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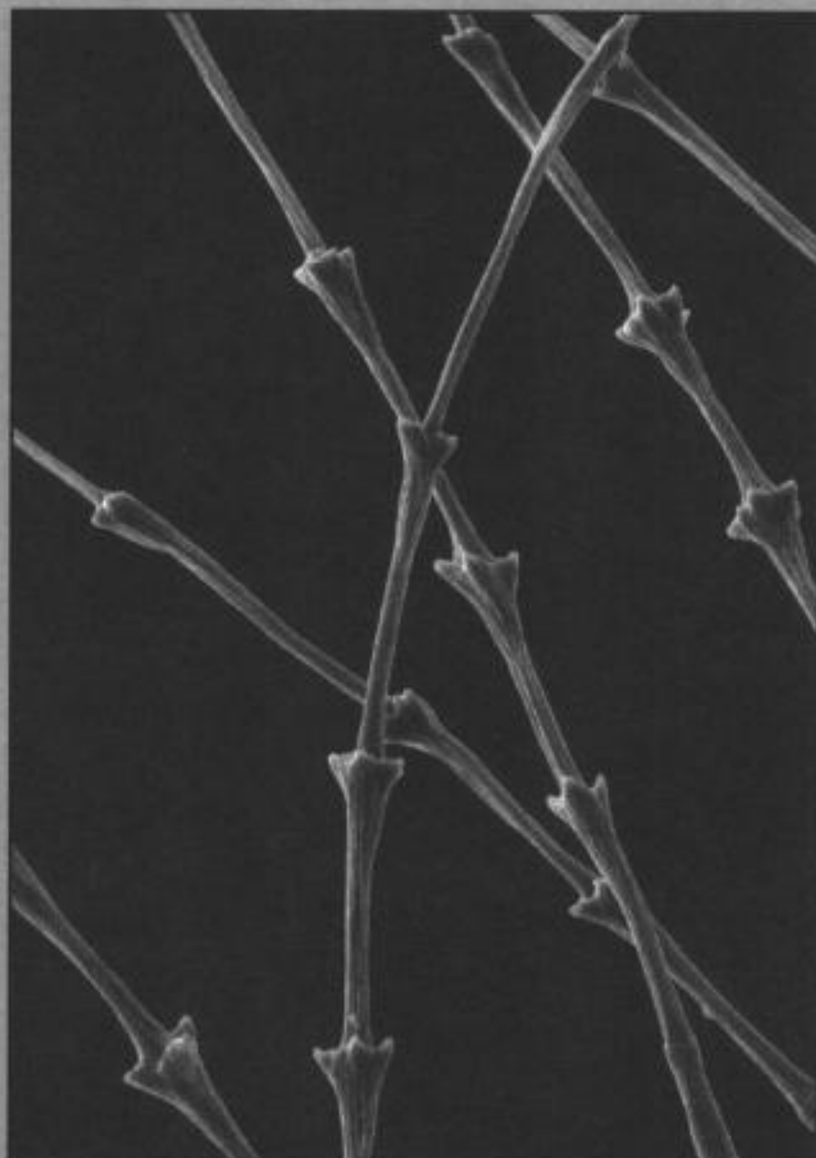

A Descriptive and Phylogenetic Analysis of Plumulaceous Feather Characters in Charadriiformes

by

Carla J. Dove

A DESCRIPTIVE AND PHYLOGENETIC ANALYSIS OF PLUMULACEOUS FEATHER CHARACTERS IN CHARADRIIFORMES

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Cover: Plumulaceous barbules of *Larus atricilla* (Laughing Gull) showing expanded nodes of true down. (SEM photo by Susann Braden.)

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A DESCRIPTIVE AND PHYLOGENETIC ANALYSIS OF PLUMULACEOUS FEATHER CHARACTERS IN CHARADRIIFORMES

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TABLE OF CONTENTS

ABSTRACT.—The variation in microscopic characters of plumulaceous feathers is well known to be useful as an aid in species identifications. However, until now, the phylogenetic significance of these characters has not been thoroughly investigated. In the first part of this study, electron and light microscopy were used to examine the range of variation in downy feather characters of more than 145 species of shorebirds (Charadriiformes) and outgroup taxa. The major results of Part 1 demonstrate that similarities and differences exist in the microscopic features within this order, that different downy types (true down vs. contour feather down) of the same individual may have different microscopic structures, that some shorebirds have villi (previously unknown on the barbule bases of this group), and 38 microscopic feather characters are deemed useful for phylogenetic study. In Part 2, parsimony analysis was used to assess the phylogenetic value of these characters by comparing feather results to hypotheses based on osteological data and traditional classification. Three different taxa lists are analyzed using the computer software PAUP, Star (*) version. Although initial analyses of 111 taxa and 38 feather characters found more than 10,000 equally parsimonious trees, the analyses provided evidence that feather characters were tracking some natural groupings in this order. Additional analyses on two smaller sets of taxa used feather characters alone (38 characters), osteological characters alone (68 characters), and a combination of both character types to search for shortest trees. The final reduced-taxa analysis shows that feather character tree statistics and character indices are comparable to those of skeletal characters. Incongruence in tree topologies is noted in the placement of plovers with sandpipers according to feather characters. Indices of total-evidence trees for 154 shortest trees are higher than either of the data sets alone. Convergence in microscopic feather characters of loons and auks has been documented here for the first time and a functional hypothesis for nodal morphology is proposed. In this study of Charadriiformes, microscopic feather characters prove to be comparable to osteological characters in tracking phylogeny. However, better results are achieved when the data sets are combined. These results support the utility of microscopic feather characters in phylogenetic studies and in microscopic identification of avian species from fragmentary evidence.

INTRODUCTION

. . . were it not for the fact that *Archaeopteryx* was feathered, this creature would have been classified unhesitatingly as a reptile.—Parkes (1966)

Although different organisms have converged on methods of flight, birds are most notably known to have evolved the intricate, delicate, extraordinarily complex and interlocking appendages of the integument known as feathers. The fact that *Archaeopteryx lithographica* had feathers indistinguishable from those of modern birds was instrumental in the early classification of this fossil animal. Even recent controversies of bird–dinosaur relationships have cited the presence of feathers on fossil specimens of theropods as "unambiguous" proof that birds descended from dinosaurs (Ji et al. 1998). The evolutionary achievement of the early invention of feathers serves the dual function of thermoregulation and flight, thereby contributing greatly to the success of the avian class of vertebrates. In addition to these primary functions, feathers are exceptionally diverse in many other respects. The extreme length of the tail feathers of the Crested Argus (*Rheinardia ocellata*); the extraordinary beauty of the upper tail coverts of the male

Indian Peafowl (*Pavo cristatus*); the camouflaged plumage of the Whip-poor-will (*Caprimulgus vociferus*); the iridescence of the hummingbirds; and the multitude of intricate feather patterns, colors, shapes, and textures used in sexual displays, all contribute to the complexity, diversity, and beauty of feathers. Not surprisingly, one then should look to this structure for information pertaining to the evolution of birds.

Chandler (1914, 1916) was one of the first to examine and describe the microscopic variation of downy feather barbs among many different groups of birds. He relied on studies of pennaceous feather structure by Nitzsch (1867) and pterylology (the arrangement of feathers in definite areas of growth) as a base for his detailed work on the taxonomic significance of microscopic structures of both downy and pennaceous feathers. Chandler's (1916) early studies showed that the microstructures of feathers varied enough to allow group designation from feather structures alone. Chandler (1916) was also the first to note the applied importance of identifying species of birds from feathers seized by U.S. Customs agents.

The feather identification technique gained importance as an applied science in the early 1960s when Roxie Laybourne, researcher at the Smithsonian Institution, was called upon to identify bird remains recovered from the crash of a Lockheed Electra aircraft at Logan International Airport (Lipske 1982). When Laybourne identified the culprits of that crash (which killed 62 people) as European Starlings (*Sturnus vulgaris*), the aviation industry began to search for ways to control birds on airfields and reduce the risk of damage to engines. Bird strike identification is currently the most demanding application of feather identification. On average, 2,600 bird strikes per year cause $40 million worth of damage to military aviation alone (LeBoeuf 1997). If the species of birds involved in bird strikes is known, airfield personnel can implement habitat management schemes that discourage bird use of airfields, and aircraft manufacturers can better design engines and aircraft to withstand the impact of bird collisions.

By studying the variation in microscopic plumulaceous (downy) feather characters such as barb and barbule length, nodal morphology, and pigmentation patterns in conjunction with whole-feather characters of size, texture, color, and pattern, positive identification of species of birds is possible from fragmentary feathers. This is done by comparing the unknown sample to a museum collection of study skins and/or a microslide reference collection of known species. The identification of species by use of micro- and macroscopic feather characters, together with circumstantial evidence (locality, date, time of day) pertaining to the unknown sample, has led to the field of forensic ornithology.

Throughout the years, the ability to determine species of birds from feather fragments has been applied to various disciplines: archeological studies of excavated artifacts (Hargrave 1965; Messinger 1965), determination of food habits from prey remains (Day 1966; Gilbert and Nancekivell 1982; Griffin 1982; Ward and Laybourne 1985; Joy et al. 1994), forensic science investigations (Davies 1970; Deedrick and Mullery 1981), examination of food contaminants (Olsen 1981), identification of fossil feather remains (Bennike and Dyck 1986; Steadman 1988; Humphrey et al. 1993; Laybourne et al. 1994), law enforcement and customs cases (Laybourne, pers. comm.), anthropological studies of feathered artifacts (Dove 1998a; Laybourne, pers. comm.), and analysis of bird–aircraft collisions (Manville 1963; Laybourne 1974; Rosalind and Grubh 1986; Brom 1991).

Although these studies demonstrated the applied importance of using feather characters for bird identifications, none fully explored the systematic potential of these characters, despite Chandler's (1916:385) early statement on the taxonomic value of feather characters: "... the morphology of feathers, in other words, the epiphyology of birds, is as valuable from a taxonomic point of view as is osteology, myology, or the systematic morphology of any other organ or system of organs of the body."

In contrast to very early studies that focused on pennaceous feather structure, more recent researchers have started to seriously investigate the taxonomic and systematic significance of the microstructures of plumulaceous feathers. The fact that interspecific variation exists in microscopic characters of downy barbs of feathers is now well documented (Chandler 1916; Messinger 1965; Day 1966; Reaney et al. 1978; Robertson et al. 1984; Horton 1990; Brom 1991; Dove 1994, 1997, 1998b; Laybourne et al. 1994; Shamoun 1994). These investigations have focused on the plumulaceous part of the feather because this is where the most diagnostic variation is observed. A reasonable a priori assumption for the observed differences in feather types (pennaceous vs. plumulaceous) is due to function. Because one of the main functions of feathers is to aid flight, evolutionary and environmental restrictions act to limit the amount of variation the pennaceous feather can undergo and still perform optimally. For example, a finite number of ways exists in which a hooklet can vary and still function as an interlocking structure. Plumulaceous feathers, on the other hand, are located at the base of the contour feather and are more protected from environmental influences by the overlapping pennaceous feathers. This arrangement may explain why we see more variation in plumulaceous feathers—these structures are more free from functional constraints.

Chandler (1916) and Messinger (1965) voiced concerns about intraspecific variation in vane symmetry and within-vane variation of the same feather. Dove (1997) examined plumulaceous barbs of North American plovers and showed that if the same vane region of feathers from the same feather tract position is studied across taxa, then it is possible to use plumulaceous feather characters to discriminate closely related species. Gilroy (1987) studied the variation of the plumulaceous barbs among feather tracts of the Rock Dove (*Columba livia*) and found diagnostic characters with little variability in all 52 tracts surveyed. These studies provide quantitative proof that microscopic feather characters can be used to aid in species identification and therefore may have some phylogenetic significance.

Although Brom (1991) and Shamoun (1994) provided general descriptions of a few diagnostic feather characters for a wide variety of birds, they did not conduct computer-assisted cladistic analyses to describe interrelationships, phylogenies, or character evolution of plumulaceous feathers. Although the phylogenetic significance of microscopic feather characters has been strongly suggested by Brom (1991) for a few "good" identifiable characters (e.g., 'detachable nodes,' villi, and flexules), he did not test those characters in combination with other microscopic feather characters or in conjunction with other data sets to identify convergence or parallelism (homoplasy). Thus, even though microscopic feather characters are well known to aid in species identification, the identifiable characters have yet to be shown to be linked to phylogeny. It is now time to begin investigations of the phylogenetic significance of microscopic feather characters. One step in such an investigation is to conduct a comprehensive, detailed description of the microscopic variation of downy feather characters in a large, monophyletic group of birds.

This study primarily will describe in detail the microscopic differences of plumulaceous feather characters observed in the avian order Charadriiformes (shorebirds and allies) and secondarily will test the phylogenetic informativeness of these characters. Although Dove (1997) has shown that microscopic differences exist at the generic level, this study will explore the phylogenetic significance of multiple feather characters at various taxonomic levels. Analysis of this type is necessary to determine whether feather characters track history as opposed to other adaptive or environmental influences. This type of study would not have been possible without previous studies that addressed very basic questions concerning variation in feather characters, and previous phylogenetic studies of the Charadriiformes using other traditional means of analysis to support monophyly in this order of birds.

The order Charadriiformes is interesting for phylogenetic study because the large order is cosmopolitan in nature and includes diverse morphological types. The species of this order inhabit a wide variety of environments and habitats, thus providing interesting ecological specialities. The order Charadriiformes also presents a unique opportunity for study because the results from the feather character analysis can be compared with two recent and comprehensive phylogenetic studies of shorebird relationships; one based on molecular data (Sibley and Ahlquist 1990) and the other on reanalysis of Strauch's 1978 osteological data (Chu 1995). These studies, together with the substantial amount of systematic research done in the past, makes this order one of the most well-studied groups of birds. An evaluation of the phylogenetic significance of microscopic feather characters is necessary to corroborate the feather identification technique, search for additional characters for phylogenetic studies, and test the significance of these characters for systematic and evolutionary investigations of birds. The order Charadriiformes provides an ideal base for such a study.

REVIEW OF CHARADRIIFORM SYSTEMATICS

Charadriiformes comprise the largest nonpasserine order of living birds. Recent sources (Sibley and Ahlquist 1990; Sibley and Monroe 1990) cite 85 genera and 366 species. The group is generally referred to as the waders, gulls, terns, and auks, but also includes several less familiar types (seedsnipes, sheathbills, and others). According to Sibley and Ahlquist (1990), the families of Charadriiformes currently include Pteroclidae (sandgrouse), Thinocoridae (seedsnipes), Pedionomidae (Plains-Wanderer), Scolopacidae (sandpipers and allies), Rostratulidae (painted-snipes), Jacanidae (jacanas), Chionididae (sheathbills), Burhinidae (thick-knees or stone curlews), Charadriidae (plovers and allies), Glareolidae (pratincoles and coursers), and Laridae (gulls and terns) under which Alcinae (auks) are given subfamilial rank. The most recent significant changes to the order include the addition of the sandgrouse by Fjeldså (1976) and the inclusion of the Plains-Wanderer by Olson and Steadman (1981) with DNA support of both additions by Sibley and Ahlquist (1990). A complete historical review of this order, going all the way back to the 1700s, can be found in Sibley and Ahlquist (1990), but for the purposes of this study only significant changes and additions to taxonomy and classification are reviewed in detail here.

Huxley (1867), who studied skull characteristics, focused on higher-level systematics and was the first to unite the birds currently included in Charadriiformes (waders, gulls, and auks). The next major work on this group of birds occurred in the early part of the 20th century when Lowe (1914) began publishing a long series of papers (see Sibley and Ahlquist 1990 for references) on the anatomy of previously unstudied species in the order, skeletal characters useful for systematic study, and plumage patterns and pterylosis in many different shorebirds. Lowe's work (1931) concluded that the order consisted of 19 families and included combining several families of Gruiformes (Gruidae, Psophiidae, Otididae, Burhinidae, and others) as a suborder with the Charadriiformes in an order that he designated Telematoformes. Peters (1934) recognized 16 families with the larger family groups of Charadriidae, Scolopacidae, and Laridae split into several subfamilies and gave alcids subordinal rank. Mayr and Amadon (1951) listed 10 families, most of which were not subdivided, and suggested that the order, which they called Laro-Limicolae, could be connected with cranes through Burhinidae, Jacanidae, and Thinocoridae. They gave the scolopacids, phalaropes, avocets, and painted-snipes subfamily status under Charadriidae. Wetmore (1960) divided the Charadriiformes into three suborders: Alcae (auks), Lari (gulls and terns) including jaegers and skimmers, and Charadrii (plovers, sandpipers, and allies). However, Wetmore (1960) agreed with Moynihan (1959) on ranking Rynchopidae (skimmers) as a separate family by citing distinct osteological peculiarities, bill morphology, and a unique vertical orientation of the pupil in the eye.

Lower taxonomic levels, such as designations of species relationships to families, subfamilies, and genera, are well established by studies such as those by Bock (1958), in a generic review of the plovers; Kitto and Wilson (1966) on the unique *S*-malate dehydrogenase enzyme in Charadriiformes; Jehl (1968a) on the relationships of Charadrii based on color patterns of the downy young; Zusi and Jehl (1970) on generic relationships of three Charadrii species; Maclean (1972a) on display postures in Charadrii; Christian et al. (1992a) in biochemical systematics of Australian dotterels and plovers (Charadriidae) and also (1992b) on the biochemical relationships between three of the main groups (Charadrii, Scolopaci, Lari) within the order; behavioral studies by Phillips (1980) and Ward (1992); clutch size in Charadrii by Maclean (1972b); the affinities of *Eudromias* to *Charadrius* (Nielsen 1975); the systematic position of the surfbird (Jehl 1968b); and the morphology of the syrinx in five families of the order (Brown and Ward 1990).

Despite these detailed studies, the interrelationships of the higher taxa within this order are still poorly understood and highly disputed. In recent years, authors have attempted to clarify interrelationships by conducting detailed phylogenetic studies involving many taxa. In the last 20 years, two major publications using different character data sets have resulted in hypotheses of the phylogenetic relationships of Charadriiformes. The first was an extensive character compatablitiy study by Strauch (1978) based on 70 mostly osteological characters of 227 taxa, which were reanalyzed extensively by Chu (1995). The next major classification of this group of birds was proposed by Sibley and Ahlquist (1990), who used DNA–DNA hybridization techniques to assess the phylogenetic relationships of birds of the world. Sixty-nine species of shorebirds were part of their comprehensive study.

Strauch's (1978) character compatibility analysis study identified three major

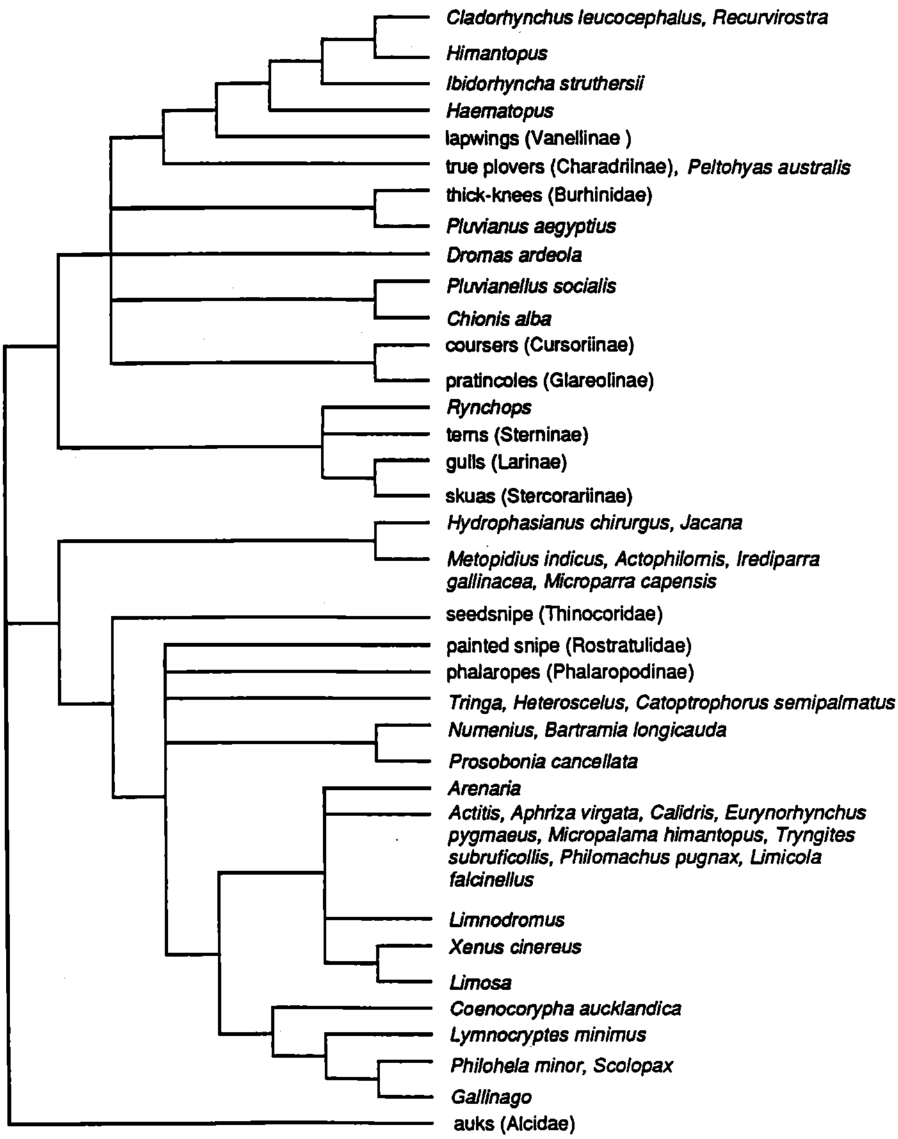


FIG. 1. Strauch's hypothesis of charadriiform phylogeny based on compatibility analysis of osteological characters (from Chu 1995, fig.1).

groups within Charadriiformes: Scolopaci, Charadrii (including larines), and Alcae (Fig. 1; from Chu 1995, fig. 1). In this study, Strauch found the Jacanidae to be a sister taxon to the sandpiper-like birds and the Thinocoridae to be a sister taxon to scolopacine waders. His Charadrii consisted of two clades, one, an unresolved polytomy of Glareolidae (coursers), Burhinidae (thick-knees), *Dromas ardeola* (Crab Plover), *Chionis alba* (Snowy Sheathbill), and the charadriine waders (including avocets and allies); the other clade included Stercorariidae, Laridae, and Sternidae.

Strauch's (1978) original character-coded matrix has been reanalyzed in at least three different publications. Mickevich and Parenti (1980) criticized Strauch's methods of character compatibility in a philosophical sense and re-evaluated his data set using a different method (Wagner tree parsimony). The results of their analysis differed from Strauch's in having two major groups, with Alcae as one clade and everything else as another, and they restructured Strauch's tree, which had three monophyletic clades, making one of those clades (Charadrii) paraphyletic with respect to another (Scolopaci). They reconstructed *Chionis* and *Pluvianellus socialis* to be a sister taxon of gulls, terns, skuas, skimmers, glareolids, thick-knees, and *Dromas ardeola.*

Björklund (1994) made the second attempt at reanalyzing Strauch's data by reducing the number of taxa to obtain better resolution within major groups with parsimony analysis and successive approximations weighting. In his analysis, the family Alcidae was found to be a sister group to the rest of the clade and the scolopacine and charadriine waders were monophyletic and formed distinct sister groups. A clade comprising *Chionis* (including *Pluvianellus socialis*) and *Dromas ardeola* was placed as sister taxa to *Glareola* plus scolopacines and charadriines. Two taxa (*Glareola* and Burhinidae) failed to group with the other plover-like birds, differing from the analyses of Strauch (1978) and Mickevich and Parenti (1980). Jacanidae were embedded within the scolopacine clade.

The third and most comprehensive reanalysis of Strauch's (1978) data was conducted by Chu (1995). Chu's study used parsimony analysis and re-examined and modified Strauch's coding decisions with regard to the criticisms of Mickevich and Parenti (1980). Although Chu (1995) recognized those criticisms, he also pointed out major flaws in the review by Mickevich and Parenti, which he attributed to their erroneous rejection of many characters. Chu's study agrees with that of Mickevich and Parenti by placing the alcids at the base of the charadriiform clade, whereas Strauch depicted this group as part of a basal trichotomy. In a reduced-matrix version, Chu agreed more with Strauch in placing all other charadiiform-like birds in two groups: scolopacines (sandpiper-like) and charadriines (plover-like). Chu's analysis supported five sandpiper lineages, placed *Dromas ardeola* (Crab Plover) with the gull-like birds, and grouped the sheathbills with *Pluvianellus socialis* (Magellanic Plover) within the plover-like group (Fig. 2; from Chu 1995, fig. 6).

Sibley and Ahlquist (1990) were the first to apply the technique of DNA–DNA hybridization to estimate the relationships of 69 species of shorebirds as part of their encompassing study on molecular systematics of birds of the world. Although the methods and results of their phylogenetic analysis have been widely criticized by ornithologists and molecular biologists (for example, Cracraft 1987; Houde 1987; O'Hara 1991; Lanyon 1992), their study remains one of the most recent and comprehensive hypotheses of shorebird relationships. Additionally, their study offers an alternative approach to traditional morphological studies by using genetic characters to estimate phylogeny.

