Acrocephalus palustris</i>	Marsh Warbler	9-17	0.5-1.0	37-46
<i>A. schoenobaenus</i>	Sedge Warbler	8-18	0.5-1.3	36-43
<i>A. arundinaceus</i>	Great Reed Warbler	22-53	0.7-1.3	32-42
<i>Hippolais icterina</i>	Icterine Warbler	8-16	0.6-1.2	31-41
<i>Sylvia nisoria</i>	Barred Warbler	19-30	0.7-1.3	27-42
<i>S. curruca</i>	Lesser Whitethroat	9-21	0.6-1.2	34-47
<i>S. communis</i>	Whitethroat	8-23	0.5-1.3	33-46
<i>S. borin</i>	Garden Warbler	12-28	0.5-1.2	35-46
<i>S. atricapilla</i>	Blackcap	11-27	0.5-1.4	37-45
<i>Phylloscopus inornatus</i>	Yellow-browed Warbler	4-8	0.6-1.1	38-45
<i>P. sibilatrix</i>	Wood Warbler	6-14	0.5-1.0	35-45
<i>P. collybita</i>	Chiffchaff	5-11	0.5-0.9	36-46
<i>P. trochilus</i>	Willow Warbler	5-13	0.5-1.0	39-50
<i>Regulus regulus</i>	Goldcrest	4-7	0.6-1.1	40-51
<i>R. ignicapillus</i>	Firecrest	4-9	0.5-1.0	38-49
<i>Muscicapa striata</i>	Spotted Flycatcher	10-20	0.6-1.2	34-44
<i>Ficedula parva</i>	Red-breasted Flycatcher	7-14	0.5-1.0	40-50
<i>F. hypoleuca</i>	Pied Flycatcher	9-19	0.5-1.1	32-46
<i>Panurus biarmicus</i>	Bearded Tit	12-18	0.5-1.2	38-46
<i>Aegithalos caudatus</i>	Long-tailed Tit	5-11	0.5-1.2	40-49
<i>Parus palustris</i>	Marsh Tit	7-14	0.6-1.5	34-44
<i>P. montanus</i>	Willow Tit	7-12	0.5-1.0	36-48
<i>P. cristatus</i>	Crested Tit	8-13	0.6-1.1	44-53
<i>P. ater</i>	Coal Tit	7-16	0.6-1.1	39-52
<i>P. caeruleus</i>	Blue Tit	9-16	0.6-1.1	43-52
<i>P. major</i>	Great Tit	14-22	0.6-1.2	38-47
<i>Sitta europaea</i>	Nuthatch	17-28	0.6-1.1	33-43
<i>Certhia brachydactyla</i>	Short-toed Treecreeper	7-14	0.5-1.3	37-50
<i>Oriolus oriolus</i>	Golden Oriole	52-96	0.7-1.6	21-31
<i>Lanius collurio</i>	Red-backed Shrike	23-38	0.9-1.6	29-35
<i>L. excubitor</i>	Great Grey Shrike	31-81	0.9-1.5	27-34
<i>L. senator</i>	Woodchat Shrike	21-45	0.7-1.4	26-36
<i>Garrulus glandarius</i>	Jay	121-199	1.2-2.5	25-33
<i>Pica pica</i>	Magpie	131-300	0.6-1.9	27-39
<i>Nucifraga caryocatactes</i>	Nutcracker	110-200	0.8-1.4	27-34
<i>Corvus monedula</i>	Jackdaw	123-281	0.8-1.6	28-40
<i>C. frugilegus</i>	Rook	225-595	1.0-2.0	25-30
<i>C. corone corone</i>	Carrion Crow	322-695	1.0-2.4	23-34
<i>C. c. cornix</i>	Hooded Crow	440-611	0.9-2.6	26-36
<i>C. albus</i>	Pied Crow	474-612	0.8-2.1	21-29
<i>C. corax</i>	Raven	798-1560	1.0-2.2	21-29
<i>Sturnus vulgaris</i>	Starling	49-122	0.6-1.3	31-41
<i>Passer domesticus</i>	House Sparrow	19-37	0.9-1.6	28-38
<i>P. montanus</i>	Tree Sparrow	15-29	0.6-1.3	32-40
<i>Fringilla coelebs</i>	Chaffinch	15-39	0.5-1.4	33-44
<i>F. montifringilla</i>	Brambling	15-37	0.6-1.2	35-43
<i>Serinus serinus</i>	Serin	9-14	0.6-1.1	34-43
<i>S. canaria</i>	Canary	8-17	0.5-1.0	42-52
<i>Carduelis chloris</i>	Greenfinch	20-37	0.7-1.1	35-45
<i>C. carduelis</i>	Goldfinch	12-22	0.6-1.2	36-46
<i>C. cannabina</i>	Linnet	16-24	0.7-1.0	35-44
<i>C. flavirostris</i>	Twite	13-21	0.7-1.4	35-43
<i>C. flammea</i>	Common Redpoll	9-23	0.7-1.4	43-52
<i>Loxia curvirostra</i>	Crossbill	24-48	0.7-1.3	35-44
<i>Pyrrhula pyrrhula</i>	Bullfinch	16-36	0.5-1.4	40-49
<i>C. coccythraustes</i>	Hawfinch	41-70	0.6-1.2	28-39
<i>Calcarius lapponicus</i>	Lapland Bunting	16-36	0.6-1.1	38-47