Sibley and Ahlquist (1990) found the Charadriiformes to constitute two groups, the birds similar to sandpipers and those similar to plovers (Fig. 3; from Chu 1995, fig. 9). Alcids were placed within the plover group. The plover-like group was divided into two groups: one consisted of the plovers, lapwings, stilts and avocets, oystercatchers, thick-knees, and *Chionis*; the other included the coursers and pratincoles, *Dromas ardeola,* auks, and larids. In the tree of Sibley and Ahlqu-

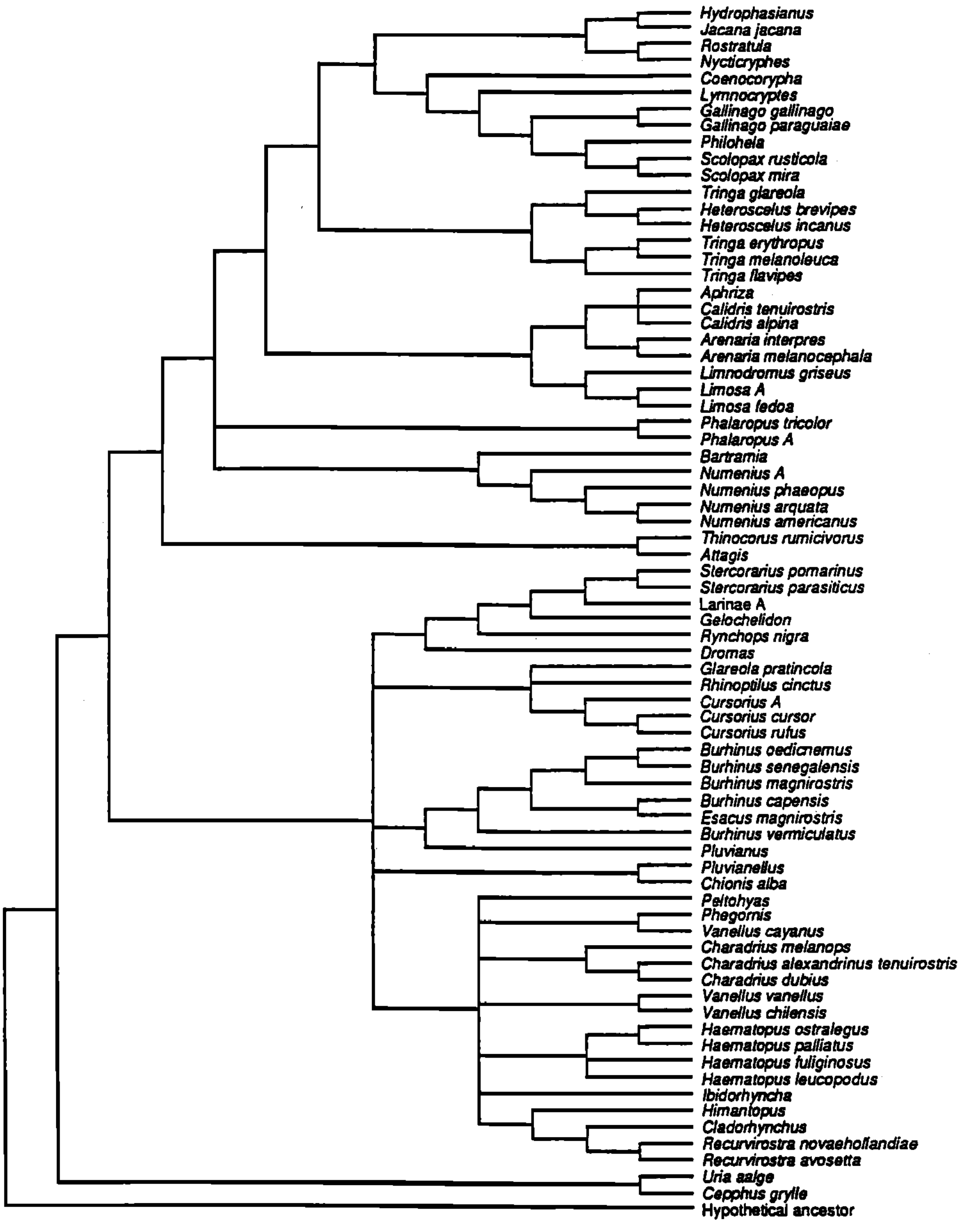


FIG. 2. Chu's (1995) hypothesis of charadriiform phylogeny based on parsimony analysis of Strauch's revised osteological characters (from Chu 1995, fig. 6).

ist, the seedsnipe/Plains-Wanderer group was most similar to the sandpiper group, and the jacana/Greater Painted-snipe group was most similar to the seedsnipe/ Plains-Wanderer clade.

Therefore the most recent analyses of charadriiform phylogeny have depended on reanalysis of Strauch's (1978) study, or on the highly criticized methods and results of Sibley and Ahlquist (1990). The objective of the current analysis is to

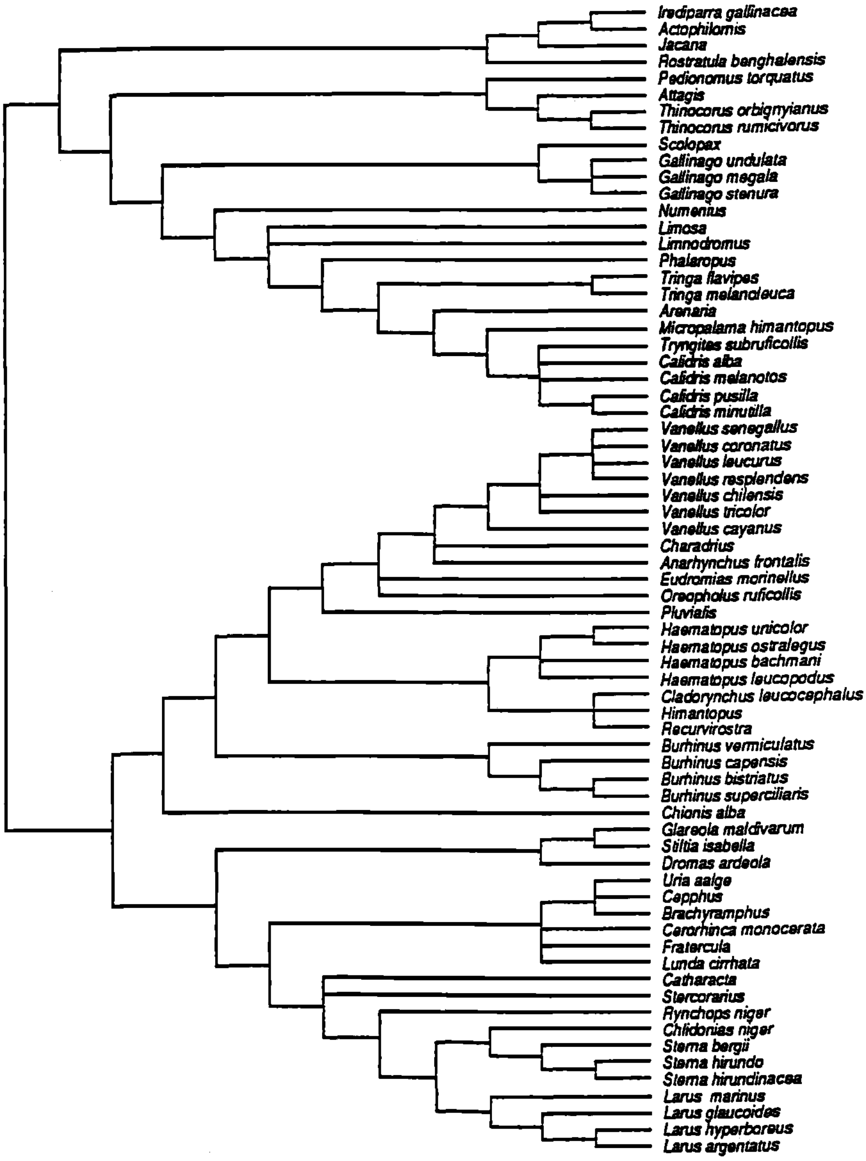


FIG. 3. Sibley and Ahlquist's 1990 hypothesis of charadriiform phylogeny (from Chu 1995, fig. 9).

introduce a new set of characters with which to analyze this avian order. The primary purpose of this study is to describe the variation in morphological structures of downy feathers in the avian order Charadriiformes. The original contribution lies in the analysis of the microscopic feather characters using phylogenetic methods to determine the evolutionary informativeness of those characters. The data in this study were examined in two ways. First, two character data sets were analyzed separately to assess the performance of osteological and feather characters independently, and to later determine the contribution of each set of characters to the whole. Then, the data sets were analyzed simultaneously in a total-evidence analysis according to the arguments of Kluge (1989). The intent here is not to present a "true" phylogeny based solely on microscopic feather characters, but rather to investigate how well feather characters track phylogeny when compared with other types of data (e.g., skeletal, DNA). The need for new characters in phylogenetic analyses is best summarized in Chu's (1995:193) statement concerning controversies over recent charadriiform phylogenetic hypotheses: "[I]t is the addition of new characters, and not a comparison of trees, that will prove the final arbiter in any discussion over which estimates of relationships are most strongly supported."

PART 1

A DESCRIPTIVE SURVEY OF DOWNY FEATHER CHARACTERS IN CHARADRIIFORMES

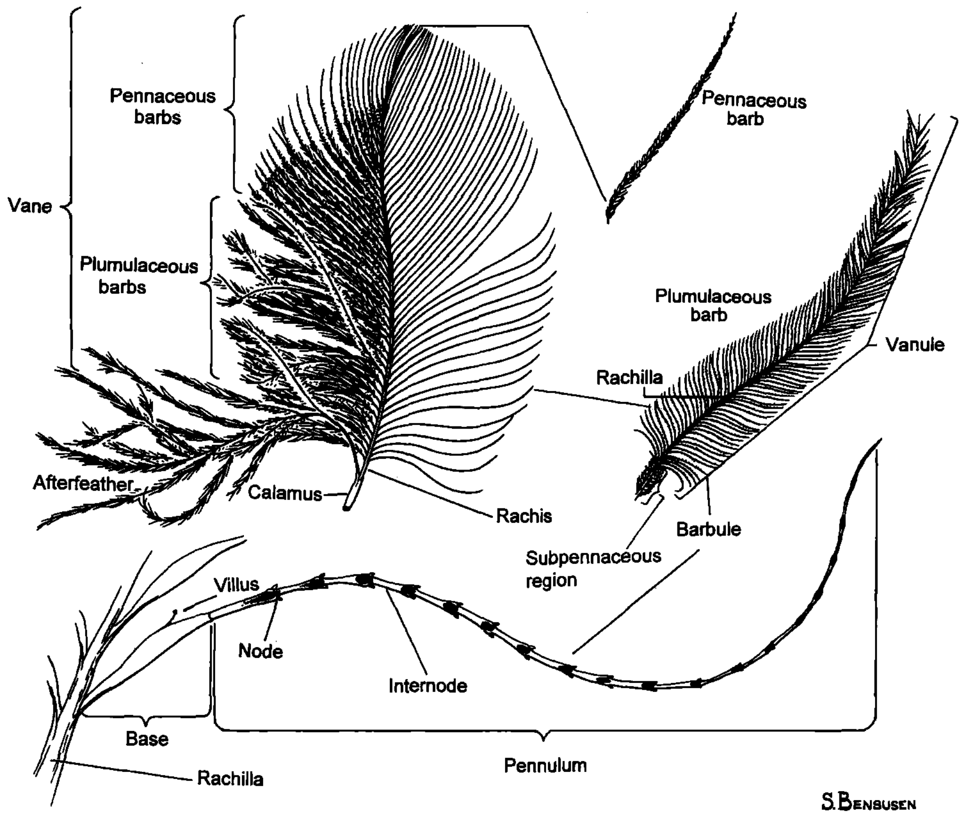
The results of character-based methods of analysis depend on the quality and scoring of the characters that are being analyzed. In fact, when incongruent phylogenies are encountered, character selection and coding are often the first aspect of the analysis to be scrutinized, and delimitation of characters remains the most challenging and influential aspect of phylogenetic inference (Pogue and Mickevich 1990).

Because multiple microscopic feather characters have never been used in a phylogenetic reconstruction of any group of birds, a detailed investigation of the microscopic variation in plumulaceous (downy) feather characters must be the first step in any attempt to assess the significance of such characters. The purpose of this descriptive study is to provide basic knowledge of the range of character variation within Charadriiformes and outgroups (Gruiformes, Gaviiformes, Columbiformes) and to serve as a base for defining microscopic feather characters for phylogenetic study.

During the course of this investigation, certain microscopic feather features warranted further investigation and study with the scanning electron microscope (SEM). The results of studies on pigmentation in different down types, base cell composition, and villi are provided at the end of the results of this section.

Feather Structure

Contour feathers consist of a rachis with vanes on either side and, in most birds, an afterfeather (Fig. 4; from Laybourne et al. 1994, fig. 1). Most vanes are composed of both stiff, pennaceous barbs that interlock and make up the surface of a feather and plumulaceous barbs, which are commonly referred to as downy barbs. In addition to natal down, most birds have at least three types of downy feathers: contour feather down (plumulaceous), true feather down (plumules), and afterfeather down (Fig. 5). Contour feather down is fluffy in appearance and is located at the base of body feathers. Rectrices and remiges also usually have a small amount of down at the very base of the feather. True down is completely fluffy in appearance and is located beneath main feathers in between feather tracts



NODE

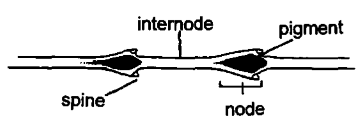


FIG. 4. Topography of a contour feather (from Laybourne et al. 1994, fig. 1) and plumulaceous node.

on the body of the bird. Afterfeather down refers to the downy barbs of the afterfeather, which is attached to the main feather at the superior umbilicus. Barbs of all down types consist of a rachilla (ramus) with vanules on either side, which, in turn, are made up of barbules. Barbules, branching from the rachilla of barbs, are the smallest division of the feather and consist of a base and a pennulum. Subpennaceous regions are only present on some contour feather down. If present, this region is located at the very base of barbs and contains barbules that have structural similarities to pennaceous feathers (long, straplike base, and pennulum with hooklets on distal vanule). See Figure 6 for location of subpennaceous region and Appendix 1 for feather terminology.

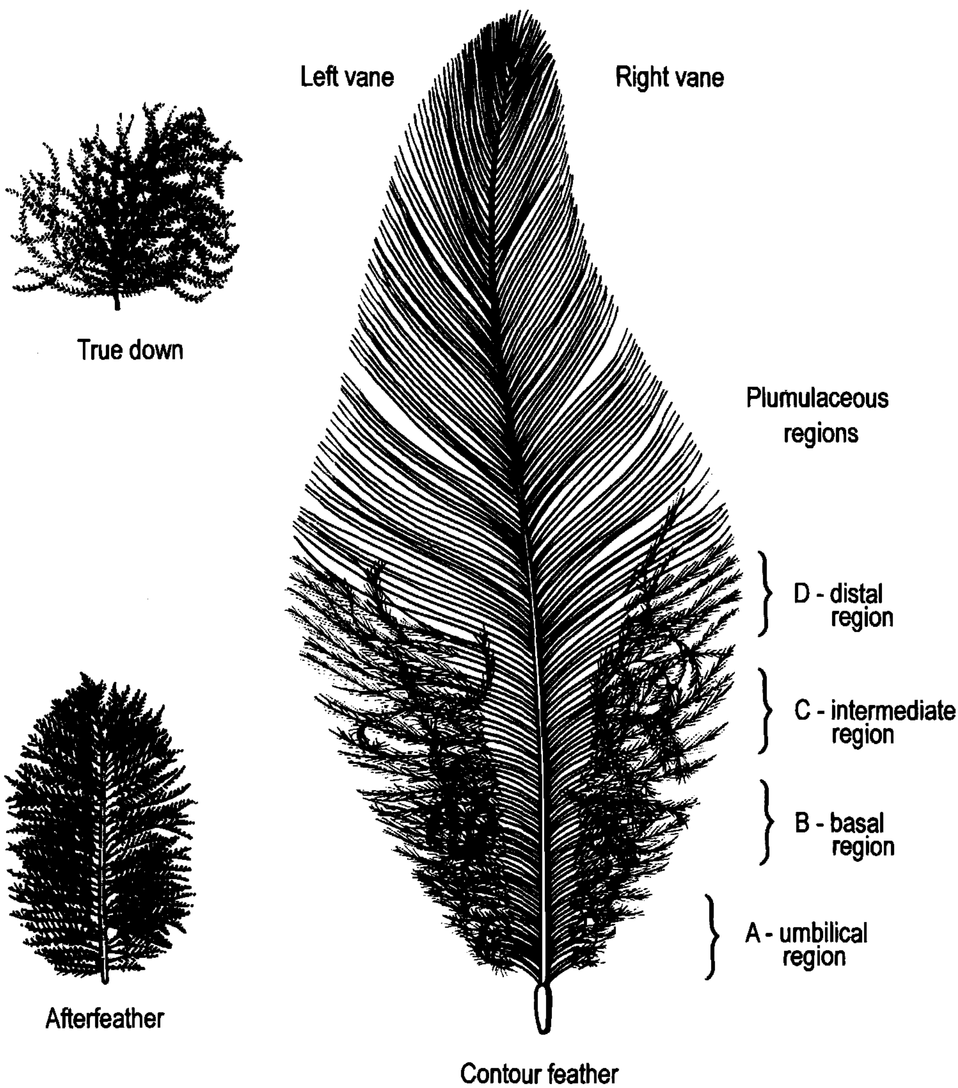


FIG. 5. Types of downy barbs (true down, afterfeather, contour feather) with plumulaceous regions shown on contour feather.

METHODS

A detailed description of feather characters for each species selected for study was conducted using qualitative observations, light microscopy (LM), and SEM. After an initial list of all possible microscopic characters was created, index cards with barbule sketches of nodal distribution and barbule pigmentation patterns, true and afterfeather down characteristics, and general notes of microscopic characters were made for each species examined. A large sample of as many species as possible is necessary to search for general family characteristics and to determine which characters may be useful for phylogenetic analysis. Therefore, previously prepared microscope slides from a reference collection were also exam-

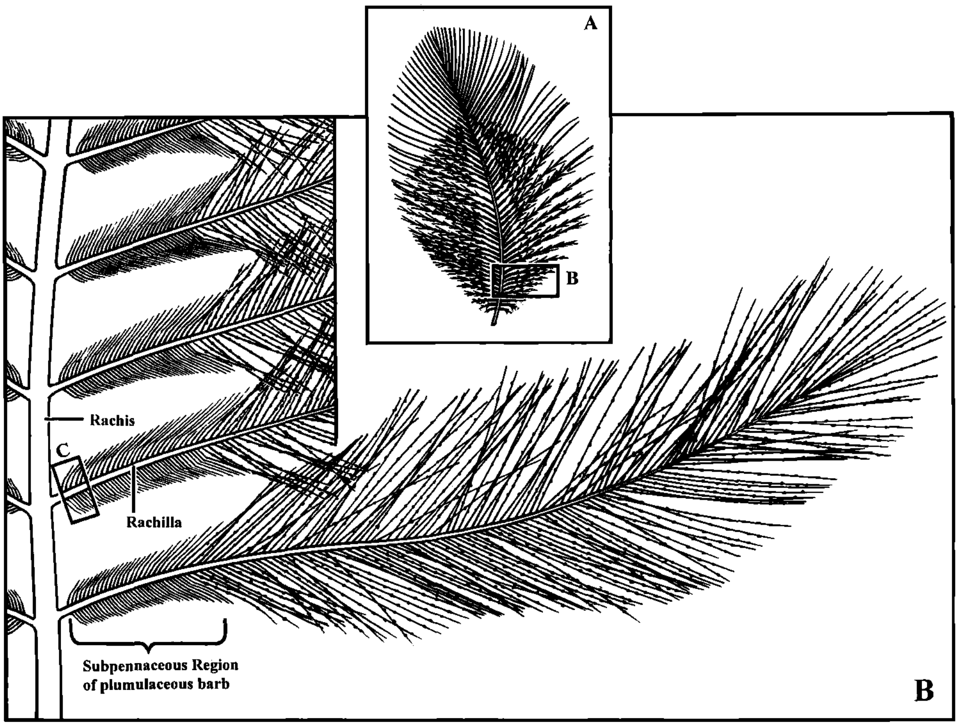


FIG. 6. Location of subpennaceous region. (*A*) Contour feather. (*B*) Plumulaceous region. (*C*) Vanules of subpennaceous region (see Fig. 141A, B). Spacing between barbs is exaggerated to allow better illustration of subpennaceous region.

ined in this descriptive part of the study and increased the sample size of charadriiform taxa to more than 145 species including 16 outgroup species. In this study of microscopic feather characters, the taxonomy of Peters (1934) and Morony et al. (1975) is followed to allow for outgroup comparison of Pteroclidae (Columbiformes).

Museum study skins of five adult males within 16 families (Morony et al. 1975) and six outgroup species (bustard, crane, coot, sandgrouse, and loon) were used for initial LM comparisons (Appendix 2; species codes follow Edwards 1982). Sandgrouse were considered outgroups in this study because of traditional placement within Columbiformes. Male specimens in breeding plumage were examined for the sake of consistency. However, because personal observation has shown that sexual or plumage variation does not affect the plumulaceous microcharacters, females and nonbreeding specimens were used when necessary. Terminology pertaining to feather topography follows Figure 4 and definitions of Appendix 1.

FEATHER PREPARATION

Light microscopy.—Only the barbs were removed from the upper left breast feathers (pectoral feather tract) of all museum specimens selected for study. Microscopic analysis was conducted on the umbilical and basal regions (shown in Fig. 5) of the plumulaceous part of the contour feather for basic character descriptions. Downy barbs from the afterfeather down and true down were also examined on one specimen of each species. LM was conducted at low (40×), mid- (100×), and high (400×) power on an American Optical compound (American Optical, Columbia, MD) or Reichert (Reichert-Yona Microscope and Instrument Company, Columbia, MD) comparison light microscope. Microslide preparation generally followed the methods described in Laybourne and Dove (1994) and Sabo and Laybourne (1994). First, a thin aqueous layer of xylene was applied to a precleaned microslide. This allowed the barbules to spread apart and facilitated microscopic analysis. Downy barbs were then removed from the feather using microforceps and placed on the xylene layer. After the xylene dried, the feather sample was covered with several drops of Flo-Texx® mounting medium (Columbia Diagnostics, Springfield, VA). Flo-Texx® is a brand-named mounting medium that is ideal for use on plumulaceous feathers because it has a refractive index similar to that of water and it does not discolor or yellow over time. Immediately after applying the mounting medium, a glass coverslip was gently placed over the Flo-Texx® and the slide was allowed to dry before microscopic examination.

In this study, 6–10 plumulaceous barbs from each individual were mounted on a single microslide in the following order: umbilical barbs, far left; basal barbs, center; intermediate barbs, far right. A total of seven microslides was prepared for each species: one slide each of five different specimens (right and left vanes) of contour feather down, one slide of afterfeather down, and one slide of true down. This allowed for examination of variation within down types and among individuals. A camera lucida was used to illustrate microscopic variation of pigmentation patterns and morphology in selected species, which are shown in illustrated barbule figures. No attempt was made to designate barbule length in the feather illustrations.

Scanning electron microscopy.—Scanning electron microscopy was used on selected species from each family to examine surface features of plumulaceous feathers and provide detailed three-dimensional images of nodal morphology and feather ultrastructure. Thirty-one charadriiform and five outgroup species were selected for SEM study of shorebird characters. Four other noncharadriiform taxa (*Eremophila, Sphyrapicus, Archilochus, Nectarina*) were studied with SEM to compare villi characteristics. For SEM examination, umbilical and basal plumulaceous regions of contour feathers (upper left breast) were sampled in all species except *Larus atricilla.* True down was studied in this species with SEM because the family Laridae has the distinction of having diagnostic characters mostly in the true down.

Because of the intense cleaning process involved in SEM study, the entire feather instead of barbs was removed from selected specimens and prepared according to Laybourne et al. (1992) with the exception that stubs were not stored in a desiccator. Feathers were blown with compressed air to remove large dirt particles, washed twice in a mild soap–hot water solution, and rinsed in warm water after each wash. After this initial cleaning, each feather was washed once in Triton® X-100 solution (Fisher Scientific, Pittsburgh, PA) and rinsed in several changes of warm water. Feathers were then placed on clean paper towels to drain and dried with compressed air. Next, the feathers were washed twice in ethanol (70–100%) and dried again with compressed air. Final drying was accomplished by directing compressed air through a mesh strainer that was inverted over feathers on a clean paper towel. Each dry feather was transferred with forceps to a labeled, clean, plastic zipper-closure bag for storage. SEM stubs were washed in

100% ethanol and dried with a linen cloth. Downy barbs were mounted on stubs with double-sided sticky tape. Smooth-surface, nonstick paper was used to gently press the barbs onto the sticky tape. The prepared stubs were sputter coated with gold palladium to a thickness of 30 nm and viewed using a Leica Stereoscan 440 (LEO) (Leica Stereoscan Leo Electron Microscopy, Inc., Thornwood, NY) scanning electron microscope with an accelerating voltage of 10 kV and a working distance of 10 mm at various magnifications (400–5,000×).

Because experience has shown that feathers prepared for SEM study do not store well over time, SEM photomicrographs serve as the permanent archival record. Images were saved to 'tif' format. Photomicrographs were made using Adobe Photoshop Version 3.0 (Adobe Systems Incorporated 1994).

Family descriptions of microscopic feather characters are mainly based on those observed in contour feather down (plumulaceous) unless otherwise noted (e.g., gulls). Character descriptions are based on morphology of proximal nodes of barbules because these generally provide the most diagnostic features. All species examined are listed at the beginning of each family heading.

Descriptive Survey

General biological and geographical summaries are provided along with microscopic feather descriptions for each family studied. Geographic distribution and general biological information are summarized from Austin (1961), Walters (1980), Harrison (1983), and Hayman et al. (1986). SEM photomicrographs and camera lucida illustrations are intermixed with the text. Illustrations of barbules are arranged with basal (top), mid- (middle), and distal (bottom) sections of barbules shown for a variety of species. Barbule and nodal morphology and pigmentation patterns are described from plumulaceous barbs of contour, afterfeather, and true down feathers. The presence of a subpennaceous region and a description of it are noted for each species and each feather type. The type of feather examined and the presence of villi is noted when applicable. Species that vary within families are discussed at the end of each family section.

Ingroups

Charadriiformes

Shorebirds, gulls, terns, and auks make up this cosmopolitan order of more than 300 species. Members of the order are found worldwide, including the polar regions. Most species inhabit coastal waters, beaches, marshes, and meadows. However, some species are pelagic, some occur inland, and some prefer freshwater habitats. General size, bill shape, and plumage are highly variable within this group. Charadriiformes are typically sexually monochromatic or exhibit only minor sex-related plumage differences except for the painted-snipes, phalaropes, and the Ruff. Because some groups and species within groups deviate from general microscopic feather patterns, a more detailed survey of each family within this order is described below.

Jacanidae

Jacana jacana (Wattled Jacana)

Jacanas are birds of tropical and subtropical continents that live near lakes or pools with surrounding low-water vegetation. Some of the eight species in this

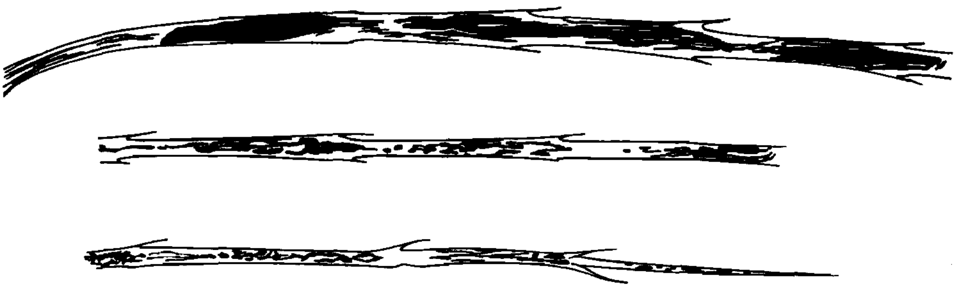


FIG. 7. Barbule of contour feather down of *Jacana jacana.*

family have a frontal shield similar to the coots and gallinules or wing spurs like some plovers (*Vanellus*).