TABLE XVIII (continuation)

Species		body weight	barbule length	N of nodes
<i>Plectrophenax nivalis</i>	Snow Bunting	22-50	0.7-1.1	36-50
<i>Emberiza citrinella</i>	Yellowhammer	18-40	0.7-1.2	32-42
<i>E. hortulana</i>	Ortolan Bunting	15-33	0.5-1.2	29-38
<i>E. pusilla</i>	Little Bunting	13-16	0.5-1.3	29-36
<i>E. schoeniclus</i>	Reed Bunting	15-28	0.7-1.4	37-46
<i>Miliaria calandra</i>	Corn Bunting	34-64	0.6-1.3	36-46

IDENTIFICATION KEY

It is strongly recommended to use this key only after studying the previous description of the characters of the 22 orders of birds examined. The key will only permit identification if some coherent barbules are present in the sample. When only detached barbules are found, the identification procedure will have to be stopped if comparisons between barbules must be made. In the case that only a very small sample is available, it may not always be certain that downy barbules are present. It must be kept in mind that barbules originating from the pennaceous portion of the feather cannot be identified with the help of this key. Some characters are diagnostic for certain groups when only one example is found (such as the occurrence of multiple nodes in Galliformes), but in other cases (such as the occurrence of villi at the basal cells in Piciformes and Passeriformes) it is recommended to look for several examples to make sure that no artifacts interfere with a correct identification.

1. Barbules possess prongs 2
- Barbules lack prongs 3
2. Barbules possess triangular (heart-shaped) nodes distally 4
- Barbules without triangular nodes distally 5
3. Barbules possess triangular (heart-shaped) nodes distally 4
- Barbules without triangular nodes distally 12
4. Barbules with triangular (heart-shaped) nodes distally:
 - ANSERIFORMES
 - nodes along <40% of barbule: DUCKS
 - nodes along 40-60% of barbule: GEESE
 - nodes along >60% of barbule: SWANS
5. Prongs longer than adjacent internodes:
 - SULIDAE
 - Prongs shorter than adjacent internodes 6