Contour feather down.—Most barbules are short and heavily pigmented throughout the entire length of the barbule (Fig. 7). Very dark pigment extends all along the barbule but is heaviest at the most basal nodes. Although pigment is more intense at the nodes, heavy stippling is typical in the internode. The pigment is often constricted to a distinct diamond-shaped point where it enters the node but at some mid-barbule nodes pigment is less intense and more stippled proximal to the pigmented node. Some mid- and distal internodes may not be as heavily pigmented. The basal cell of the barbule is pigmented. High-power microscopy (400× LM, 800× SEM) shows spines at nodes (Fig. 8). Spines are usually longer at nodes on the distal portion of the barbule (Fig. 9). Jacanas have a well-developed subpennaceous region (Fig. 10).

Afterfeather and true down.—Plumulaceous barbules of the afterfeather and true down are similar to those of contour barbules in pigmentation patterns and general morphology. However, barbules of these feather types are finer and more filamentous. No subpennaceous region is present in these down types.

Rostratulidae

Rostratula benghalensis (Greater Painted-snipe)

Painted-snipes (two species) live in tropical and subtropical marshlands. Superficially they resemble snipes and have woodcock-like rounded wings. Sexual dimorphism is somewhat marked with females being brighter.

Contour feather down.—The microscopic feather structures of *R. benghalensis* (Fig. 11) are extremely similar to those of *Jacana jacana* (Fig. 7). The main observable differences are that the plumulaceous barbules of *Jacana* are somewhat more heavily pigmented and slightly shorter, and distal nodes on barbules have a greater number of long prongs than is observed on those of *Rostratula.* Barbs and barbules of *Rostratula* are heavily pigmented throughout. Pigmentation is heavy at nodes and becomes more stippled proximal to nodes. Spines are present at nodes (Figs. 12, 13) and become longer at nodes on the distal portion of the barbule (Fig. 14). The subpennaceous region and basal cells are pigmented.

Afterfeather and true down.—The barbules of these plumulaceous feathers are similar to those of the contour feather but do not have a subpennaceous region. Plumulaceous barbs and barbules of these down types are finer than those of

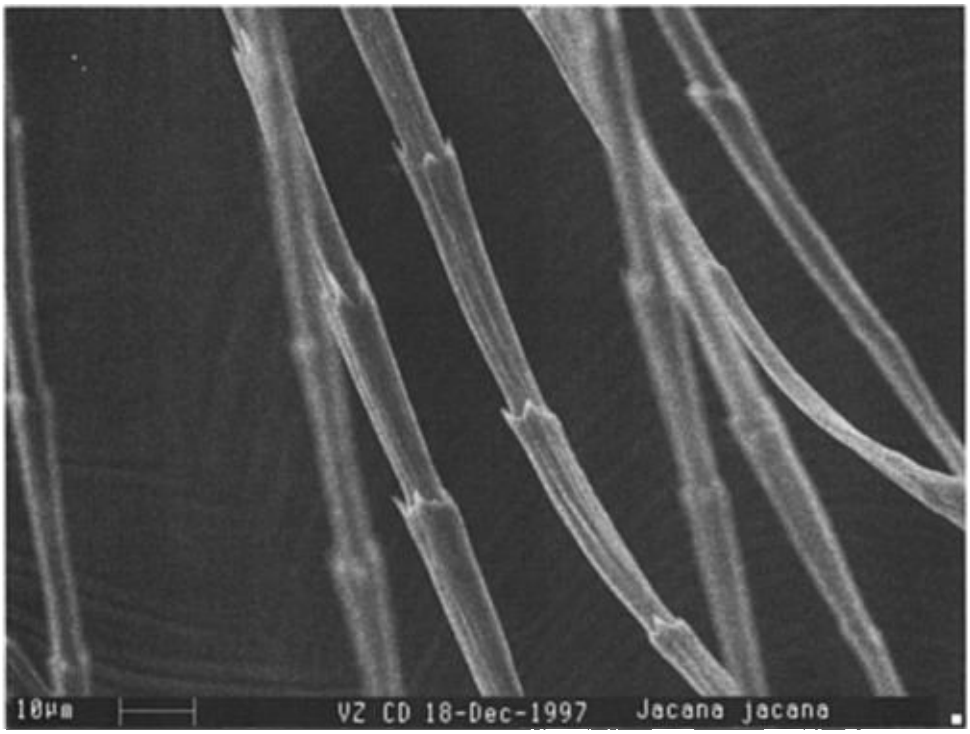


FIG. 8. Barbules of *Jacana jacana* showing short spines at basal nodes.

contour feathers. The barbules of the true down are generally shorter than those of the contour feather.

Dromadidae

Dromas ardeola (Crab Plover)

The Crab Plover is the only species in this family and is endemic to the northern and western parts of the Indian Ocean. All down types are unpigmented but the skin of this pied-plumaged bird is black.

Contour feather down.—Barbs and barbules are unpigmented (Fig. 15). Nodes are slightly expanded (Fig. 16) and visible at 200× all along the barbule. Basal nodes of barbules have blunt spines (Fig. 17) that become indistinct at the distal nodes of the barbule. Barbules are medium in length. The subpennaceous region is well developed (Fig. 18) and unpigmented.

Afterfeather and true down.—Barbules of these feather types have finer structures but are morphologically similar to the plumulaceous barbules of contour feathers. The afterfeather and true down do not have subpennaceous regions. Barbules of true down are noticeably shorter than barbules of contour feather down.

Haematopodidae

Haematopus bachmani (Black Oystercatcher), *Haematopus palliatus* (American Oystercatcher)

Oystercatchers are nearly cosmopolitan in distribution and prefer open beaches and rocky coasts. They do not occur in the polar regions or on oceanic islands.

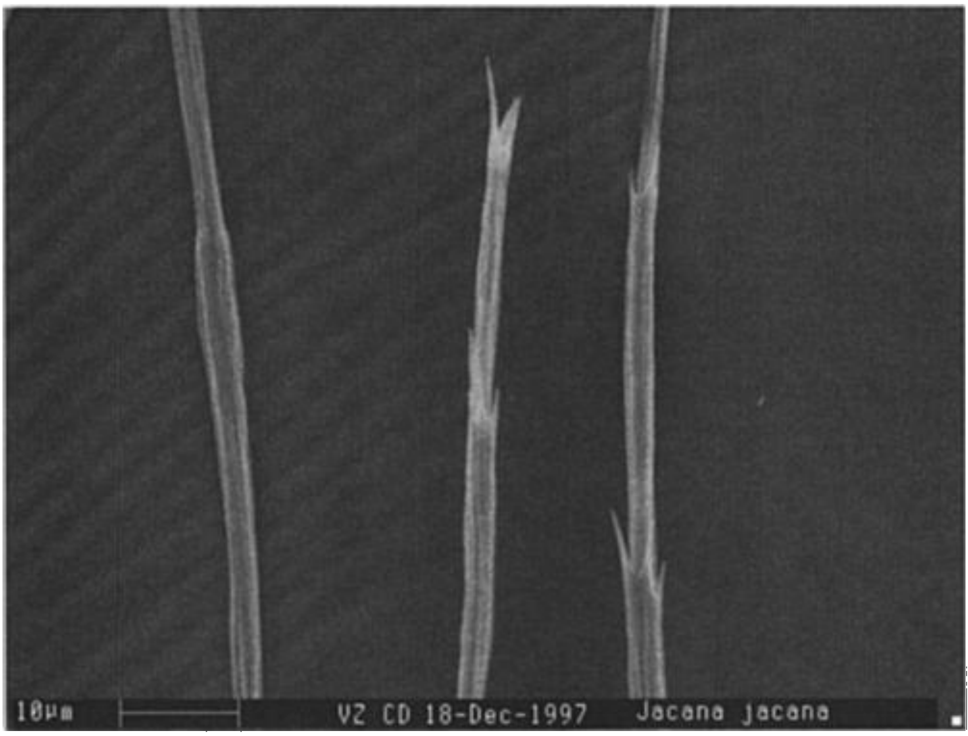


FIG. 9. Longer spines on distal nodes of barbules of *Jacana jacana*.

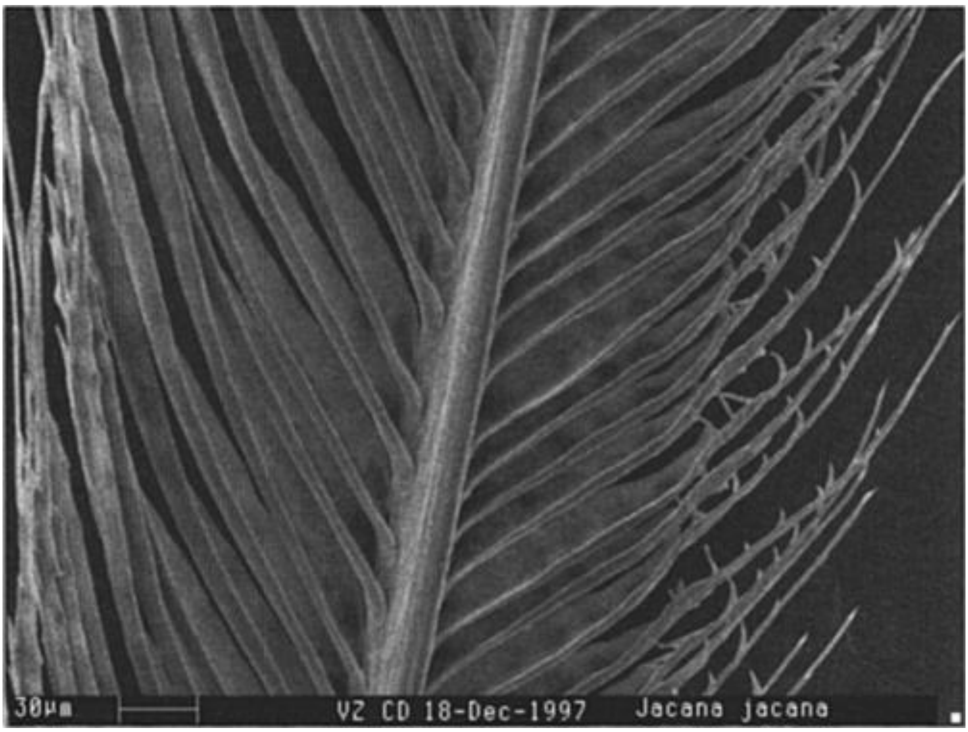


FIG. 10. Well-developed subpennaceous region of *Jacana jacana*.

FIG. 11. Contour feather down of *Rostratula benghalensis*.

Plumulaceous feather structure is examined in two species. Because the microscopic feather characters vary between the two species examined here in the manner they are pigmented, each species is described separately.

Haematopus bachmani (Black Oystercatcher)

Contour feather down.—*Haematopus bachmani* has pigmentation at nodes and internodes that extends to about the midsection of the barbules (Fig. 19), and the distal part of the barbule is typically unpigmented. Slightly expanded nodes are visible throughout the entire length of the barbule. Pigment is generally heaviest

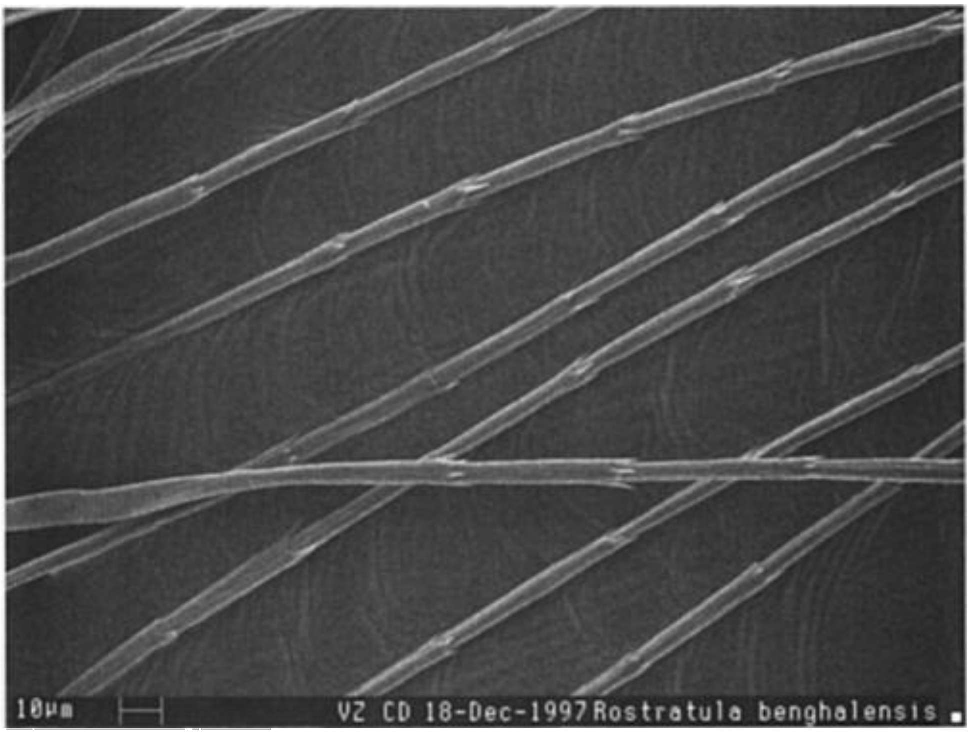


FIG. 12. Spines are present at nodes all along the barbules on *Rostratula benghalensis*.

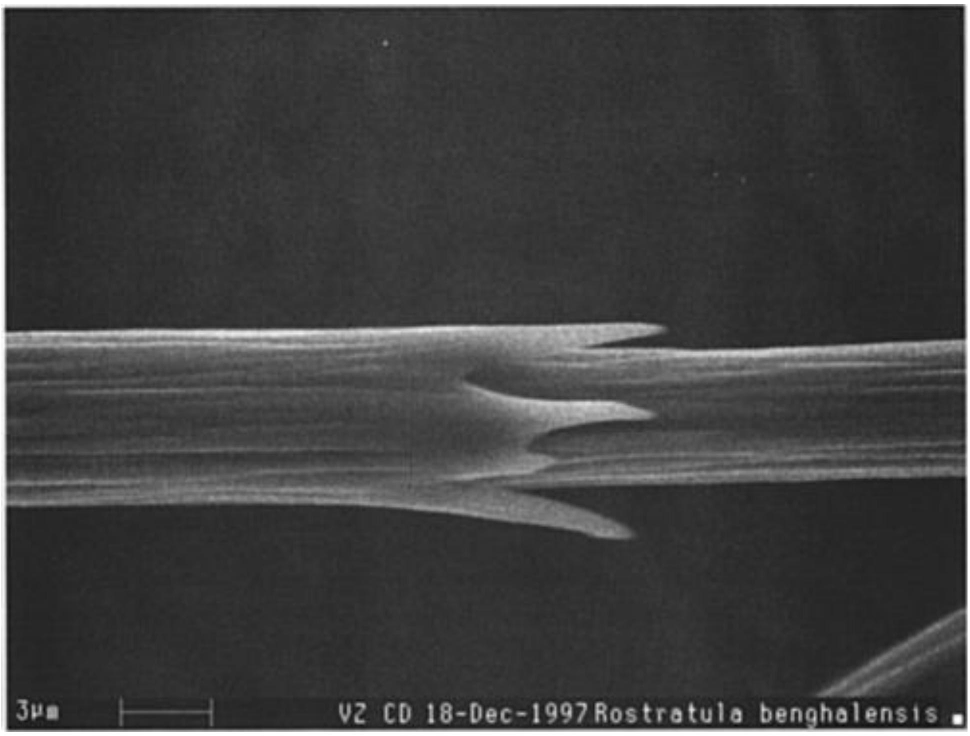


FIG. 13. Enlarged view of spined node of *Rostratula benghalensis*.

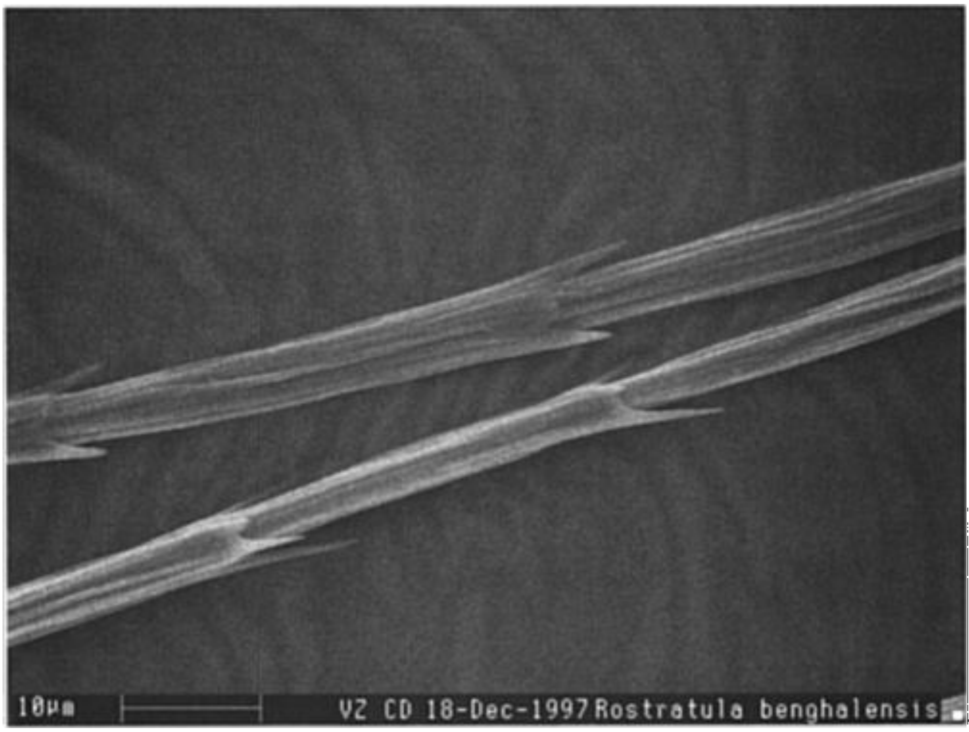


FIG. 14. Distal nodes of *Rostratula benghalensis* typically have longer spines than proximal nodes.

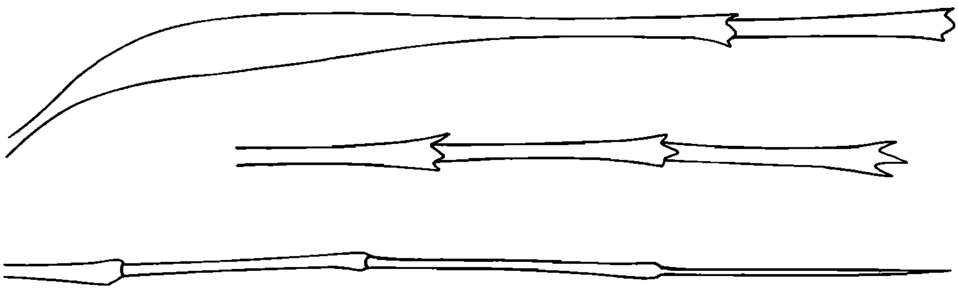


FIG. 15. Contour feather down of *Dromas ardeola.*

just below the node and tapers to heavy stippling in the internode. Basal nodes of barbules have the most pigmentation. In general, the pigmented granules are scattered throughout the proximal portion of the barbule with heavy concentrations of pigment at the nodes. Sometimes pigment is constricted to a diamond-shaped point at basal nodes of barbules. Spines are present at the basal nodes and become reduced or absent at nodes on the distal portion of the barbule. The distal part of the barbule becomes very thin and filamentous with very few scattered pigment granules. The subpennaceous region is lightly pigmented.

Villi.—Very few villi were observed on base cells of some barbules.

Afterfeather and true down.—These plumulaceous barbules are similar in appearance and pigmentation to contour feather down except that the nodes of the

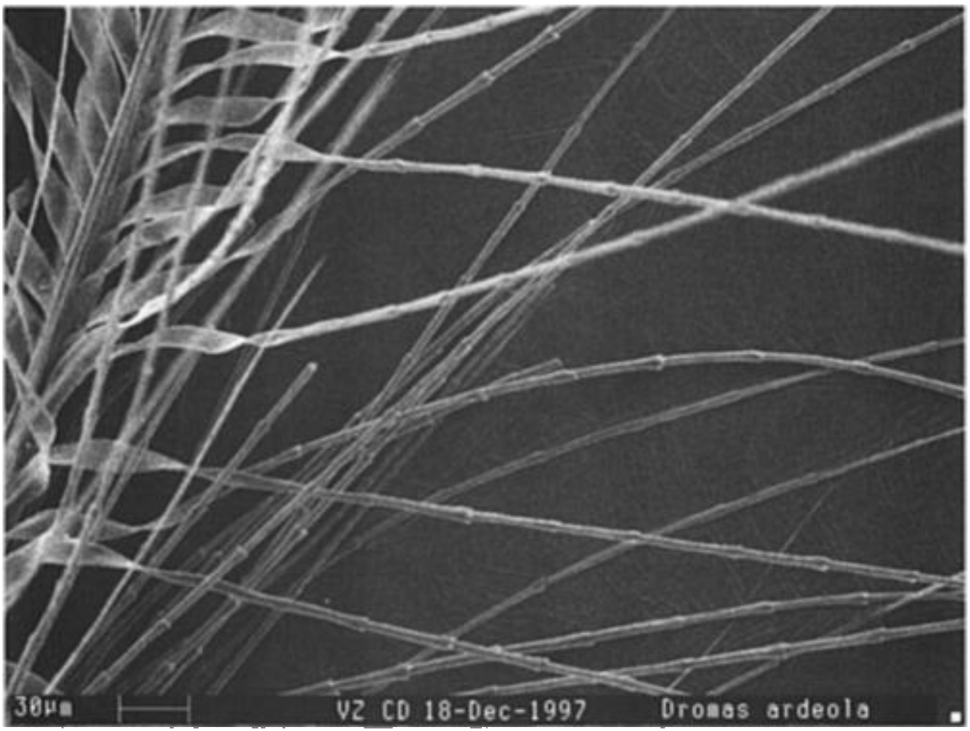


FIG. 16. *Dromas ardeola* has slightly expanded nodes all along the barbule.

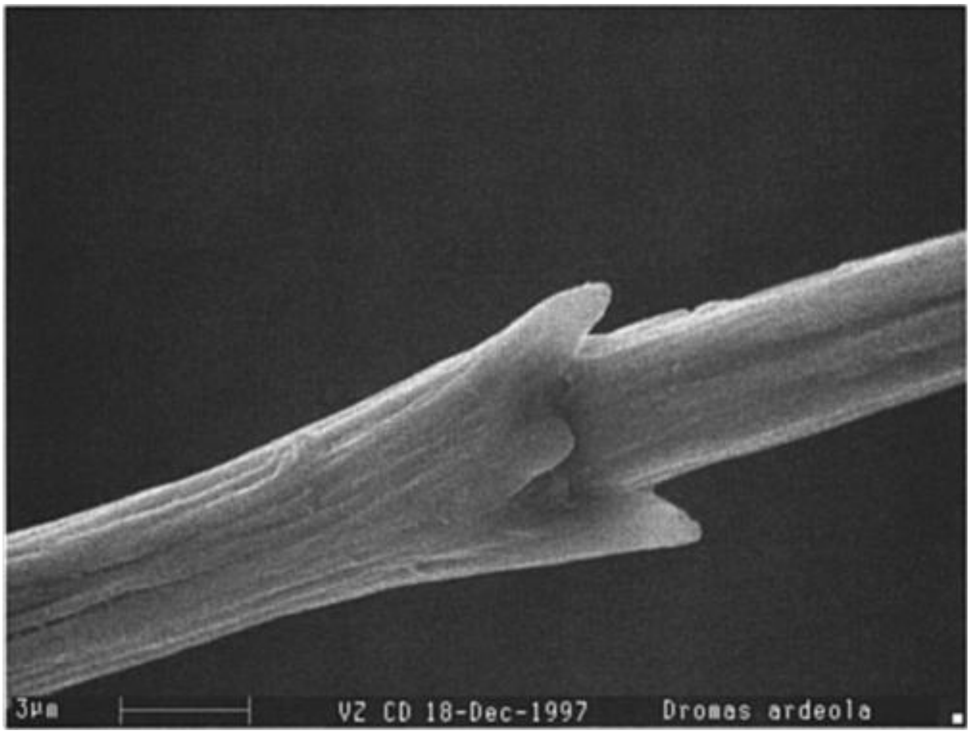


FIG. 17. Enlarged view of basal node of *Dromas ardeola* showing blunt spines.

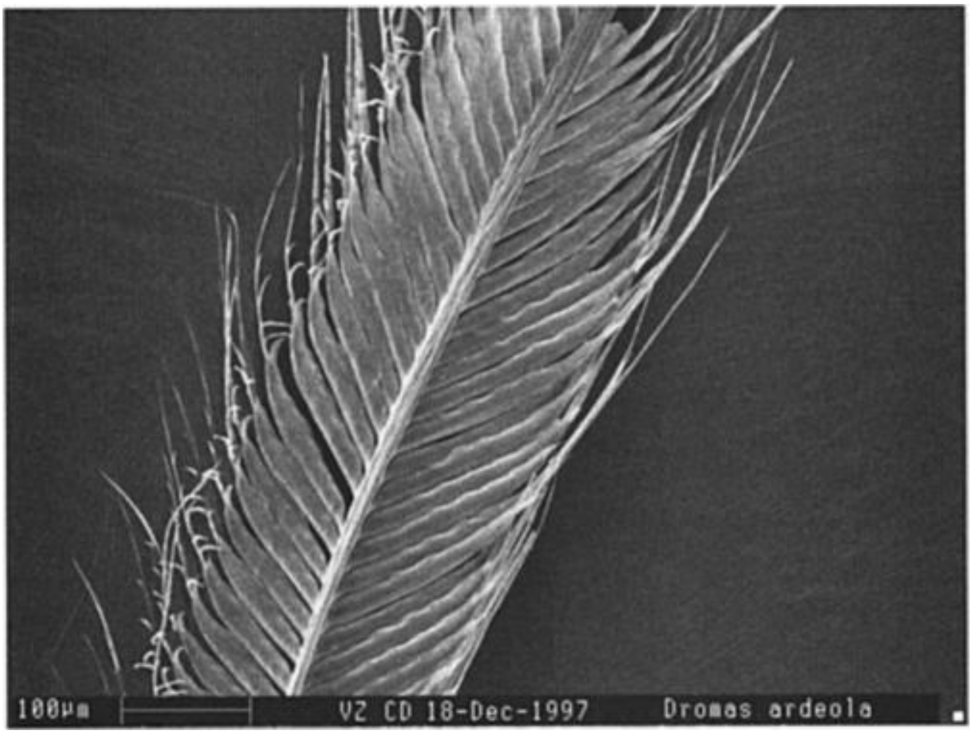


FIG. 18. Well-developed subpennaceous region of barb of *Dromas ardeola*.

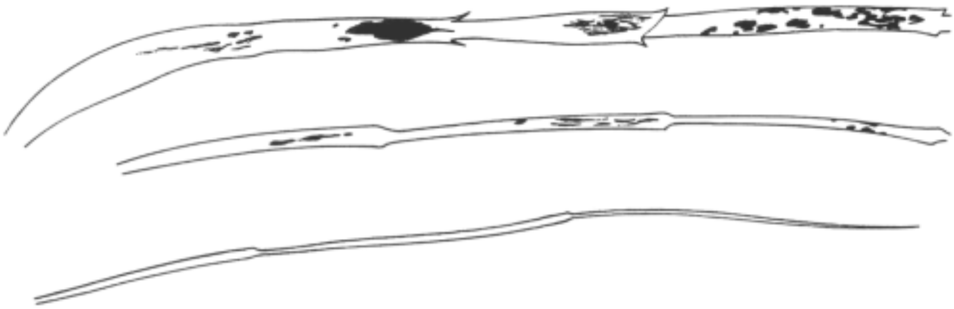


FIG. 19. Contour feather down of *Haematopus bachmani.*

true down are slightly more expanded and the barbules of the true down are shorter. No subpennaceous region occurs in either the afterfeather or true down.

Haematopus palliatus (American Oystercatcher)

Contour feather down.—This species differs from *H. bachmani* by having unpigmented contour feather down and pigmented true and afterfeather down. Nodal structures of contour down are slightly expanded and the nodes are spined at the base of the barbules (Fig. 20). The nodes and spines become indistinct on the distal portion of the barbule. No pigmentation was observed on any basal plu-

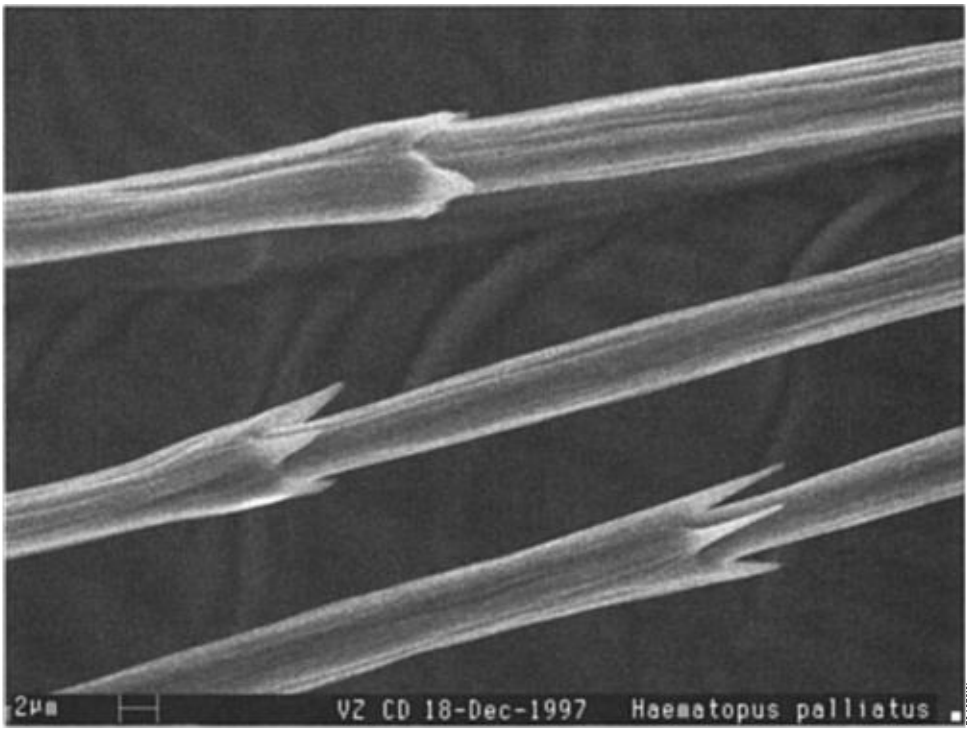


FIG. 20. Contour feather down of *Haematopus palliatus* showing slightly expanded, spined nodes at the base of barbules.

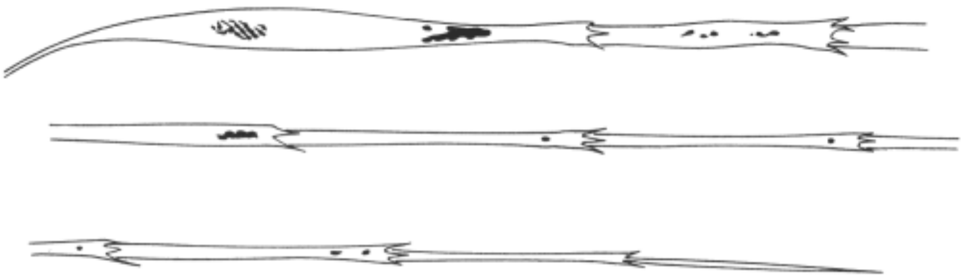


FIG. 21. Contour feather down of *Ibidorhyncha struthersii*.

mulaceous barbs of the contour feather. Barbules are medium in length and the subpennaceous region is unpigmented.

Afterfeather and true down.—In contrast to contour feather down, these feather types have pigmented plumulaceous barbs. In this way, they are similar to those observed in the downy barbules of *H. bachmani.* Afterfeather and true down of this species do not have subpennaceous regions.

Ibidorhynchidae

Ibidorhyncha struthersii (Ibisbill)

The Ibisbill is the only species in this family. Its range is restricted to glacial riverbeds in the Himalayan region and Tibetan plateau.

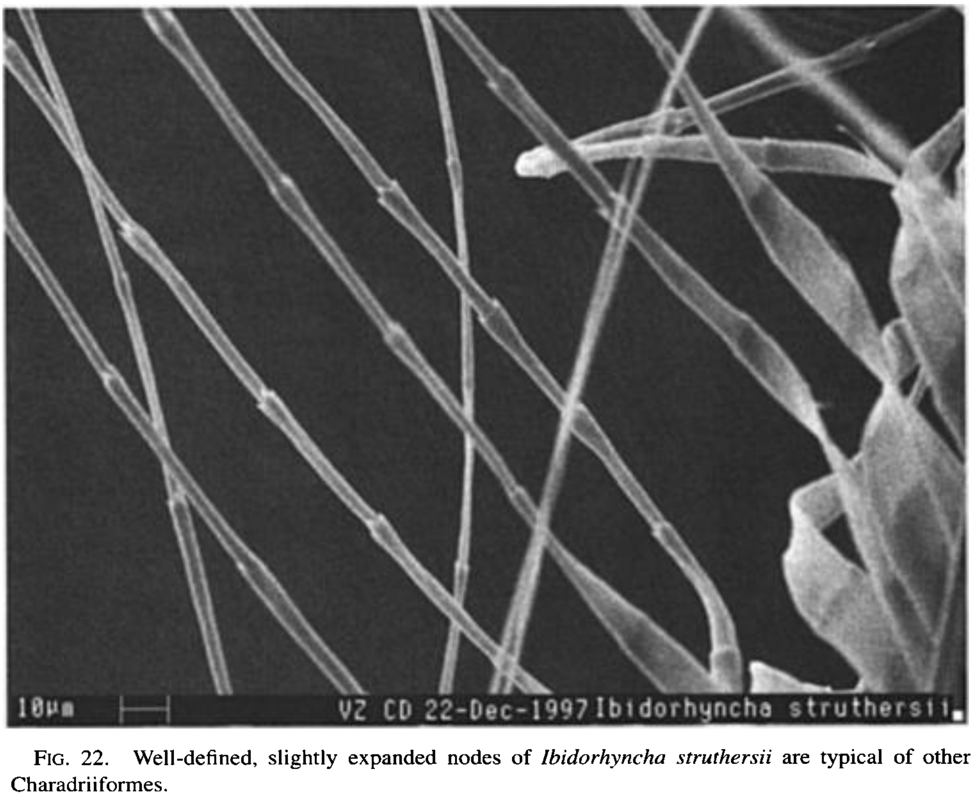


FIG. 22. Well-defined, slightly expanded nodes of *Ibidorhyncha struthersii* are typical of other Charadriiformes.

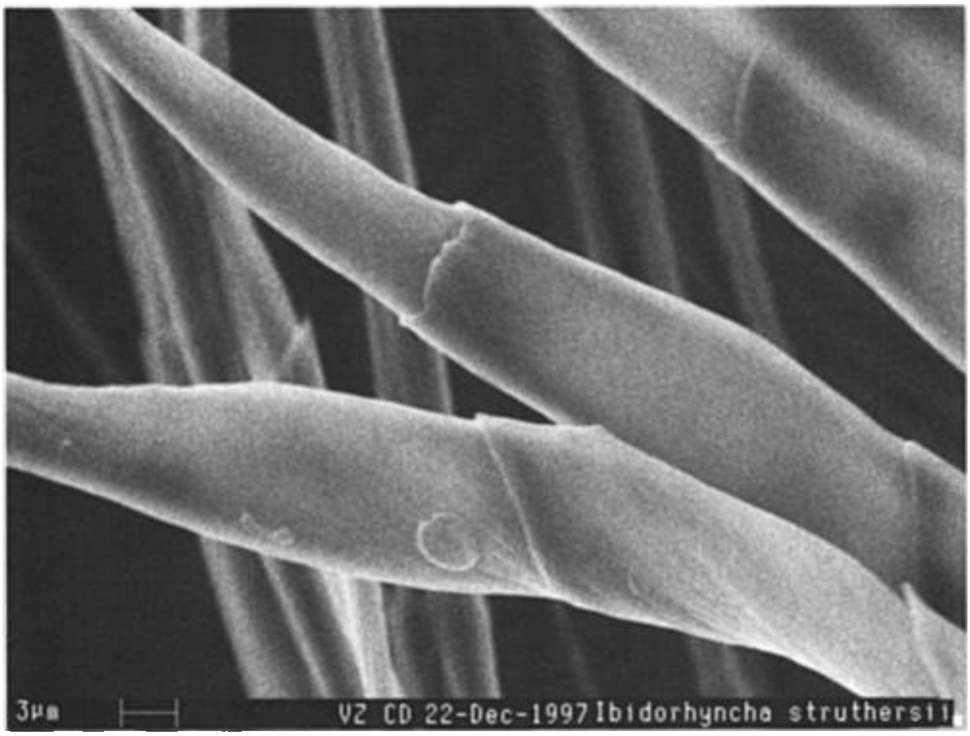


FIG. 23. Distinctly divided base cell of *Ibidorhyncha struthersii.*

Contour feather down.—The umbilical barbs usually are pigmented throughout the entire length of the barb but many of the basal region barbs had pigment only extending to half of the barb's length. Pigment is heaviest at the base of the barb and barbules. Basal barbules usually lack pigment at the very distal portion (Fig. 21). Barbules are medium in length and nodes are well defined and slightly expanded (Fig. 22). Pigment is mainly diamond-shaped and confined to nodes, but sometimes the pigment granules are stippled into the internode. Spines are most visible on basal nodes of the barbule. Base cells are distinctly divided (Fig. 23). The subpennaceous region is distinct and pigmented. In the subpennaceous region, high-power microscopy shows "pea-pods" of pigment in the base of the barbule that are concave on the ventral side of the barb (Fig. 24a) and convex on the dorsal side (Fig. 24b).

Afterfeather and true down.—The plumulaceous barbules of these feathers are microscopically similar to those of contour feather down. No subpennaceous regions are present on these feather types.

Villi.—Villi occur on the base cells of some barbules (Fig. 25).

Recurvirostridae

Himantopus himantopus (Black-winged Stilt), *Cladorhynchus leucocephalus* (Banded Stilt), *Recurvirostra americana* (American Avocet)

Stilts and avocets are a cosmopolitan group of birds that live chiefly around brackish and saline wetlands in warmer climates. The family is composed of 13 species; feathers were examined from members in all three genera.

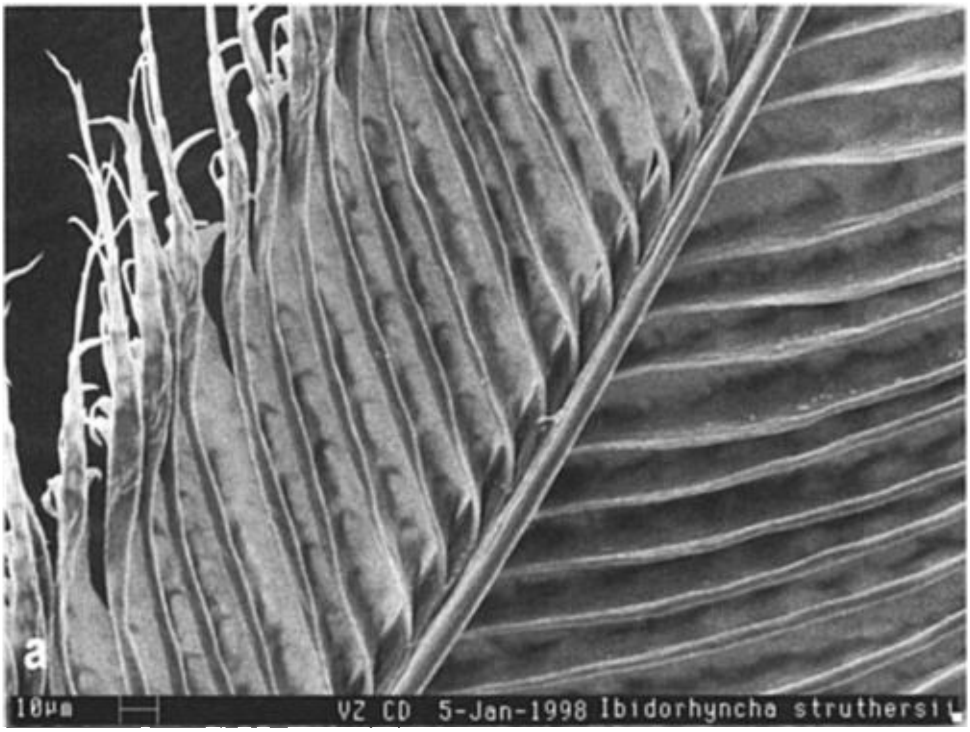


FIG. 24a. The subpennaceous region of *Ibidorhyncha struthersii* shows pigment like peas in a pod that are concave on the ventral side of the barb (a) and convex on the dorsal side of the barb (Fig. 24b).

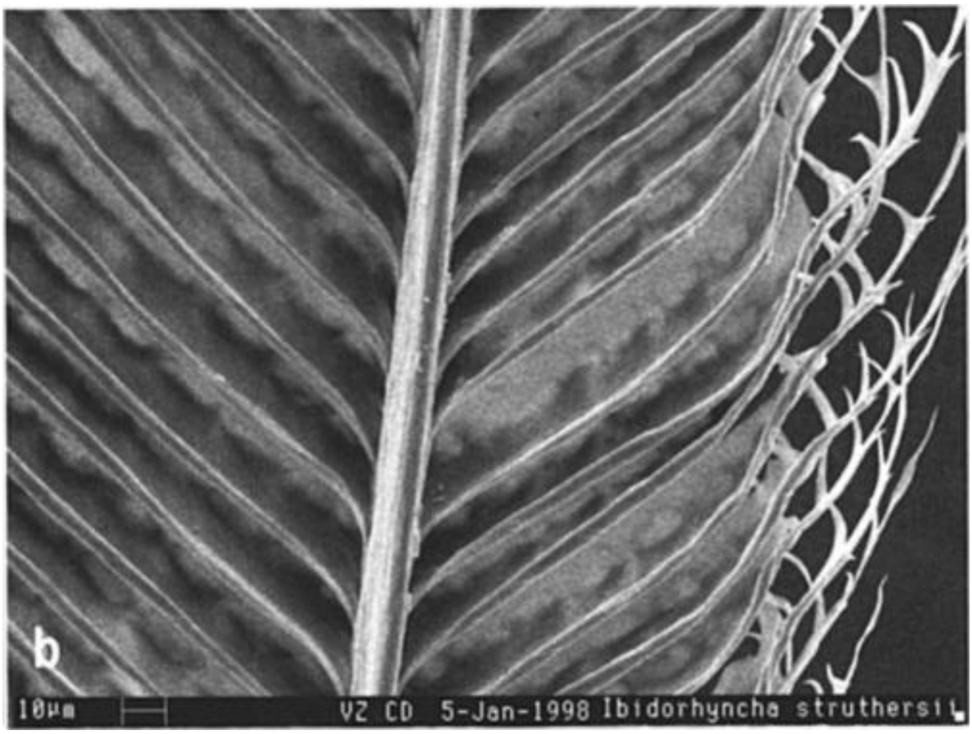


FIG. 24b.

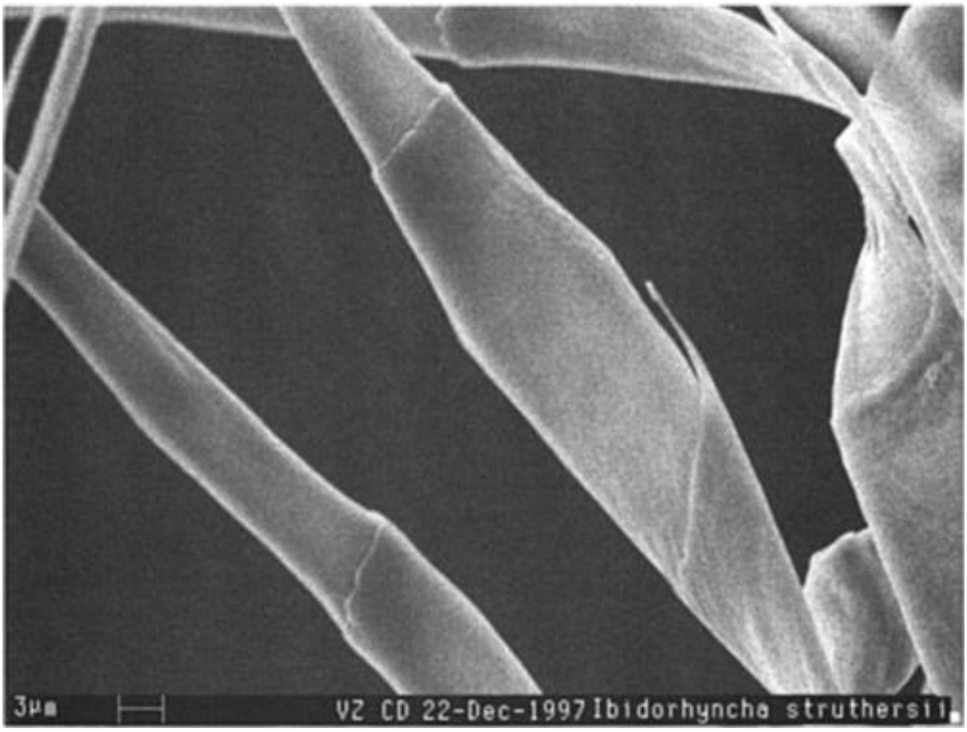


FIG. 25. Villi occur on some barbule bases of *Ibidorhyncha struthersii.*

Microscopic feather characters and pigmentation patterns of species studied here are consistently similar to each other. Contour feather down is unpigmented but the afterfeather down and true down are pigmented (Figs. 26, 27).

Contour feather down.—Nodes are slightly expanded and have small spines throughout the barbule (Fig. 28). In *R. americana* some tiny granules of pigment may be visible just below some nodes when viewed at high power (400×). Subpennaceous regions are present in contour feather down of all three species examined.

Afterfeather and true down.—The downy barbules of these feathers are pigmented similarly in all three species. Pigment is stippled, sometimes concentrated at the nodes and scattered internodally to the midsection of the barbule (Fig. 27).

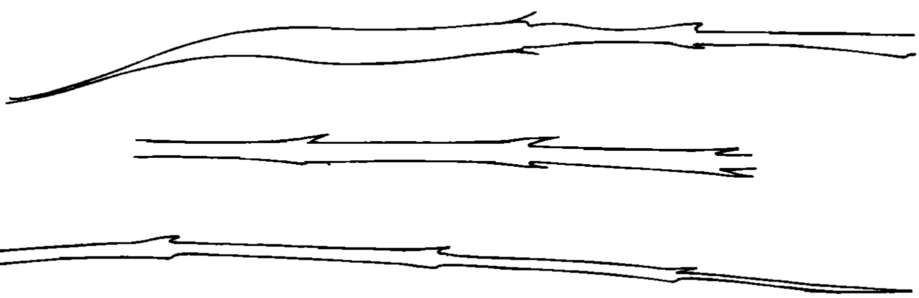


FIG. 26. Contour feather down of *Himantopus himantopus.*

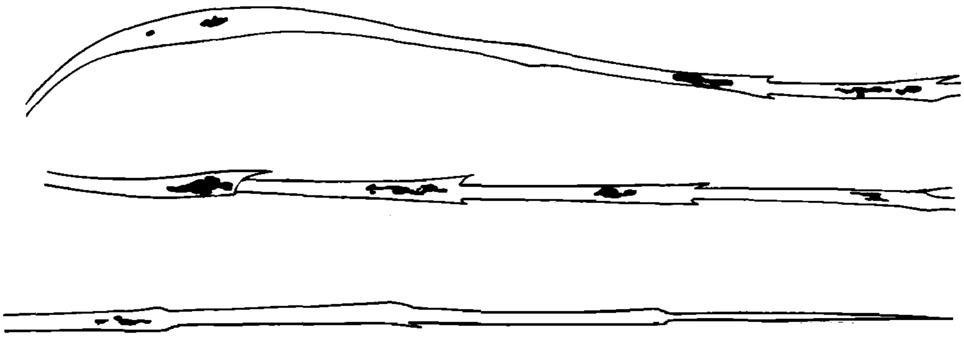


FIG. 27. Afterfeather down of *Himantopus himantopus.*

Distal portions of barbules are unpigmented. In *H. himantopus,* true and afterfeather down are more heavily pigmented than any other species studied in this family. These feather types do not have subpennaceous regions.

Villi.—Villi were found on basal barbules of *R. americana* (Fig. 29).

Burhinidae

Burhinus oedicnemus (Eurasian Thick-knee), *Burhinus senegalensis* (Senegal Thick-knee), *Burhinus vermiculatus* (Water Thick-knee), *Burhinus capensis* (Spotted Thick-knee), *Esacus recurvirostris* (Great Thick-knee)

The thick-knees are mainly birds of arid or semiarid open country of southern continents. These birds inhabit shores, riverbanks, or dry pebbly areas. Five of the nine species are examined in this study. General feather microstructure and pigmentation patterns are consistent among the species of this family, varying only in the intensity of the pigment.

Contour feather down.—Plumulaceous barbs are usually pigmented to some degree throughout the entire barb. Barbules are medium length with the pigment mostly concentrated on the basal portion of the barbule. Pigment is sparse at the distal portion of the barbule (Fig. 30). Spines occur at nodes all along the barbule (Fig. 31). Internodal pigmentation is usually heavy and stippled, sometimes forming a constricted point at the basal nodes on the barbule. The pigment is mostly internodal at the midsection of the barbule. Some of the nodes along the barbule lack pigment even though the internode is stippled with pigment. The stippled internodal pigment is usually more intense at the base of the barbule. Basal cells are stippled with pigment. Subpennaceous regions are present and pigmented. SEM examination shows deeply furrowed internodes (Fig. 32).

Of the five species of thick-knees examined, *B. vermiculatus* has the most heavily pigmented plumulaceous barbules. Pigment is also more constricted at the nodes and distinctly diamond-shaped at many nodes on the barbules. Internodal pigment is less intense than other species. *Burhinus capensis* is most similar to *B. vermiculatus* in overall microscopic feather characters. Of the species studied, *Esacus recurvirostris* has the least amount of pigment in plumulaceous barbules in this family. Pigment is lighter and mainly distributed as internodal stippling with little or no pigment at nodes.

Afterfeather and true down.—These feather types were examined in *E. recur-*

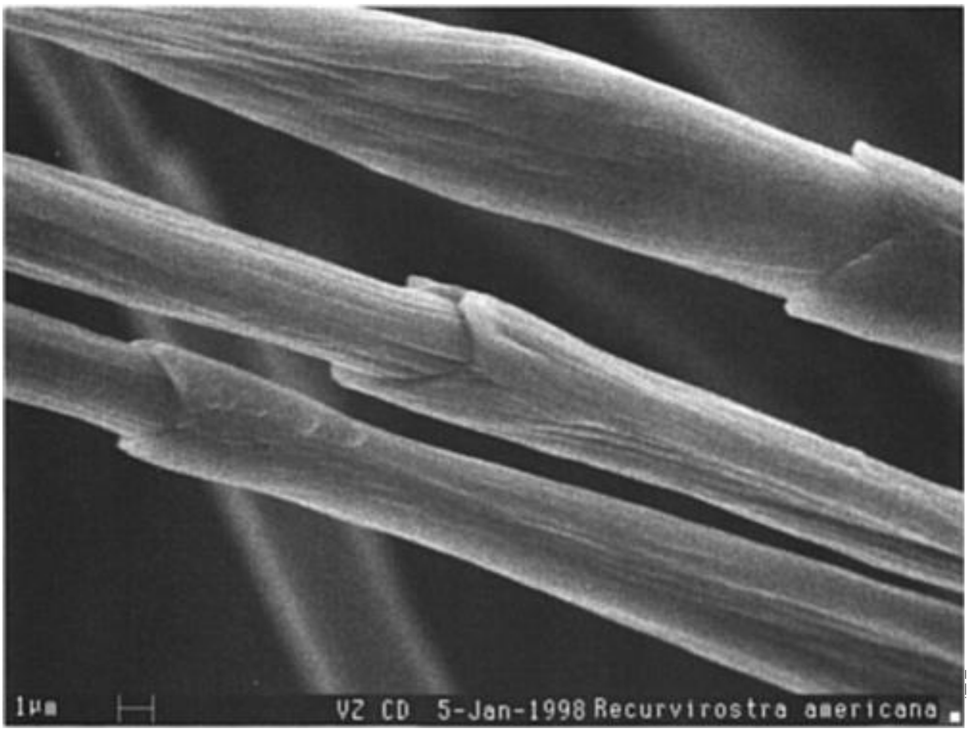


FIG. 28. *Recurvirostra americana* has slightly expanded nodes with short spines throughout the barbule.

virostris and *B. oedicnemus*. Pigmentation in these plumulaceous barbules is generally heavier than in contour feather down and barbs and barbules are finer in structure. No subpennaceous region is present in true and afterfeather down.

Glareolidae

Pluvianus aegyptius (Egyptian Plover), *Rhinoptilus chalcopterus* (Bronze-winged Courser), *Cursorius cursor* (Cream-colored Courser), *Stiltia isabella* (Australian Pratincole), *Glareola pratincola* (Collared Pratincole)

Coursers and pratincoles inhabit warm or hot climates of the Old World. Sixteen species in five genera make up this family. Coursers are fast-running birds that occupy dry habitats and feed by aerial hawking. The Egyptian Plover is found near African rivers. Feather structures were examined in all genera of this family.