6. At low magnification (50 ×) barbules clearly subdivided into enlarged nodes and internodes 7
 — At low magnification (50 ×) nodes very difficult to discern 9
7. In most barbules (basalmost of barb) nodes rapidly decrease in size over 2-6 basal internodes 8
 — No decrease in size of nodes apparent:
 PROCELLARIIFORMES, PHAETHONTIDAE
8. Barbule length >1.5 mm and nodes <18 per mm:
 PTEROCLIDIFORMES
 — Barbule length <1.5 mm and nodes >15 per mm:
 LARIDAE, STERNIDAE
9. Barbule length >3 mm, prongs usually asymmetrical:
 ACCIPITRIFORMES
 — Barbule length <3 mm 10
10. Prongs only at one side of the majority of barbules:
 PODICIPEDIFORMES
 — Prongs at both sides of barbules 11
11. Barbule length >1.7 mm:
 CICONIIDAE, ARDEIDAE, GRUIDAE
 — Barbule length <1.7 mm:
 GAVIIFORMES, PELECANIDAE, FREGATIDAE,
 PHALACROCORACIDAE, THRESKIORNITHIDAE,
 PHOENICOPTERIFORMES, HAEMATOPODIDAE,
 RECURVIROSTRIDAE, STERCORARIIDAE, ALCIDAE
12. At low magnification (50 ×) barbules clearly subdivided by enlarged nodes and internodes 17
 — At low magnification (50 ×) no conspicuous subdivision into nodes and internodes 13
13. At low magnification (50 ×) barbules visible as strongly pigmented threads 14
 — Barbules filamentous and not strongly pigmented 15
14. Barbule length >1.7 mm:
 CAPRIMULGIFORMES
 — Barbule length <1.7 mm:
 APODIFORMES
15. Barbule length >1.7 mm 16
 — Barbule length <1.7 mm:
 HAEMATOPODIDAE, RECURVIROSTRIDAE
16. At higher magnification (150 ×), at the basal part of the barbules some enlarged nodes are visible which decrease in size over a short distance:
 ACCIPITRIFORMES, OTIDIDAE
 — At higher magnification (150 ×) a subdivision of the barbules is visible, but proximally the nodes are not more enlarged than elsewhere:
 CICONIIFORMES
17. Villi present at the basal cells 18
 — Villi absent at the basal cells 19
18. Villi recurved and sharply pointed:
 PICIFORMES
 — Villi blunt, knobbed, or finger-like:
 PASSERIFORMES
19. Multiple nodes present:
 GALLIFORMES
 — Multiple nodes absent 20
20. Nodes along entire length of barbules, not plate-like in shape 21
 — Nodes flattened and plate-like in shape; only at most basal barbules reaching tip of barbule, but usually not present along entire length (the remaining part being smoothly filamentous):
 COLUMBIFORMES
21. Pigment located in spots just proximal of globular nodes and barbules very long and slender:
 CUCULIFORMES
 — Pigment located in nodes 22
22. In the basalmost barbules nodes abruptly decrease in size over short distance 23
 — No reduction in size of basalmost nodes 24
23. Barbule length >1.7 mm (barbules often in clews), most nodes elongate in shape:
 STRIGIFORMES
 — Barbule length <1.7 mm and reduction in size of nodes more pronounced in one of the two vanules:
 RALLIDAE
24. Both pigmented and unpigmented nodes occur within one feather or even in one barbule 25
 — Barbules uniform in pigmentation 26
25. Barbules slender and wavy, internodes kinky:
 PSITTACIFORMES
 — Barbules not slender and wavy, short internodes not kinky:
 CHARADRIIDAE, *Numenius*, *Calidris*, *Tringa*, *Limosa*,
Arenaria, *Philomachus*
26. Barbules very slender and wavy (often in clews), nodes small and rounded:
 FALCONIFORMES
 — Barbules straight, nodes not rounded:
 CORACIIFORMES, TURNICIDAE, GLAREOLIDAE,
Scolopax, *Gallinago*, *Lymnocyptes*, *Phalaropus*

CONCLUSIONS

Using the structure of the downy barbules of feathers one can usually establish the order to which a given bird belongs. The described characters proved to be very uniform within monophyletic taxa, but show striking differences between birds that occupy comparable habitats (e.g. Gaviiformes, Podicipediformes, Anseriformes, Rallidae, and Alcidae), leading to the conclusion that these characters are not highly adaptive.

In several groups the distribution of nodal structures along the barbules is related to the size of the bird. Within the Falconidae, Galliformes, Rallidae, Laridae, Sternidae, Psittaciformes, Strigiformes, Coraciiformes,

Piciformes, and Passeriformes, a tendency has been found that larger birds possess fewer nodes per mm barbule than smaller birds.