Contour feather down.—Barbs and barbules are pigmented throughout their lengths except in *Pluvianus,* in which these structures are totally unpigmented. Basal nodes of barbules of the other species studied here have diamond-shaped pigmentation that constricts into a point in the node (Fig. 33). The shape of the pigment becomes more rounded at the nodes toward the mid- and distal sections of the barbule. Pigmentation often extends from the node posteriorly into the internode at the basal nodes of barbules but is more confined to the node at the midsection of the barbule. Typically, expanded nodes are prevalent all along the barbule. Mid-nodes are large when viewed with LM and SEM, making the inter-

FIG. 29. Villi occur on the base of some basalmost barbules in *Recurvirostra americana.*

node width appear narrow (Fig. 34). Numerous, expanded nodes are characteristic of this family (Fig. 35) with the exception of *Pluvianus,* which has only slightly expanded nodes (Fig. 36). The subpennaceous region is very reduced or absent. Spines are present at nodes all along barbules.

Nodes are expanded most dramatically on barbules of *Glareola pratincola.* The basal nodes of barbules of *G. pratincola* have large flared transparent processes surrounding the pigment that generally taper to smaller size toward the midsection and distal portion of the barbule. True down of this species has greatly expanded basal nodes that resemble the patterns observed in gulls.

Pluvianus aegyptius is atypical of this family in microscopic feather characters. All down types of this species are unpigmented. Nodes are only slightly expanded all along the barbule. Spines are visible at almost all of the nodes on barbules.

FIG. 30. Contour feather down of *Burhinus oedicnemus.*

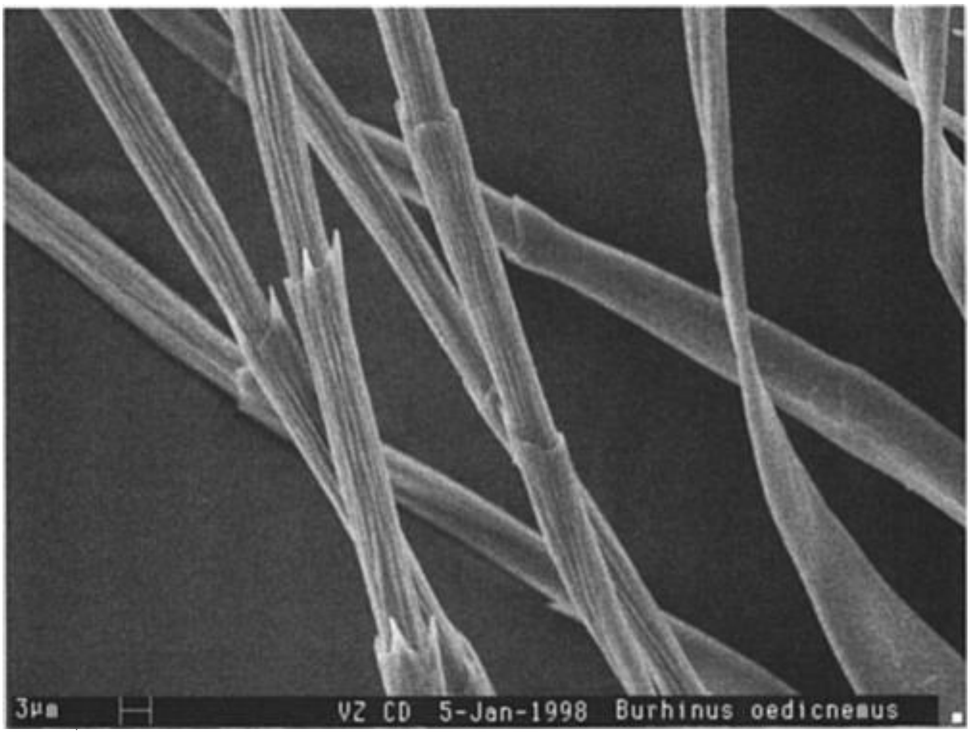


FIG. 31. Thick-knees (Burhinidae) typically have slightly expanded nodes with distinct spines all along the barbule.

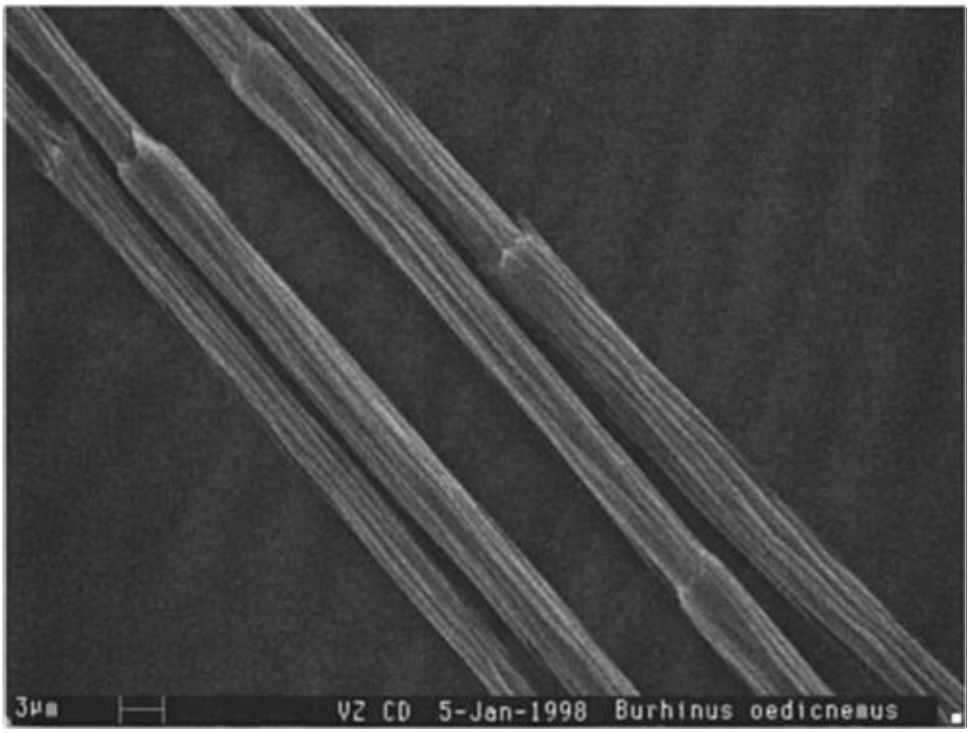


FIG. 32. Scanning electron microscopy examination at 1,860× shows deeply furrowed internode of *Burhinus oedicnemus*.

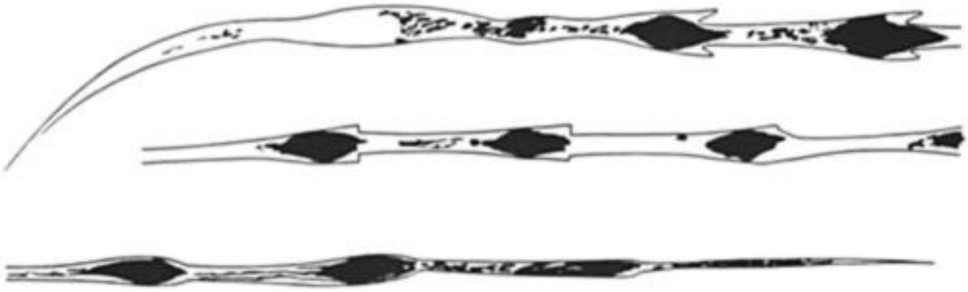


FIG. 33. Contour feather down of *Cursorius cursor*.

The subpennaceous region is short but more developed than in other species in this family. Internodes throughout the barbule appear more deeply furrowed when viewed with SEM in *Pluvianus* (Fig. 37) than in other glareolids. Contrary to Chandler's (1916) observation, this study of only plumulaceous microstructures does not support the position that glareolids are similar to herons (Ardeidae).

Afterfeather and true down.—These down types are generally similar to contour feather down in the species studied except that the afterfeather down and true down are finer and no subpennaceous region is present. These down types are unpigmented in *P. aegyptius* and true down varies somewhat in *Glareola pratincola.*

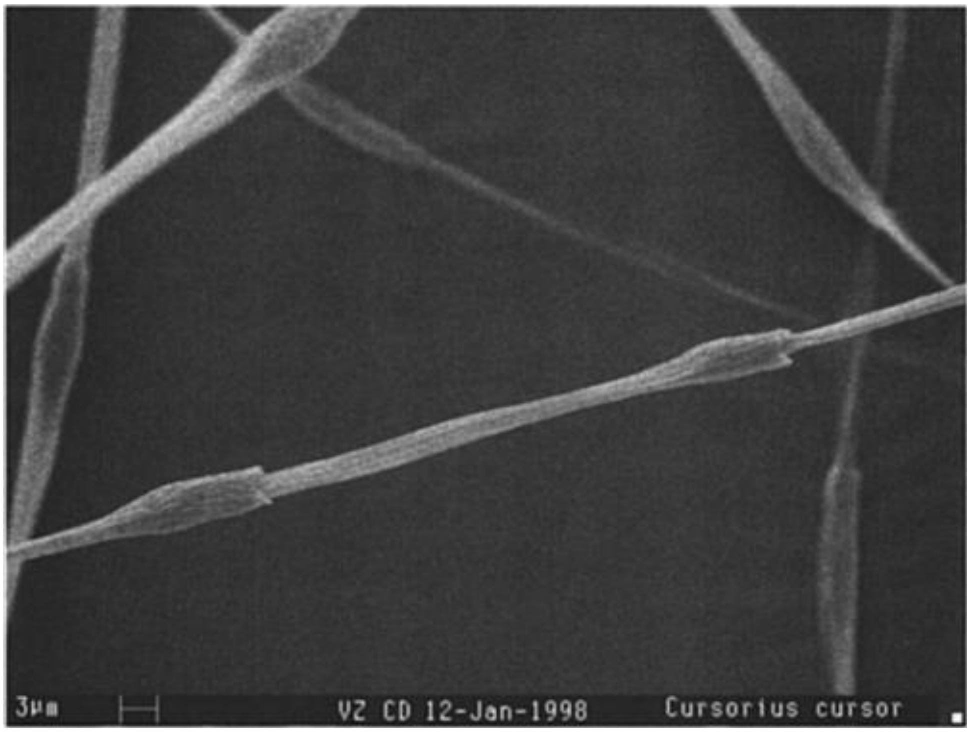


FIG. 34. Mid-nodes of coursers (Glareolidae) are typically large, making the internode appear very narrow.

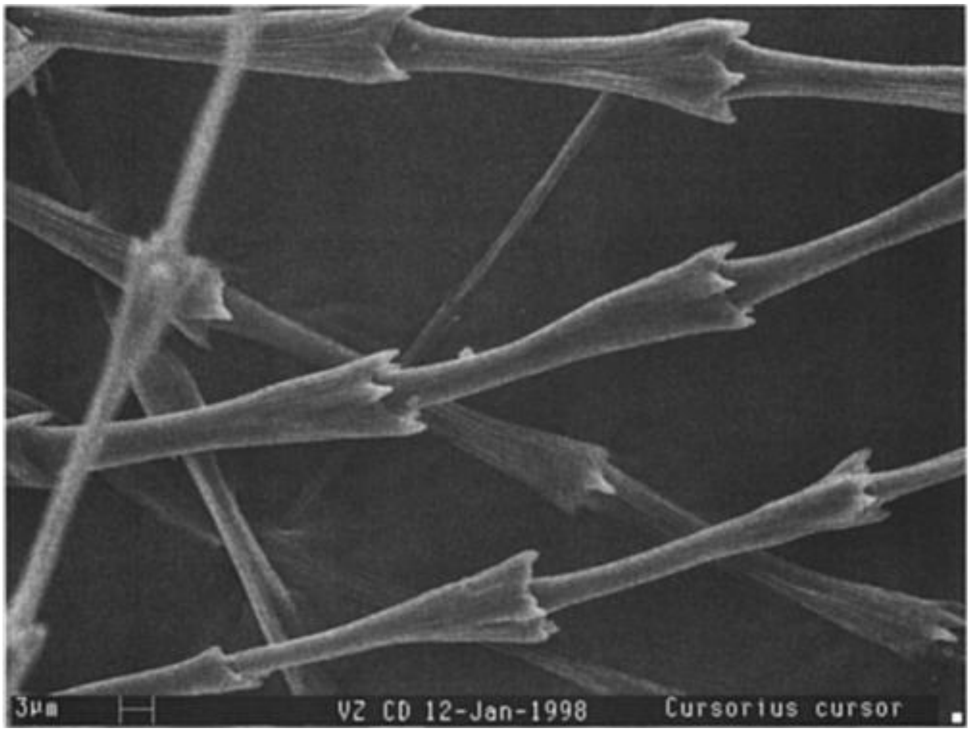


FIG. 35. Coursers (except *Pluvianus*) have many very expanded nodes that are consistently large all along the barbule.

FIG. 36. ***Pluvianus aegyptius*** differs from other members of Glareolidae by having much less expanded nodes.

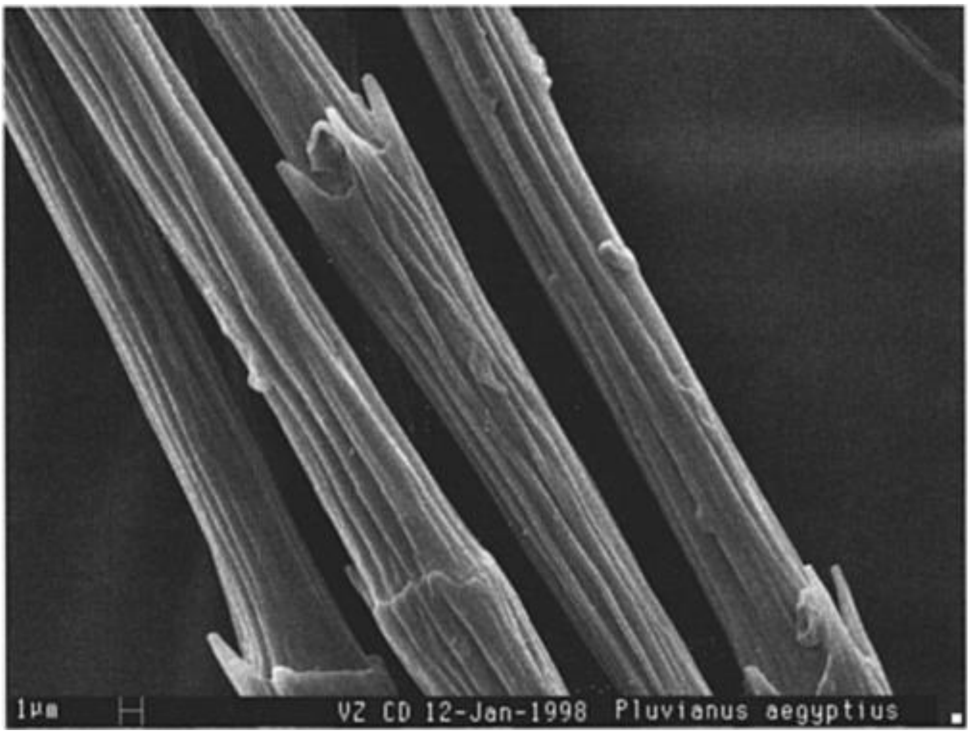


FIG. 37. Furrowed internode of barbules of *Pluvianus aegyptius*.

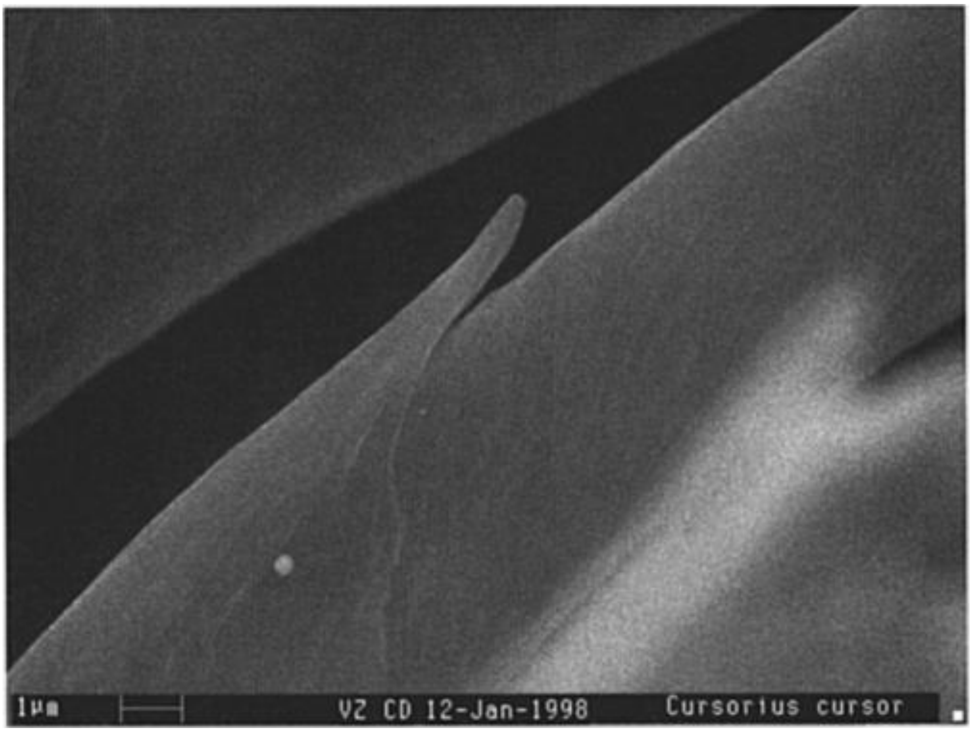


FIG. 38. Villi occur on basalmost barbules of some members of the family Glareolidae (e.g., *Cursorius cursor*).

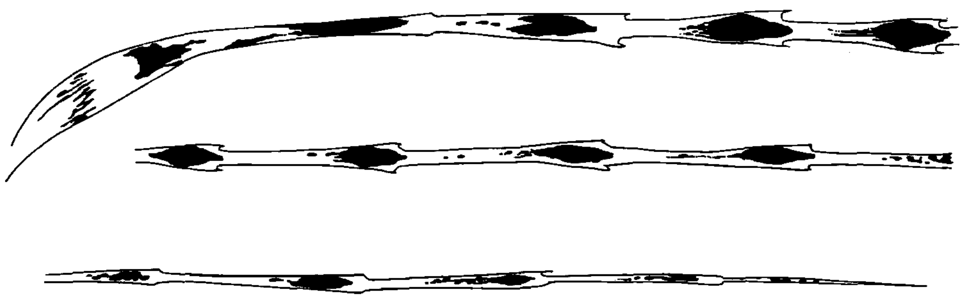


FIG. 39. Contour feather down of *Charadrius vociferus.*

Villi.—Villi were found in *Stiltia isabella* and *Cursorius cursor* (Fig. 38) at the base of the barbule on umbilical barbs.

Charadriidae

Vanellus vanellus (Northern Lapwing), *Vanellus crassirostris* (Long-toed Lapwing), *Vanellus spinosus* (Spur-winged Lapwing), *Vanellus indicus* (Red-wattled Lapwing), *Vanellus lugubris* (Senegal Lapwing), *Vanellus cayanus* (Pied Lapwing), *Vanellus chilensis* (Southern Lapwing), *Vanellus albiceps* (White-headed Lapwing), *Pluvialis dominica* (American Golden Plover), *Pluvialis squatarola* (Gray Plover), *Charadrius semipalmatus* (Semipalmated Plover), *Charadrius dubius* (Little Ringed Plover), *Charadrius vociferus* (Killdeer), *Charadrius tricollaris* (Three-banded Plover), *Charadrius alexandrinus* (Kentish Plover), *Charadrius mongolus* (Mongolian Plover), *Charadrius montanus* (Mountain Plover), *Anarhynchus frontalis* (Wrybill), *Eudromias morinellus* (Eurasian Dotterel), *Pluvianellus socialis* (Magellanic Plover)

Lapwings and plovers make up this cosmopolitan group of about 64 species. Lapwings are absent from the Arctic and North America but otherwise can be found almost worldwide. Plovers comprise a varied group of shorebirds that are found all over the world in all sorts of habitats and in all climates. In this study, *Pluvianellus socialis* is grouped with plovers for consistency in following the taxonomy of Morony et al. (1975) and contra osteological studies of Strauch (1978) and Chu (1995, 1998) that support a *Pluvianellus–Chionis* association.

Contour feather down.—The overall microscopic feather structures of plovers (*Charadrius, Pluvialis,* some *Vanellus*) are very similar to each other. Barbules are usually short to medium in length with spines at the nodes and many expanded, usually pigmented, nodes throughout the barbule (Figs. 39, 40). The main variation among species exists in the amount and distribution of pigment along the barbs and barbules. Some species (*C. vociferus, C. montanus, C. tricollaris*) are typically heavily pigmented throughout both the barb and barbules, whereas other species (*C. alexandrinus, Anarhynchus frontalis*) are usually not completely pigmented on the distal portions of the barb or barbules. Pigment is typically concentrated into a diamond-shaped point at the nodes in this family. The basal nodes of barbules are the most characteristic in the shape of the pigment, but mid- and distal nodes often also have diagnostic diamond-shaped pigment. In some species mid- and distal nodes of barbules may have more round-shaped

FIG. 40. Contour feather down of *Pluvialis squatarola.*

pigment clusters with trailing internodal pigmentation. Basal cells of barbules usually have stippled or spotted pigment. Subpennaceous regions are present in all plover species examined here except *Charadrius alexandrinus* and are most often heavily pigmented, sometimes more so on distal vanules. The first node of the barbule is reduced, or unexpanded, and has round-shaped pigment that is concentrated near the distal end of the first node. Charadriids exhibit the most consistent pattern of diagnostic diamond-shaped pigmented nodes of the order (see Killdeer, Fig. 39).

Eudromias morinellus differs from *Charadrius* in having expanded nodes that flare out more from the axis of the barbule (Fig. 41). The pigment is also usually more rounded in shape at the nodes than it is in most *Charadrius* species. *Pluvialis* follows the general microscopic conformation of plovers but the nodes are more constricted, are narrower, and have more elongate pigment shape (Fig. 40). Pigment usually extends far into the internode, especially at the basal nodes of barbules. Barbules are slightly longer than *Charadrius.*

Afterfeather and true down.—These down types are similar to contour plumulaceous down in this family except some species have slightly different pigmentation patterns (more or less pigmentation) in true down. No subpennaceous region is present and the true down and afterfeather are finer in structure than the down of the contour feather.

Villi.—A few villi were observed on some of the barbule bases of umbilical barbs in *Charadrius vociferus* (Fig. 42), *C. tricollaris, C. mongolus, C. montanus,*

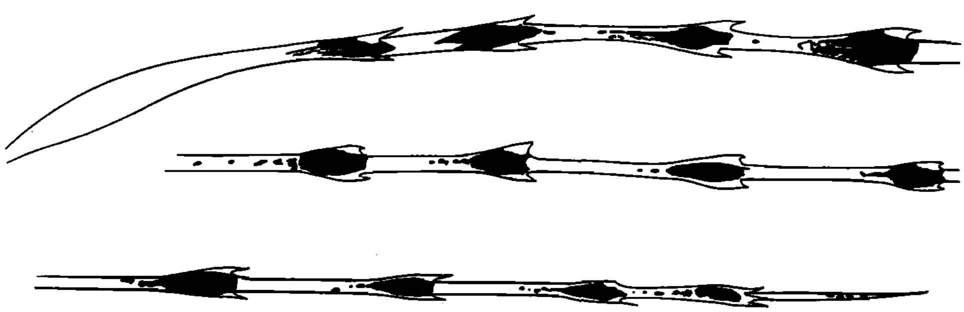


FIG. 41. Contour feather down of *Eudromias morinellus.*

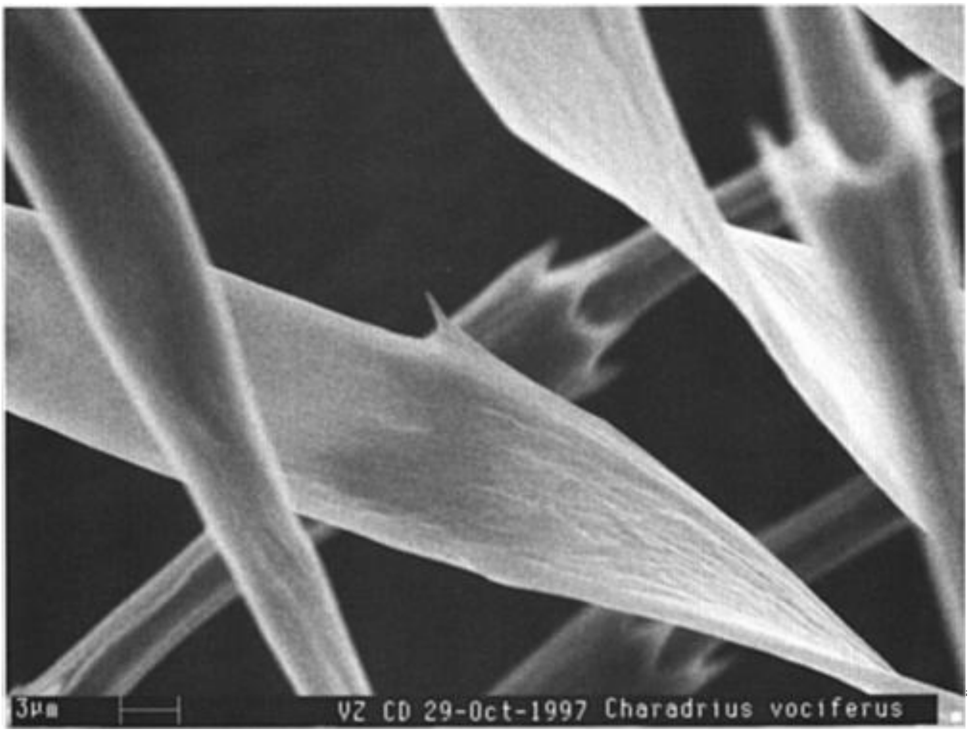


FIG. 42. *Charadrius vociferus* have villi infrequently in small numbers.