DISCUSSION

Microscopic identification of feathers is based on the observation that the fine structures of feathers from each species of bird differ just as do other characters. The more closely two species are related, the more alike the feather structures are, and conversely. It seems that the complexity of feather structures generally follows the taxonomic order, although the exact value of this set of characters for avian taxonomy remains to be evaluated. It is evident that some of the described characters unite several orders, whereas other characters separate families that are usually grouped within one (assumed) order. Groups that attract special attention are the Falconidae and the Rallidae. Their downy barbules have microstructures that are totally different from their alledged relatives, the Accipitriformes and the remaining Gruiformes, respectively.

The identification method described in this paper has been extensively applied to the study of collisions between birds and aircraft (bird strikes). In combination with the method of comparing feathers with bird skins, it usually leads to identification at order-, family-, or species-level. The level of identification is further influenced by the presence or absence of additional information, such as time of the season, time of the day, height, and location. Applied to bird strike analysis, this method is a major improvement of existing methods of identification. In 97% of all cases ($N = 658$) the order could be established (in the remaining 3% a bird strike usually could be confirmed, but the material was not sufficient for further identification), in 47% of the cases the species could be established (Brom, 1984). For bird strike analysis it is very useful that in several groups of birds a tendency exists that larger birds have fewer nodes per mm of barbule than smaller birds. In this way an indication of the weight of

the bird can be obtained without exactly knowing the actual species involved. This is important as weight is a key factor in the analysis of bird strikes (Buurma, 1984). For example, within the Passeriformes crows can always be distinguished from small songbirds. In a similar way, a distinction can be made between ducks, geese, and swans in the family Anatidae.

In contrast to mammals, the phylogeny of birds is still very imperfectly understood (see e.g. the discussion between Cracraft, 1981, and Olson, 1982). Owing to the constraints of flight, the general morphology of birds is less diverse than that of mammals (discussed by Wyles et al., 1983). The application of the method of phylogenetic analysis is hindered by the difficulty in recognizing clearly character states that are either plesiomorphic or apomorphic.

Recently the amino-acid sequence of the eye lens protein α -crystallin A was studied in 19 bird species, belonging to 14 orders (Stapel et al., 1984). This study provided new evidence that the Ratites are the sister-group of all other birds. However, the resolution of the method is insufficient to determine the relationships of most other orders.

Comparative studies on feather keratins carried out on solubilized S-carboxymethyl (SCM) proteins show that the patterns on polyacrylamide gel electrophoresis (PAGE) are complex and that they may contain taxonomic information. Comparison of these patterns for 45 genera belonging to the Anseriformes led to the production of a dendrogram of intraordinal relationships (Brush, 1976a, b). Some feather keratin monomers are species specific, whereas others are tissue specific and appear to be characteristic of various feather parts such as the vane or rachis, or are typically found in the pennaceous or downy portion of the feather (O'Donnell, 1973; O'Donnell & Inglis, 1974; Fraser & MacRae, 1976; Busch & Brush, 1979).

Studies on the internal structure of shafts and barbs (by means of transverse sectioning) suggest that the cellular arrangements in medulla and cortex constitute a taxonomically important character: these configurations are con-

stant within a species, differ from related species only in detail, and include a basic pattern common to all species of a family (Frank, 1939; Auber & Appleyard, 1955; Auber & Mason, 1955; Auber, 1957, 1959, 1964; Swales, 1970; Dyck, 1977).

A more detailed study of the ptilomorphology (both external and internal) might answer the questions (a) to what extent are feather characters adaptive, and (b) which characters are to be considered primitive and which are derived. These aspects of phylogenetic analysis will require a detailed comparative study which may lead to new data with a bearing on the relationships of the higher taxa of birds. The fact that the general structure of barbules often does not vary within entire orders or families makes these characters suitable for phylogenetic studies at higher levels. The value of this study will reside in the possibility to apply it as an independent test to the results of several recent studies that are mainly based on a molecular approach (e.g. Lewin, 1985; Sibley & Ahlquist, 1986; Stapel, 1986).

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