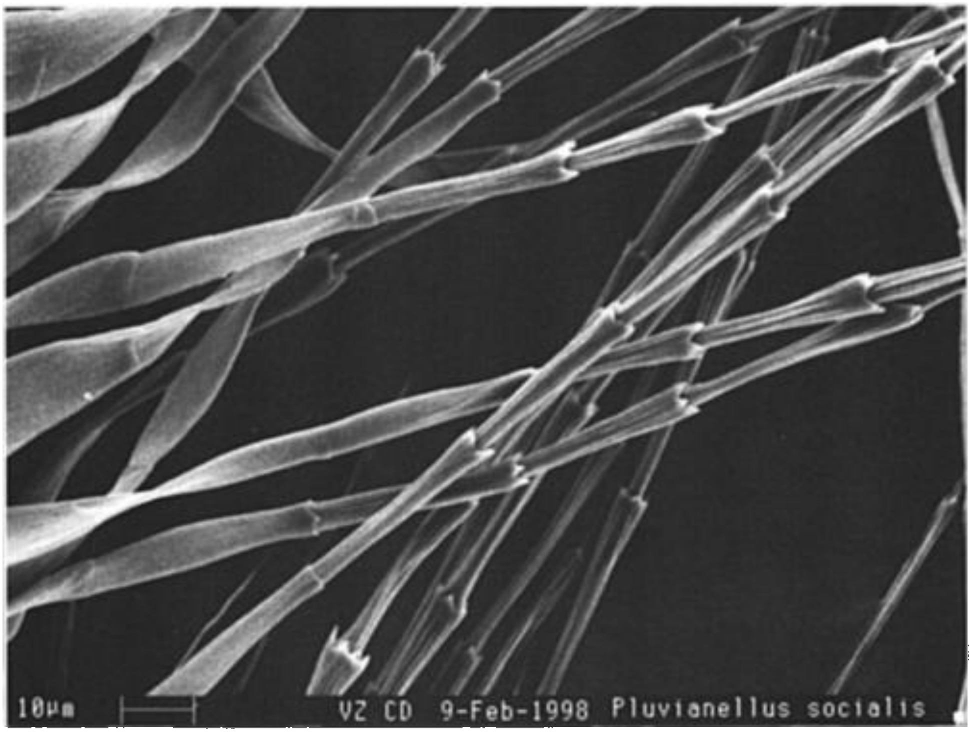


FIG. 43. *Pluvianellus socialis* is similar to plovers in overall microstructure (e.g., slightly expanded, spined nodes).

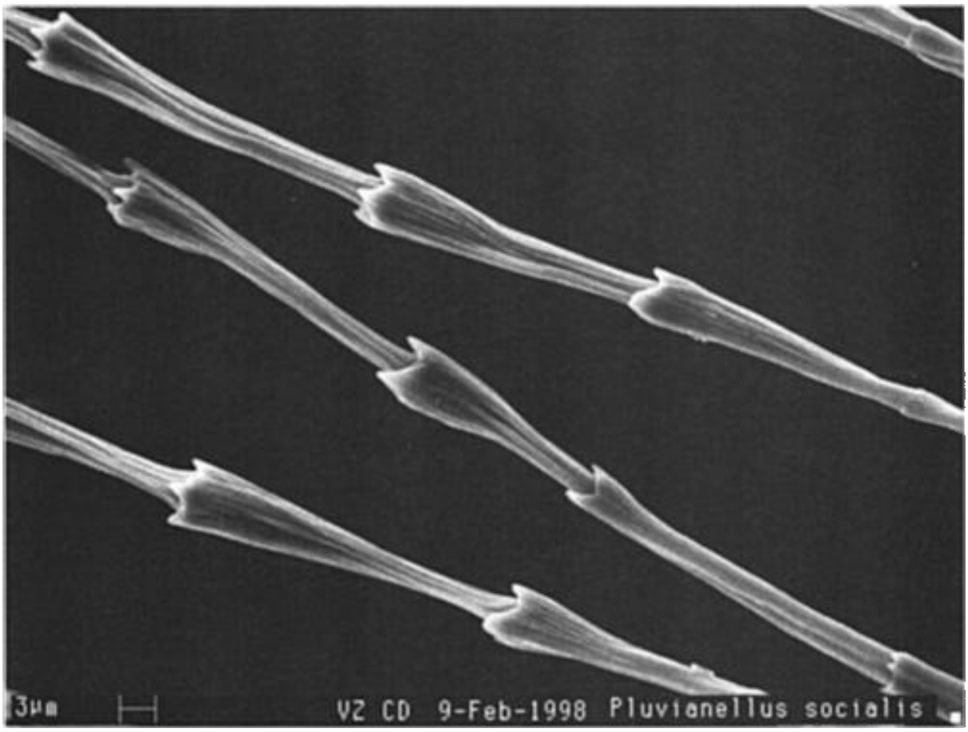


FIG. 44. *Pluvianellus socialis* differs from other plovers in having short internodal distances at basal nodes of barbules.

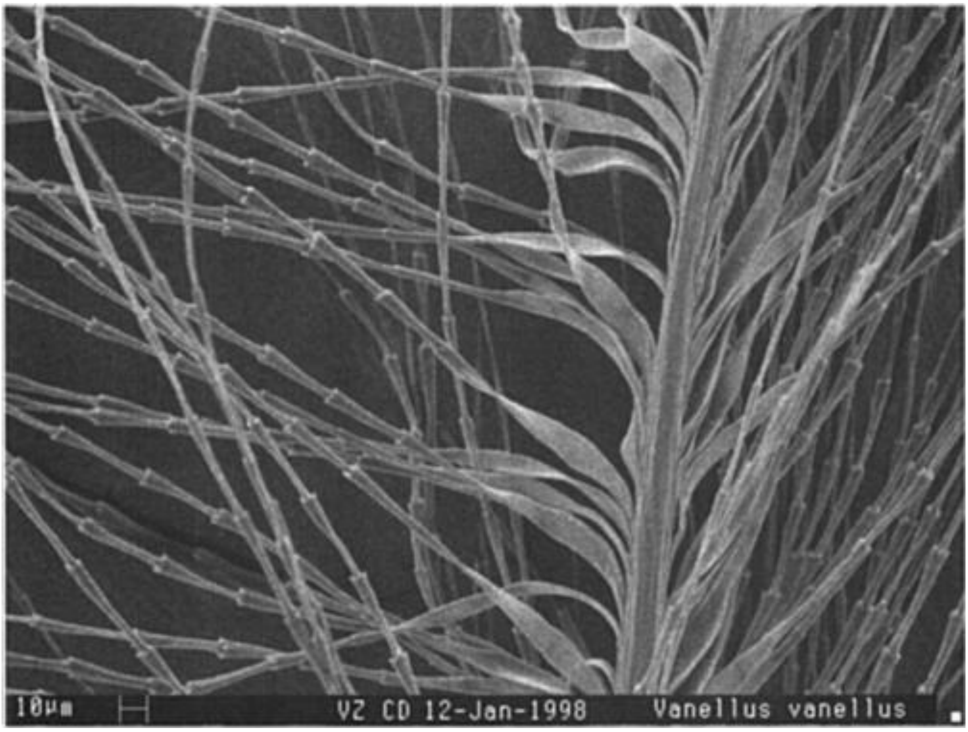


FIG. 45. Lapwings (Charadriidae) are extremely variable in pigmentation patterns but show basic microstructural framework similar to other members of the family.

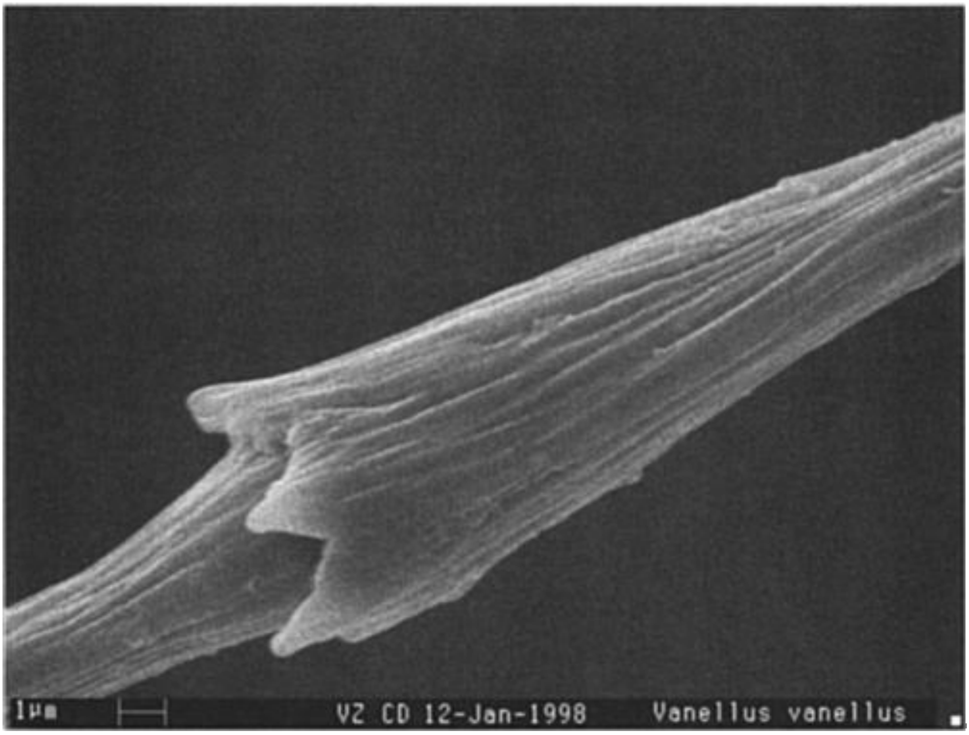


FIG. 46. Typical node of *Vanellus vanellus* showing short spines.

Vanellus indicus, V. lugubris, Anarhynchus frontalis, Pluvialis squatarola, and *Eudromias morinellus.*

Pluvianellus socialis is similar to other plovers in overall microstructure (Fig. 43). The most striking difference is in the short internodal distance at basal nodes of barbules (Fig. 44). The subpennaceous region of this species is present but not well developed and is difficult to distinguish.

The microscopic feather structures of lapwings (*Vanellus*) are the most variable of any group in this family. Although the basic microstructural framework of barbules is similar to that of other members of the family (expanded nodes, spines at nodes throughout, medium length barbules; Figs. 45, 46), the pigmentation patterns vary widely among the species. In some species both nodes and internodes are heavily pigmented (*V. vanellus,* Fig. 47), whereas others are typically

FIG. 47. Heavily pigmented nodes and internodes of *Vanellus vanellus.*

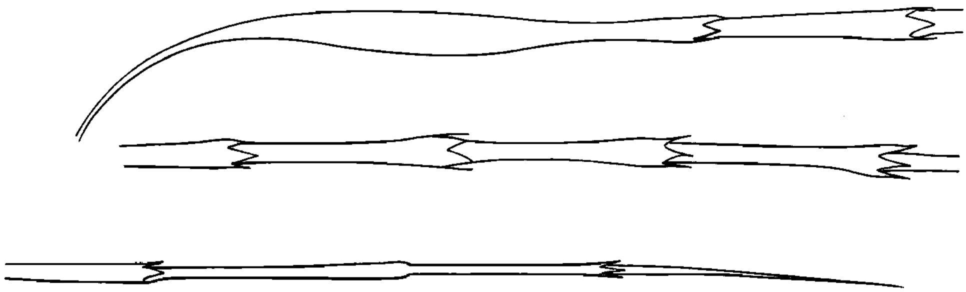


FIG. 48. Nodes and internodes of *Vanellus cayanus* that are typically devoid of pigment.

totally void of pigment (*V. cayanus,* Fig. 48), and still others are somewhat intermediate in pigmentation (*V. indicus, V. lugubris*). Pigment is typically constricted, or narrow and diamond-shaped at the node with much trailing pigment into the internode, especially at basal and mid- nodes. Internodal stippling is also common at mid- and distal nodes. *Vanellus* is more similar to *Pluvialis* than to *Charadrius* in overall microstructure. Although most species have similar true down and afterfeather down pigmentation, variation also occurs in this character. *Vanellus cayanus* has heavily pigmented true down, whereas afterfeather down is only pigmented near the base of the barb; contour feather down is usually unpigmented. The true down of *V. chilensis* has more expanded nodes, with pigment more confined to nodes when compared with contour feather down of this species. Variation in pigmentation patterns of all down types makes this group one of the most difficult to identify microscopically.

Scolopacidae

Limosa haemastica (Hudsonian Godwit), *Numenius americanus* (Long-billed Curlew), *Bartramia longicauda* (Upland Sandpiper), *Tringa nebularia* (Common Greenshank), *Tringa flavipes* (Lesser Yellowlegs), *Catoptrophorus semipalmatus* (Willet), *Xenus cinereus* (Terek Sandpiper), *Actitis macularia* (Spotted Sandpiper), *Heteroscelus incanus* (Wandering Tattler), *Prosobonia cancellata* (Tuamotu Sandpiper), *Arenaria interpres* (Ruddy Turnstone), *Phalaropus lobatus* (Red-necked Phalarope), *Phalaropus tricolor* (Wilson's Phalarope), *Scolopax rusticola* (Eurasian Woodcock), *Scolopax minor* (American Woodcock), *Gallinago nigripennis* (African Snipe), *Gallinago gallinago* (Common Snipe), *Lymnocryptes minimus* (Jack Snipe), *Limnodromus griseus* (Short-billed Dowitcher), *Aphriza virgata* (Surfbird), *Calidris canutus* (Red Knot), *Calidris alba* (Sanderling), *Calidris pusilla* (Semipalmated Sandpiper), *Calidris minutilla* (Least Sandpiper), *Calidris bairdii* (Baird's Sandpiper), *Calidris alpina* (Dunlin), *Eurynorhynchus pygmeus* (Spoonbill Sandpiper), *Limicola falcinellus* (Broad-billed Sandpiper), *Micropalama himantopus* (Stilt Sandpiper), *Tryngites subruficollis* (Buff-breasted Sandpiper), *Philomachus pugnax* (Ruff)

Sandpipers and allies are a large group of shorebirds that are commonly divided into at least four and sometimes up to 10 subgroups: Tringinae (tattlers, curlews, godwits, willets), Arenariinae (turnstones), Scolopacinae (snipe and woodcock), and Calidridinae (sandpipers). More than 85 species are recognized in this family,

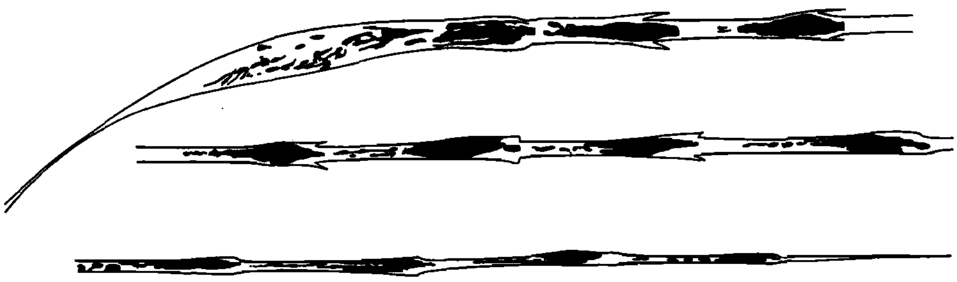


FIG. 49. Contour feather down of *Tringa nebularia*.

which is essentially restricted to the Northern Hemisphere (excluding a few snipe). They are mainly found in aquatic, swampy, or seashore environments.

Because the Scolopacidae constitutes a large group of species, highly variable microcharacters are to be expected. To describe and compare the variation in feather characters in this survey, this family has been divided into five subgroups (Tringinae, Arenariinae, Scolopacinae, Gallinagoninae, Calidridinae).

Although scolopacids exhibit many variations in feather microstructures, they also have many similarities to each other and to members of the Charadriidae. The nodal pigment shape and the way the pigment trails into the internode (with internodal stippling in Tringinae) in some species is generally most similar to that of the charadriids. However, calidridines usually have pigment that is more confined to the nodes and not extensive in the internodal areas of the barbule. The nodes of most scolopacids are usually pigmented all the way to the very distal portions of the barbules. Because many of the scolopacids overlap charadriids in pigmentation patterns and micromorphological features, separation of some of these groups is impossible based on microstructure alone.

Tringinae

Microscopic characters are similar among the species of Tringinae (tattler, curlews, godwits, and willet) examined in this study.

Contour feather down.—Pigment is dark and barbules are heavily pigmented with much trailing or stippled internodal pigment (Fig. 49). Nodes are slightly expanded with diamond-shaped pigment, which is typically constricted to a point in the node. The transparent area around the node is very apparent and most of the nodes along the barbule have distinct spines. Pigment is less intense at the

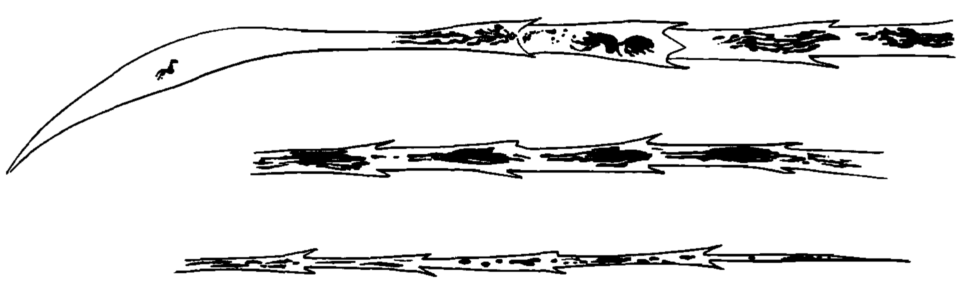


FIG. 50. Contour feather down of *Numenius americanus*.

node and more stippled internodally in *Numenius americanus* (Fig. 50) and *Limosa haemastica.* Some specimens of *Numenius americanus* have unpigmented distal portions of barbules.

Midsection nodes of barbules are more narrow or elongate than rounded in *Bartramia longicauda* and *Catoptrophorus semipalmatus.* At the distal portion of the barbules in *Bartramia* the pigment is very heavy and the nodes are closer together than in other species in this group. A unique feature of *Bartramia* is that the last cell on the barbule (distal cell) has multiple spines at the tip (Fig. 51a, b) instead of a single long spine that is typical of other members of this order (Fig. 52). The only other species examined in this study with multiple spines at the tip of the distal-most cell was *Prosobonia cancellata.*

Xenus cinereus differs from other species in the order by having unpigmented true down, whereas other down types (contour and afterfeather) are fully pigmented.

Prosobonia cancellata has typical microscopic features of scolopacids with many nodes that are usually pigmented all the way to the tip of the barbule. The most characteristic features of this species are the longer than normal spines that are more numerous (five to seven) at the nodes all along the barbule (Figs. 53, 54). Nodal pigment trails into internodes all along the barbule. The most distal cells on the barbule are sometimes multispined at the very tip as in *Bartramia* (Fig. 55).

Afterfeather and true down.—These are similar to contour feather down except the overall structure is finer and no subpennaceous region is present on these feather types.

Villi.—Villi are observed on some barbules of *Tringa flavipes.*

Arenariinae

Contour feather down.—*Arenaria interpres* also conforms to general scolopacid patterns in feather microstructure except the internode at the midsection of the barbule is much thinner than other species and makes the midnodes of barbules seem larger. Pigment is diamond-shaped at the nodes and mostly confined to the nodes with little or none of the internodal pigmentation that is commonly observed in the microstructures of the Tringinae. Thus, pigmentation patterns of *A. interpres* are more similar to those of Calidridines than Tringines. Spines are most visible at the basal nodes of barbules.

Afterfeather and true down.—Microscopic structures are finer but similar to those of contour feathers. No subpennaceous region is present in these feather types.

Villi.—Villi are observed on some barbules of *A. interpres.*

Scolopacinae

Contour feather down.—The two species of the subfamily Scolopacinae examined here differ slightly in feather microstructure. Both *Scolopax minor* (Fig. 56) and *S. rusticola* have very long barbules that set them apart from all other sandpipers. Nodal and internodal pigmentation of barbules is very heavy in both

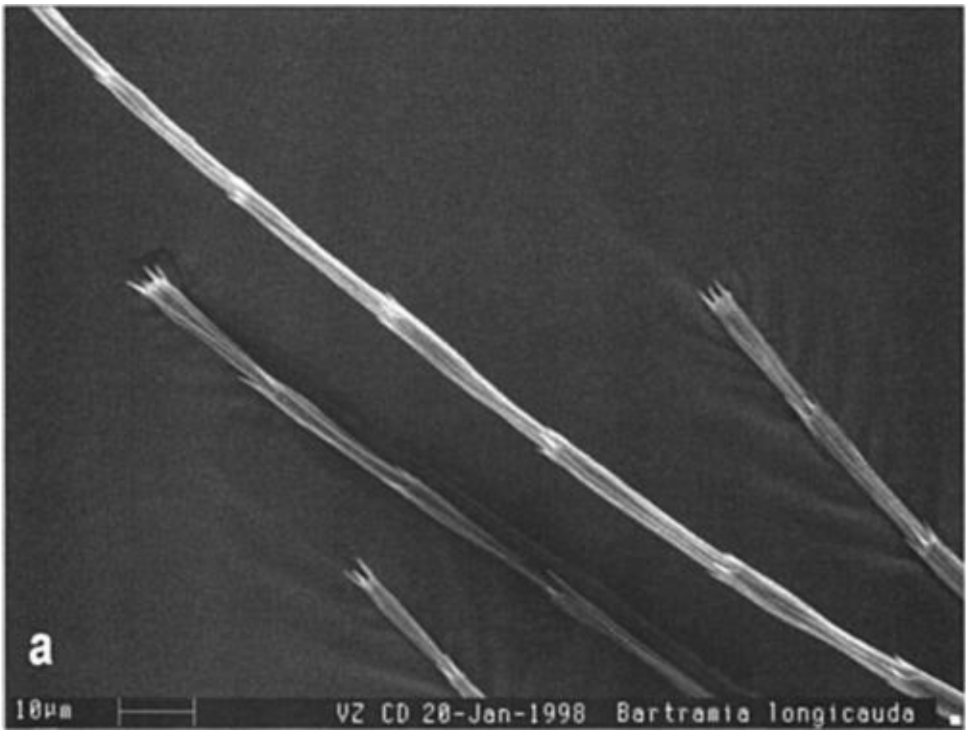


FIG. 51a. *Bartramia longicauda* has distal cells with multiple spines (a). Enlarged view of distal, multiple-spined cell (Fig. 51b).

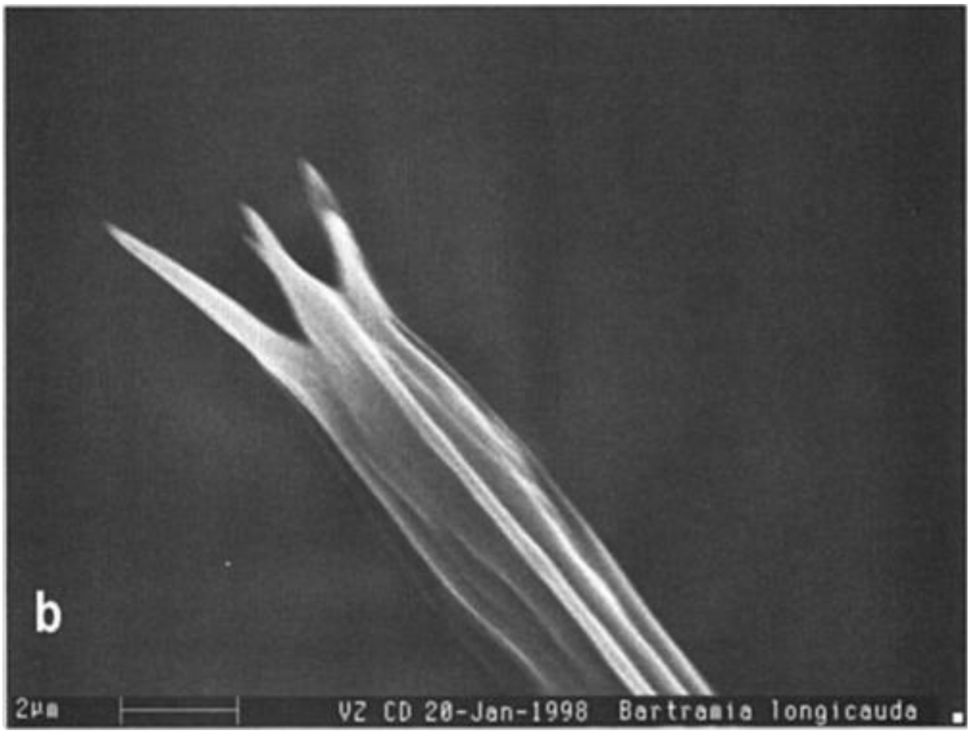


FIG. 51b.

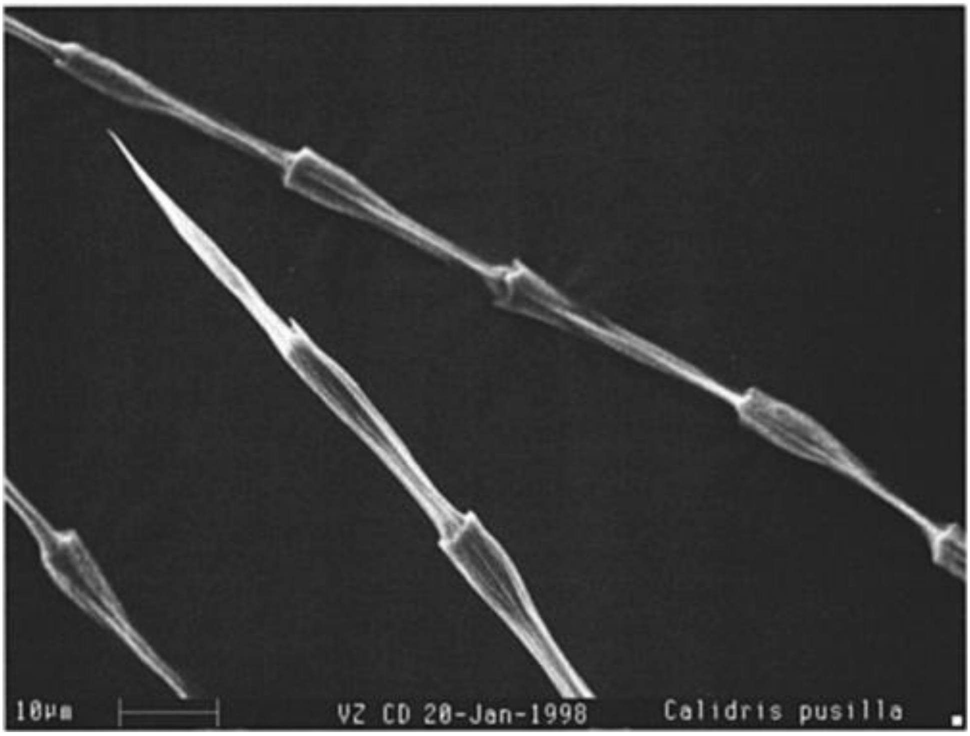


FIG. 52. Most members of the order Charadriiformes have single-spined distal cells.

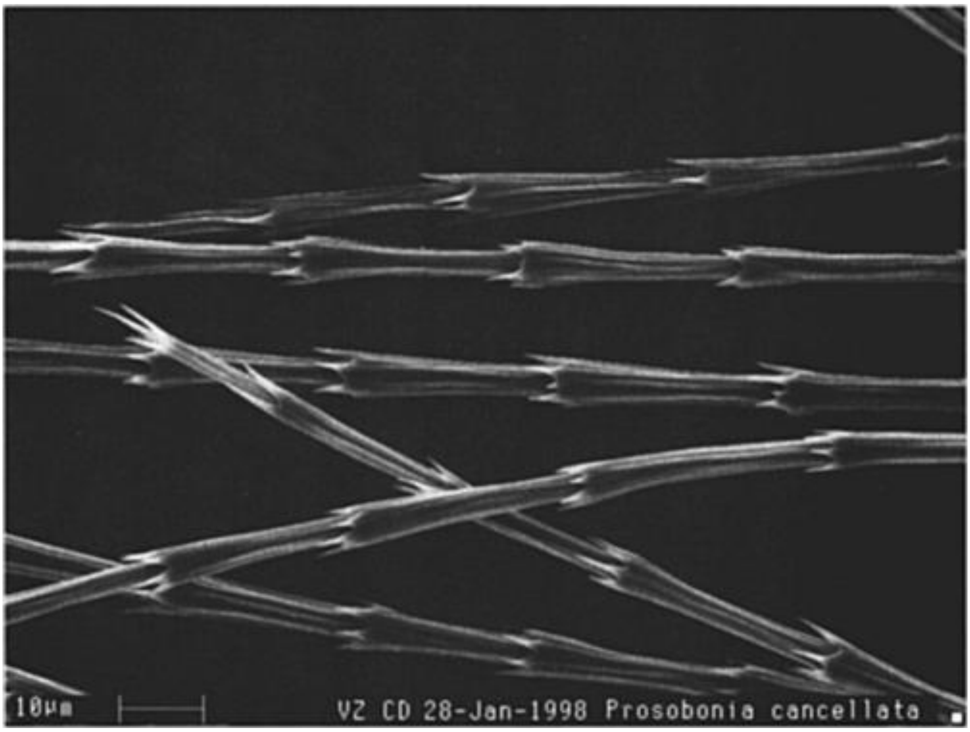


FIG. 53. *Prosobonia cancellata* differs from most members of the family Scolopacidae by having much longer spines that consistently occur on nodes all along the barbule instead of only on basalmost nodes.

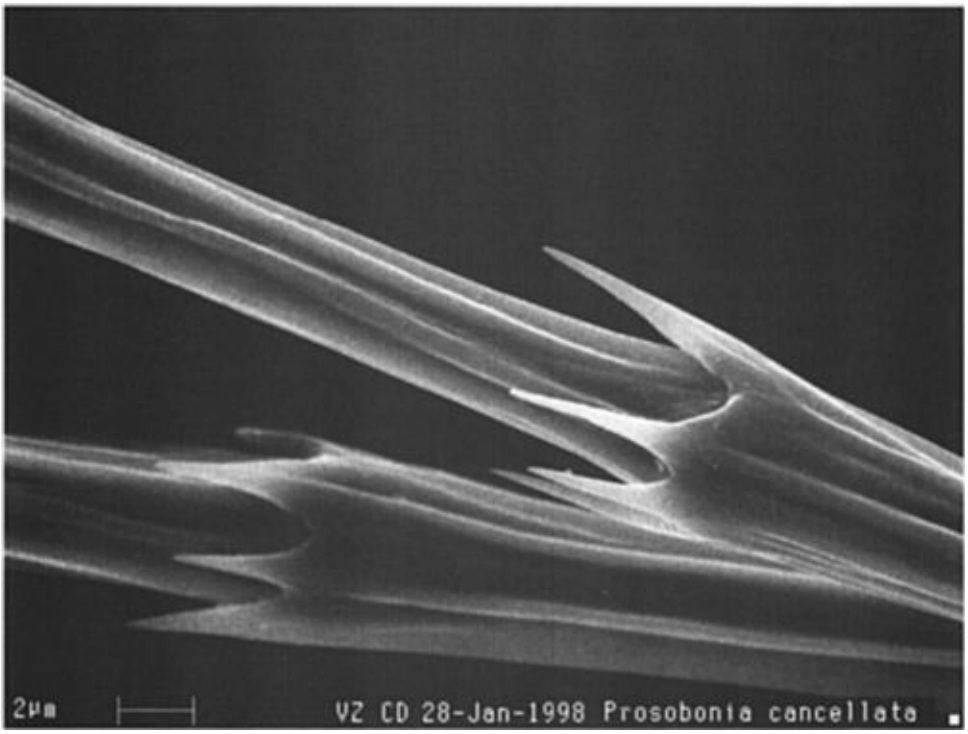


FIG. 54. Enlarged node of *Prosobonia cancellata* showing typical long spines.

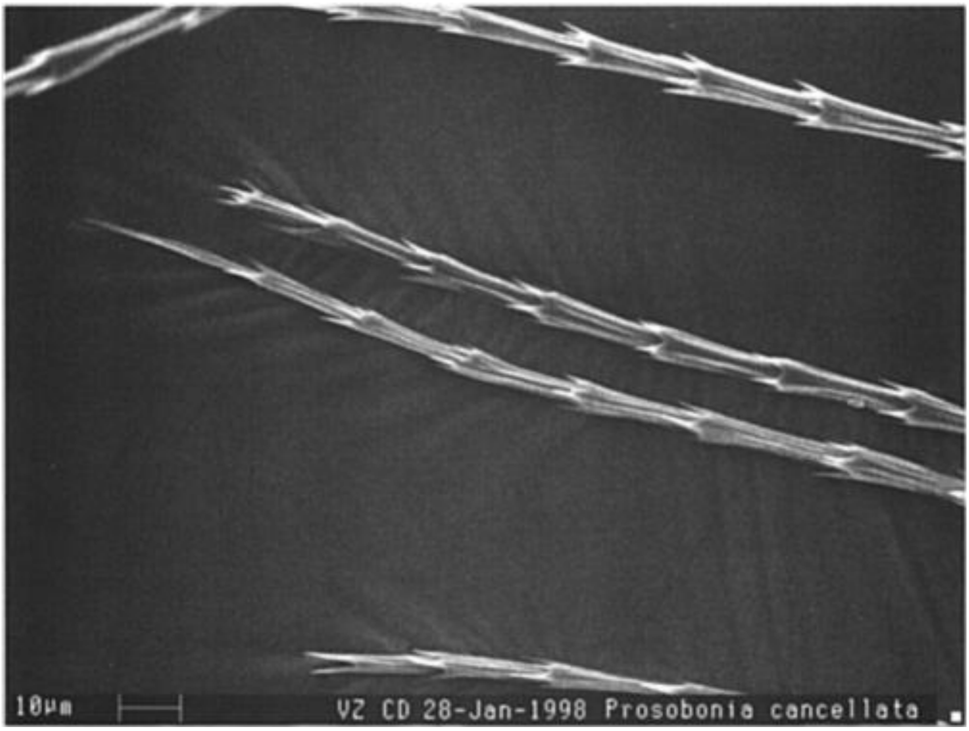


FIG. 55. Distal cells of *Prosobonia cancellata* sometimes have multiple spines as in *Bartramia*.

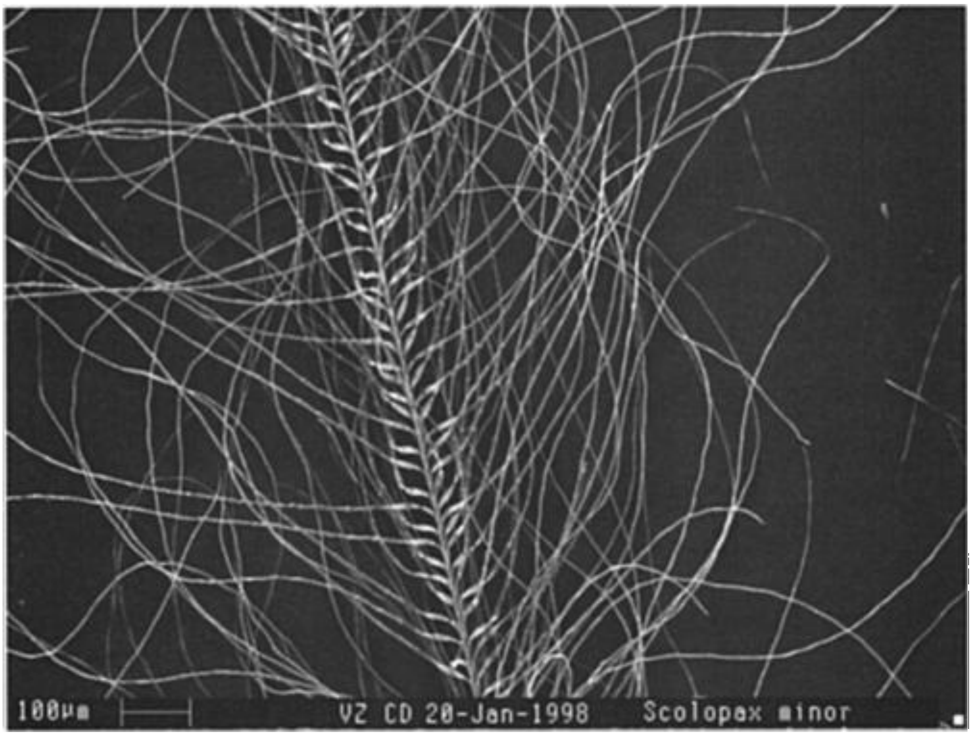


FIG. 56. Very long barbules distinguish *Scolopax* from most other shorebirds.

species (Fig. 57). Basal nodes of barbules have the pigment constricted in the node to form a diamond-shaped point but the transparent area around the nodal pigment is more distinct in *S. minor*; the node shape is more flared in *S. rusticola.* Spines are most visible on the nodes of the basal portions of barbules; nodes at distal portions of the barbule are usually inconspicuous because the tip of the barbule is thin and filamentous. However, some distal node spines can be seen at high power on *S. minor.* Midsection nodes of *Scolopax* are very narrow and oblong in shape and internode width is very narrow (Fig. 58). Subpennaceous regions are distinct on contour feather down.

Afterfeather and true down.—Afterfeather and true down are microscopically similar to contour feather down but lack subpennaceous regions and are finer in structure.

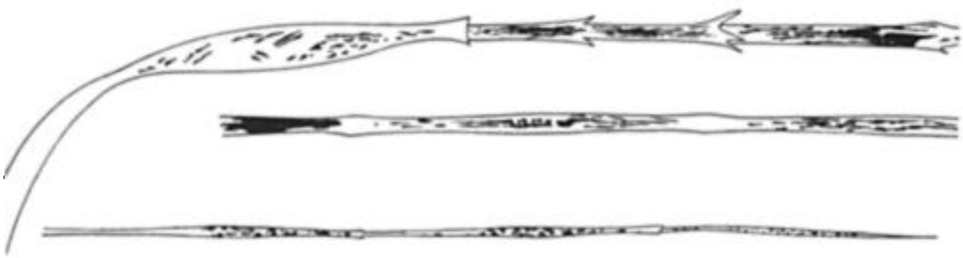


FIG. 57. Heavily pigmented nodes and internodes of contour feather down of *Scolopax rusticola.*

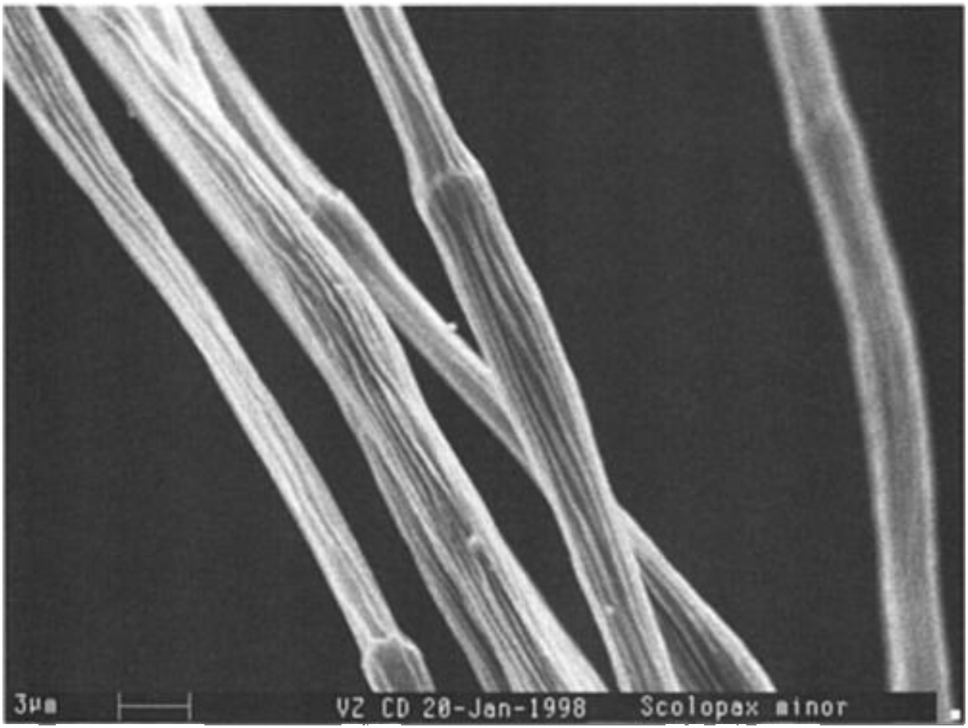


FIG. 58. Midsection nodes of *Scolopax* are long and narrow.

Gallinagoninae

The four species of the Gallinagoninae surveyed in this study are similar to each other in plumulaceous microscopic structures.

Contour feather down.—Although the barbules of contour feathers of *Gallinago* are much shorter than in *Scolopax,* they are similar to each other in having very elongate, narrow nodes at distal sections of barbules. Nodes are more expanded at the base of the barbule and become long and narrow at mid- and distal sections of the barbule (Fig. 59). Pigment is heavy and continuous throughout nodes and internodes of the barbule in all species examined in this study (Fig. 60) except *Limnodromus griseus* (Fig. 61).

Limnodromus griseus differs from the other members of this subfamily in having much less internodal pigmentation (Fig. 61). Pigment is more rounded at nodes with much internodal stippling. This internodal stippling is heavier at the basal portion of the barbule. Pigment does not connect through the node and internode as in *Gallinago* and *Lymnocryptes.* Pigment is also much heavier at the base of the barb than at the tip of the barb in *Limnodromus griseus.* Subpennaceous regions are well defined in all species studied except *Lymnocryptes.*

Afterfeather and true down.—Afterfeather and true down are similar to contour feather down in pigmentation patterns with the exception that true down is sometimes less pigmented than contour feather down at the base of barbules. These feather types do not have subpennaceous regions.

Villi.—Villi are observed in *Lymnocryptes minimus.*

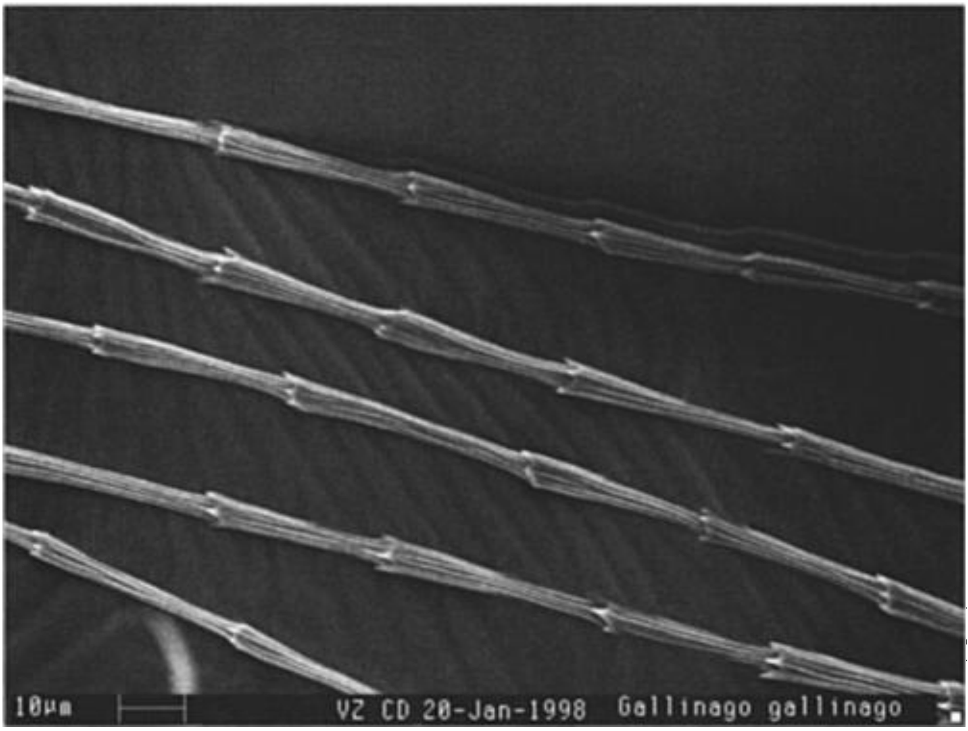


FIG. 59. *Gallinago gallinago* has slightly expanded nodes that are close together at the base but become more indistinct at the midsection (shown here) of the barbule.

Calidridinae

Microscopic characteristics are similar among the species of Calidridinae (sandpipers) examined in this study.

Contour feather down.—Plumulaceous barbules are of medium length and typically have pigmented nodes throughout the length of the barbule. Nodes are well defined, often with diamond-shaped pigment that is usually more distinctly shaped at basal nodes on barbules. Pigment shape at midsection nodes of barbules is sometimes rounder or more oblong at many nodes and less diamond-shaped. Like

FIG. 60. Contour feather down of *Gallinago nigripennis*.

FIG. 61. Contour feather down of *Limnodromus griseus*.

charadriids, the most proximal node is often reduced or smaller than the next node on the barbule (*Calidris pusilla,* Fig. 62). Spines are typically present at nodes all along the barbule but some species of *Calidris, Limicola,* and *Micropalama* do not have distinct spines at nodes on the midsection of the barbule. Instead, these species have more of a rounded projection than a spine at the node. Pigment is usually more confined at mid-nodes of barbules but sometimes extends proximal to the nodes at the basal and distal portions of the barbules. *Tryngites subruficollis* and *Limicola falcinellus* have wider basal nodes in proportion to distal nodes than other species in this group.

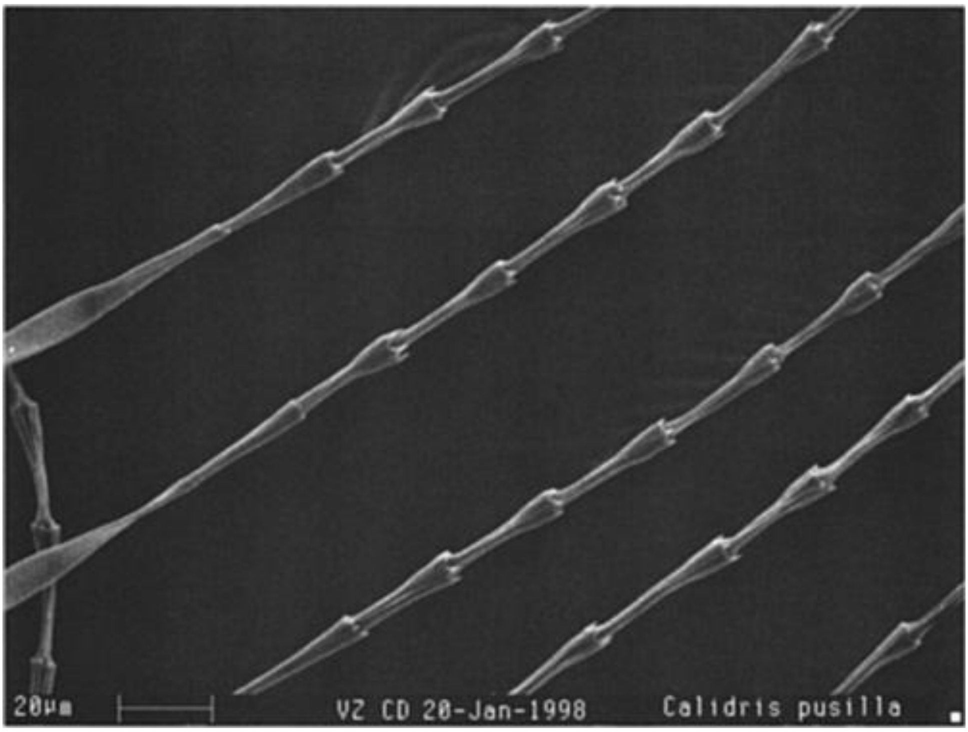


FIG. 62. Reduced first node typical of some members of the order Charadriiformes (*Calidris pusilla* is shown).

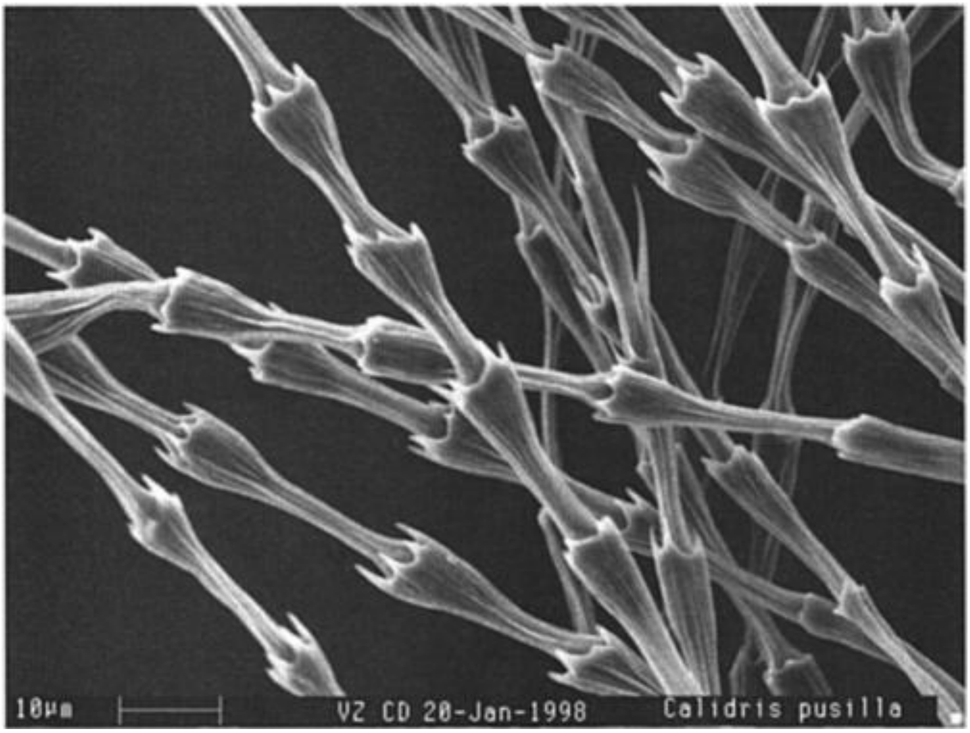


FIG. 63. Greatly expanded, spined nodes that occur all along the barbule, and short internodal length are distinguishing features of *Calidris*.

All six species of *Calidris* examined here have similar microstructures. Nodes of barbules are rounder and more expanded all along the barbule (Fig. 63) than in other members of this family. Nodes are distinct on the distal part of the barbule (Fig. 64). The genus *Calidris* has the most numerous and most expanded nodes in the family with pigment and node shape more rounded than oblong (Figs. 65, 66). *Philomachus pugnax* has longer, narrower pigment at the nodes that extends into the internode and also has relatively long barbules. Subpennaceous regions in contour feather down are present in all species examined except *Calidris pusilla*; subpennaceous regions were difficult to find in *C. minutilla.*

Phalaropes (two species) have heavier internodal pigmentation that is more prevalent throughout the barbules than in most scolopacids (Fig. 67) Barbules are relatively short with elongated pigment at the slightly expanded nodes (Figs. 68, 69). Villi are more readily observed on phalaropes than any other species examined in this study (Fig. 70) and multiple villi are common on some bases.

Afterfeather and true down.—All calidridines examined here have similar true and afterfeather pigmentation patterns to contour feather down but have finer, more filamentous barbules. No subpennaceous regions are present in these feather types.

Villi.—Villi are present in *Calidris bairdii, C. pusilla* (Fig. 71), *Eurynorhynchus pygmeus, Micropalama himantopus, Tryngites subruficollis, Philomachus pugnax,* and both species of phalaropes.

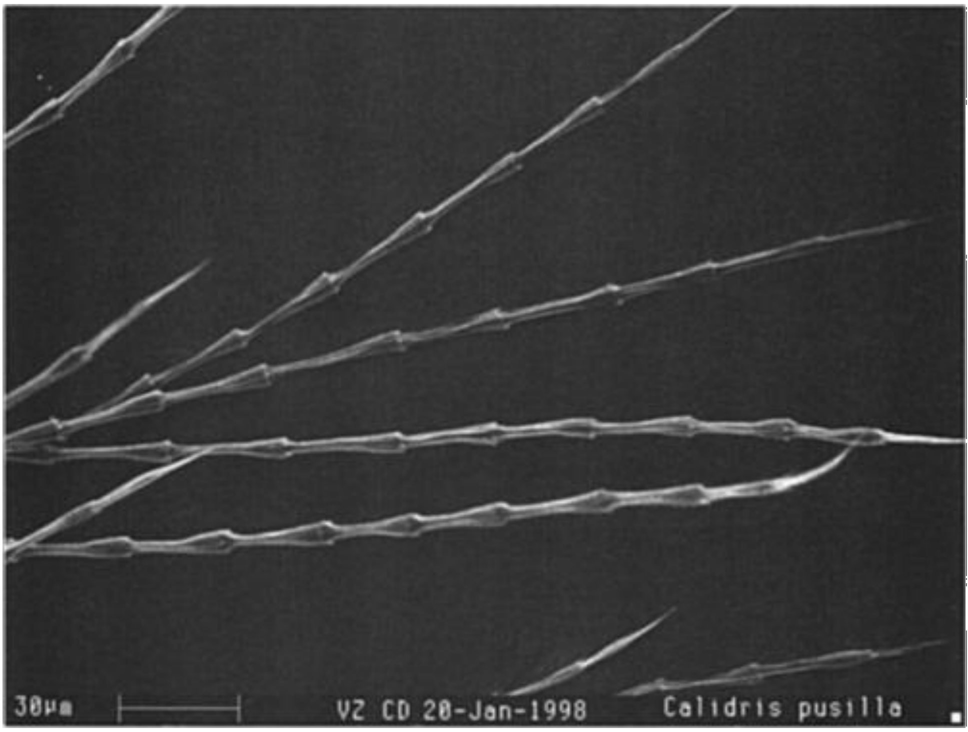


FIG. 64. Expanded nodes on the distal part of the barbule in *Calidris*.

Thinocoridae

Attagis gayi (Rufous-bellied Seedsnipe), *Thinocorus orbignyianus* (Gray-breasted Seedsnipe), *Thinocorus rumicivorus* (Least Seedsnipe)

The four species in this family range from the tundras of the Falkland Islands and Patagonia northward through the Argentine pampas, and in the barren highlands from Chile to Ecuador.

Contour feather down.—The microscopic feather characteristics of this family are diagnostic in that they have very long barbules with extremely expanded nodes that occur all along the length of the barbule (Fig. 72). The nodes are large and the pigment is confined at most nodes. The large nodes at the midsection of the barbules make the internode appear thin (Fig. 73). Of the three species studied in

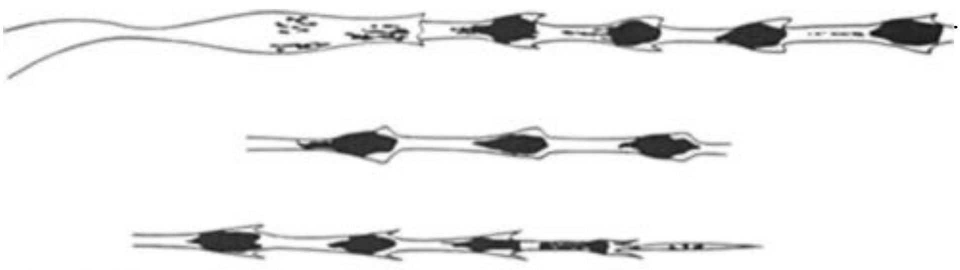


FIG. 65. Contour feather down of *Calidris minutilla*.

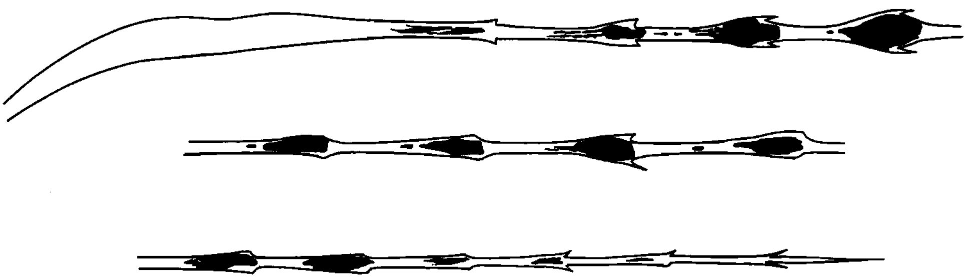


FIG. 66. Contour feather down of *Calidris alba.*

this family, *Attagis gayi* has the largest and most expanded nodes that occur all along the barbule (Fig. 74). The most distal cell of the barbule is short. None of the species studied has significant subpennaceous regions. Base cells of barbules are long, some with distinct cell division scars (Fig. 75). The combinations of the microscopic feather characteristics of this family (long barbules, large nodes, confined pigment) are very diagnostic and consistent within this order of birds.

Afterfeather and true down.—All of the down types were similar to contour feather down with the usual exception of being finer and more filamentous than other types.

This family shares few microcharacters with other members of the order. Diamond-shaped pigment at the node is apparent on basal nodes of barbules in *Thinocorus* more so than in *Attagis,* and the first cells of the former are usually reduced. *Thinocorus* has somewhat more elongate pigment at nodes than *Attagis* and nodes are closer together (Fig. 76). *Attagis* can be distinguished from *Thinocorus* by having basal nodes of barbules that are more flared and the internodal length is visibly longer (Fig. 77). Nodes of barbules in this family can be expanded so much that some of the transparent processes surrounding the pigment at the nodes appear to be downturned. At some nodes, this creates the illusion of a ringlike structure around the node because the transparent process bends downward toward the base of the barbule. Contrary to Brom's (1991) observations of *A. gayi,* this is not the same ringlike structure found in Galliformes. The nodal structures of these two groups are morphologically different, and the nodal processes of seedsnipes are firmly attached and not known to detach from the node.

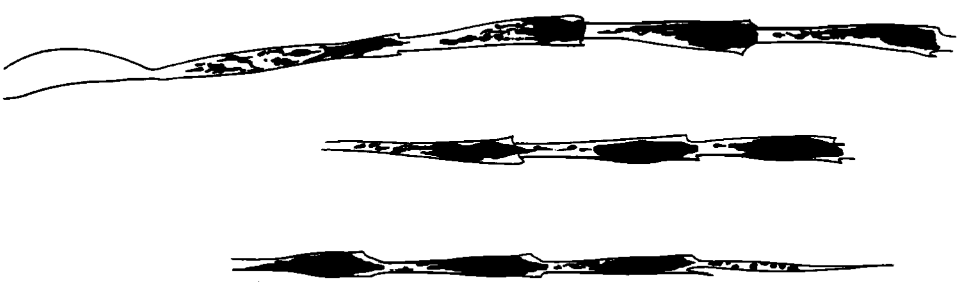


FIG. 67. Contour feather down of *Phalaropus tricolor.*

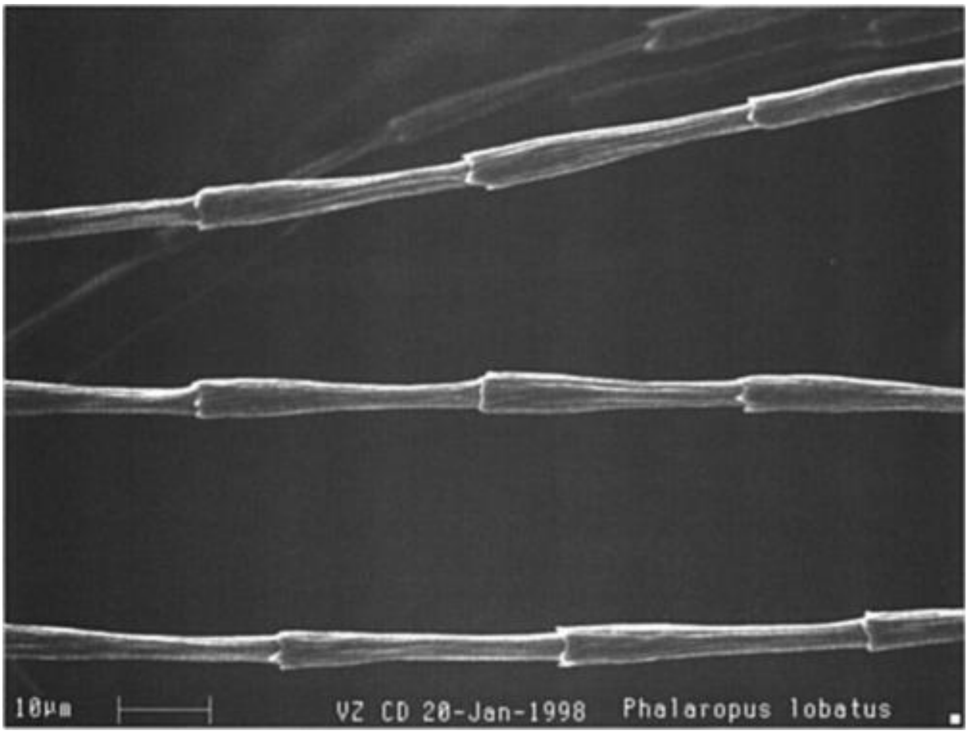


FIG. 68. Phalaropes have short barbules with slightly expanded nodes.

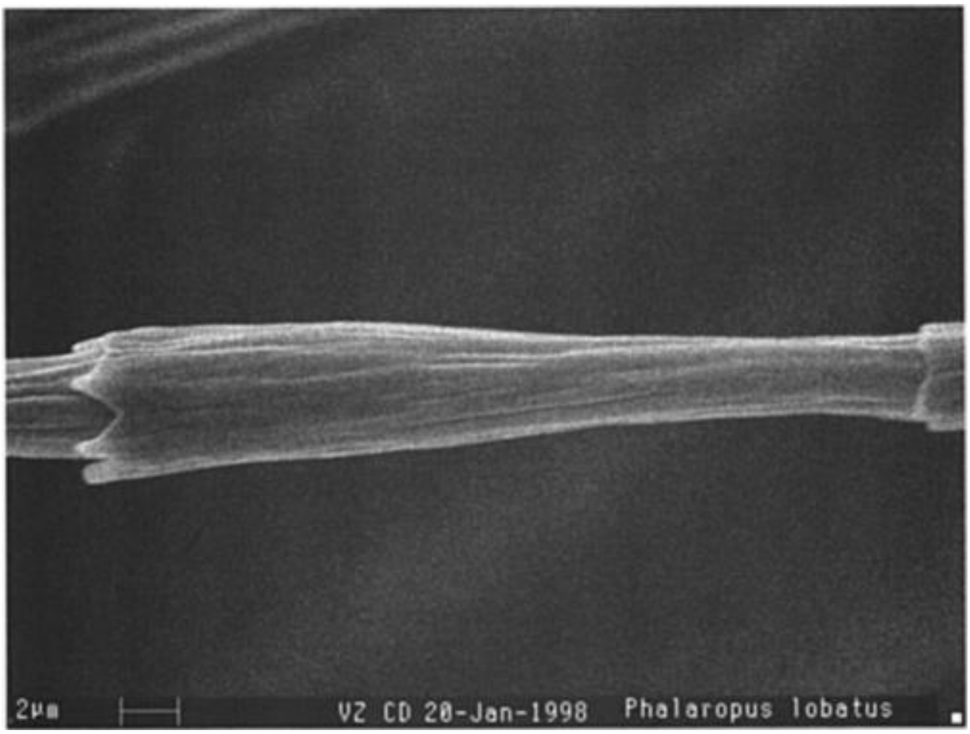


FIG. 69. Enlarged node of *Phalaropus lobatus* showing very short spines.

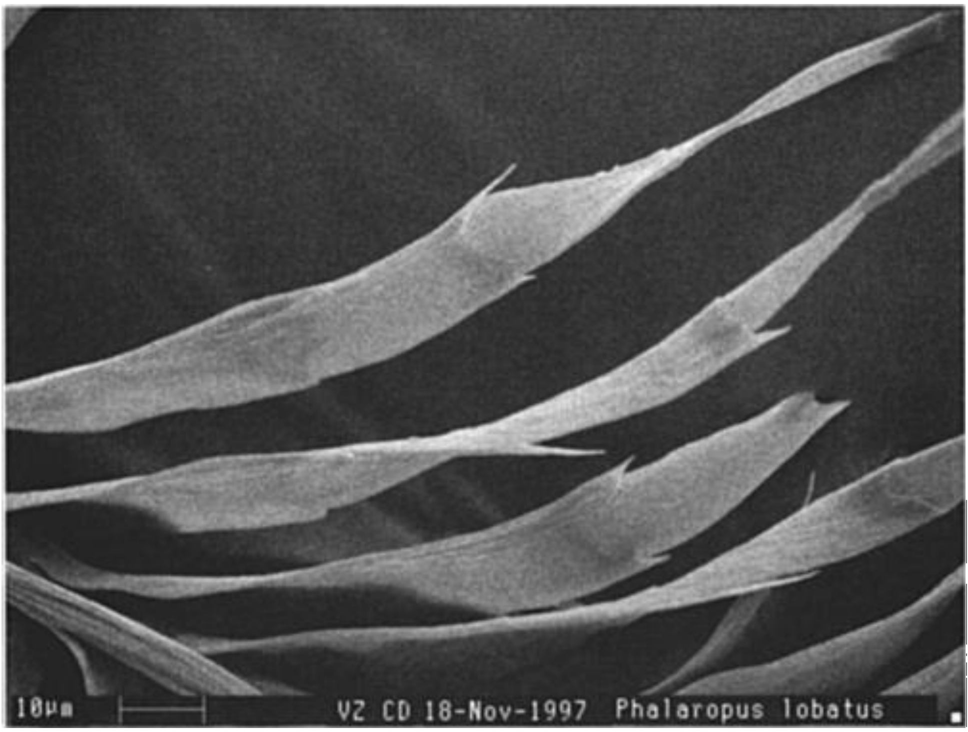


FIG. 70. Phalaropes have more villi than any other species studied in this order.

FIG. 71. Villi occur on the very basal barbules of some species of calidridines (e.g., *Calidris pusilla*).

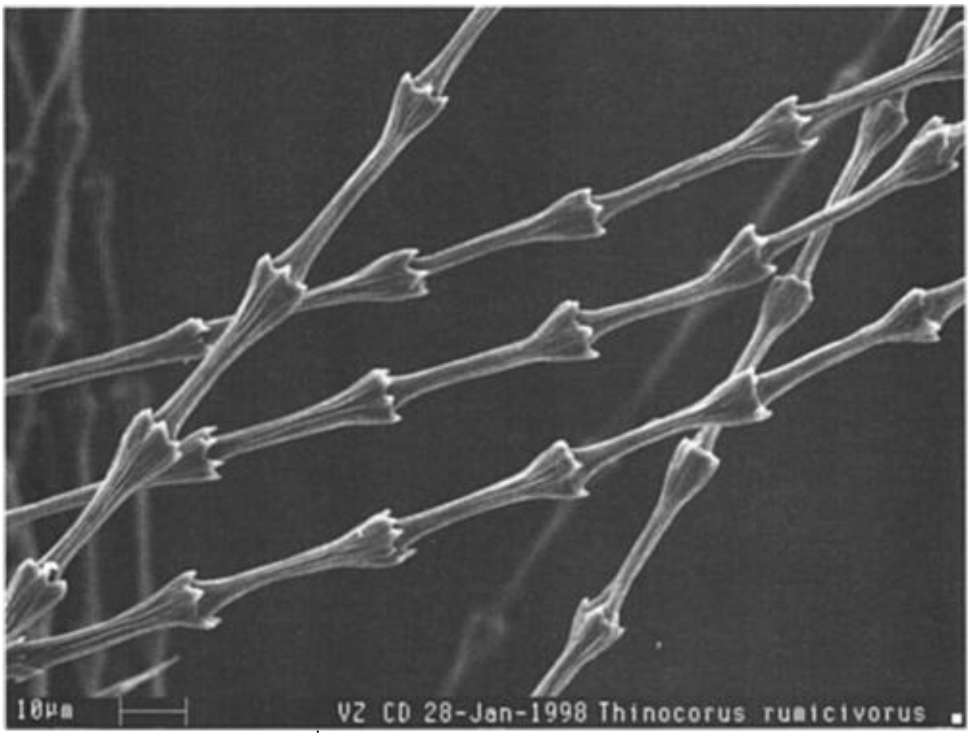


FIG. 72. Seedsnipes (Thinocoridae) typically have very long barbules with greatly expanded nodes that occur along the entire length of the barbule.

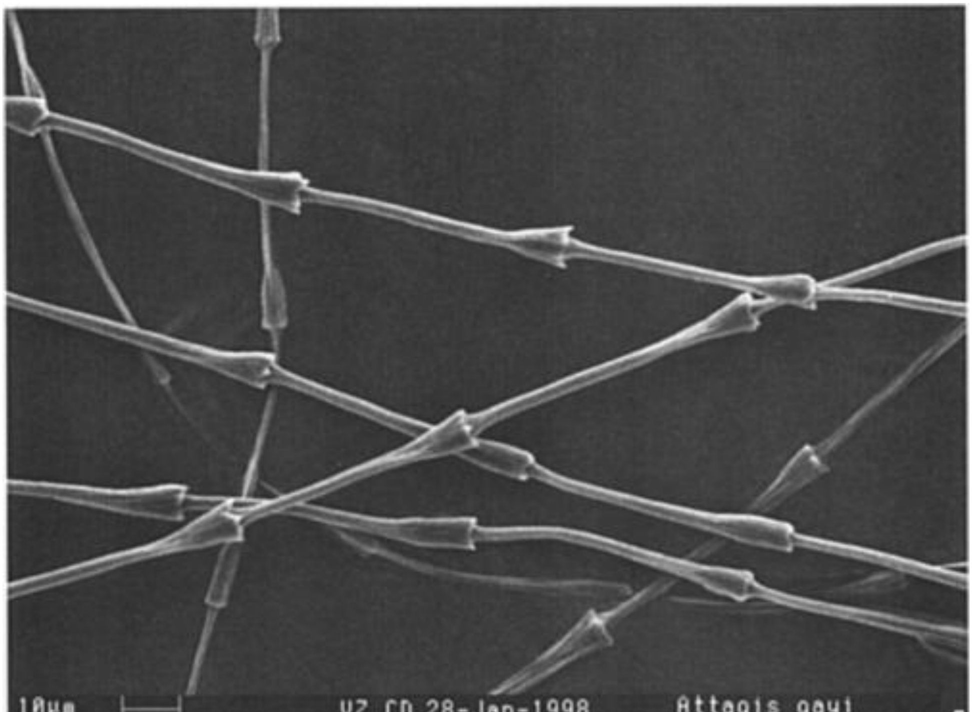


FIG. 73. Large nodes at the midsection of the barbule in seedsnipes make the internode appear very narrow as in coursers, but seedsnipes have much longer barbules.

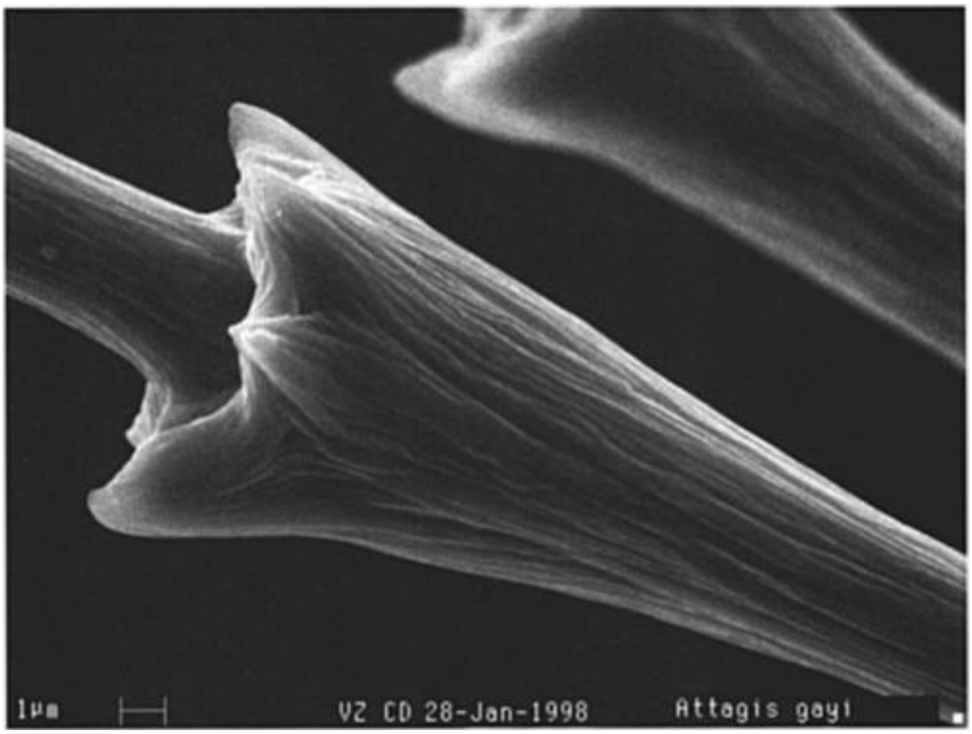


FIG. 74. *Attagis gayi* has the most expanded nodes of any species examined in this family.

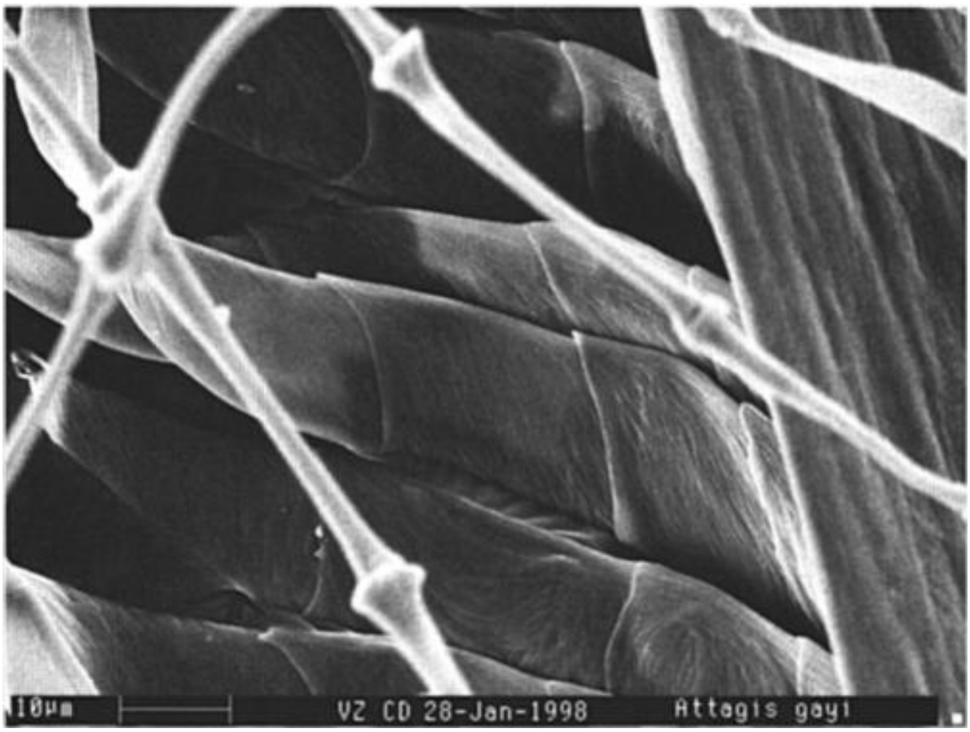


FIG. 75. Distinct cell divisions in bases of barbules may be observed in *Attagis gayi*.

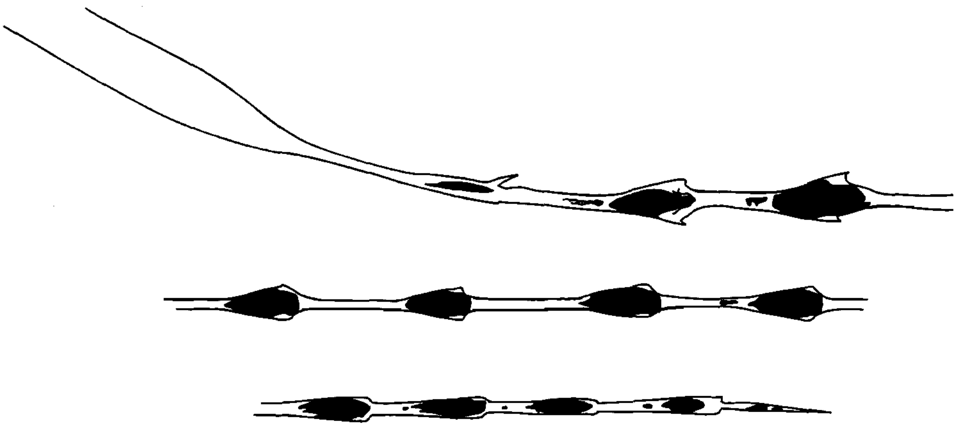


FIG. 76. Contour feather down of *Thinocorus rumicivorus.*

Pedionomidae

Pedionomus torquatus (Plains-Wanderer)

Until fairly recently, the Plains-Wanderer was classified in a completely different order (Gruiformes, family Turnicidae). *Pedionomus torquatus* is now recognized as a monotypic species in its own family within the Charadriiformes (Olson and Steadman 1981). This species resembles the buttonquails (Turnicidae) in appearance and lives in southeastern Australia.

Contour feather down.—Microscopic feather characters are not unique or drastically different from other families in the order but are generally similar to those of the scolopacids because they usually have pigmented nodes that are visible to the very distal portion of the barbules. Nodal morphology is also more similar to that of the scolopacids than that of birds in other families in this order. Barbs and barbules have pigmented, spined nodes throughout the length of the barbule (Figs. 78, 79). Pigment is often diamond-shaped at the nodes with some pigmentation trailing into the internode (Fig. 80). The first node is usually reduced (Fig. 81), and the basal cell is moderately pigmented. The subpennaceous region is not distinct.

Afterfeather and true down.—Afterfeather and true down are similar to contour feather down but have no subpennaceous regions and are finer in structure.

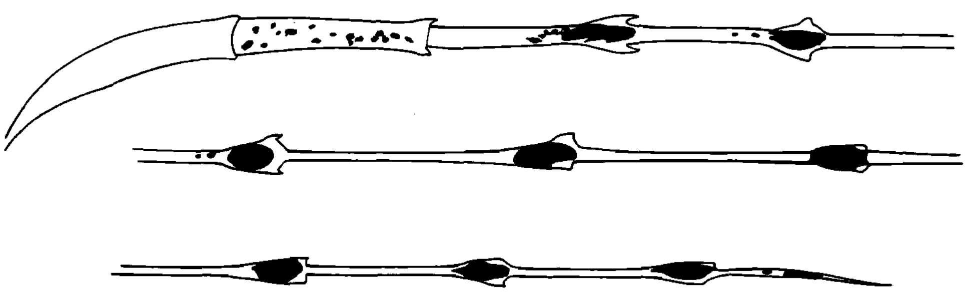


FIG. 77. Contour feather down of *Attagis gayi.*

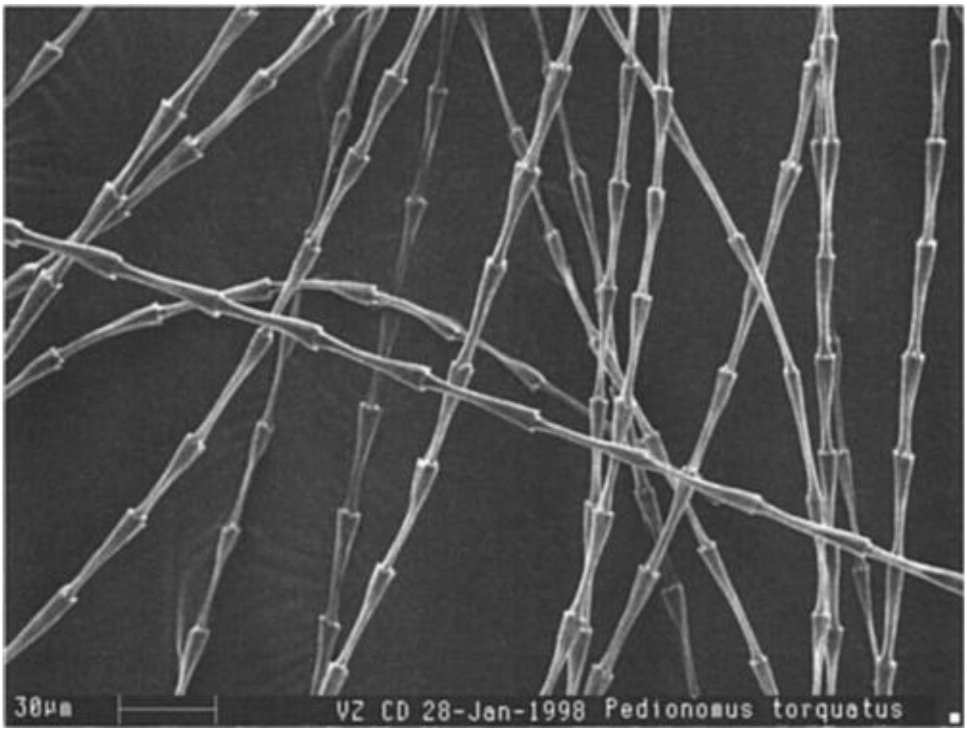


FIG. 78. Microstructures of plumulaceous feathers of *Pedionomus torquatus* are somewhat similar to some scolopacids by having many nodes all along the medium-length barbule.

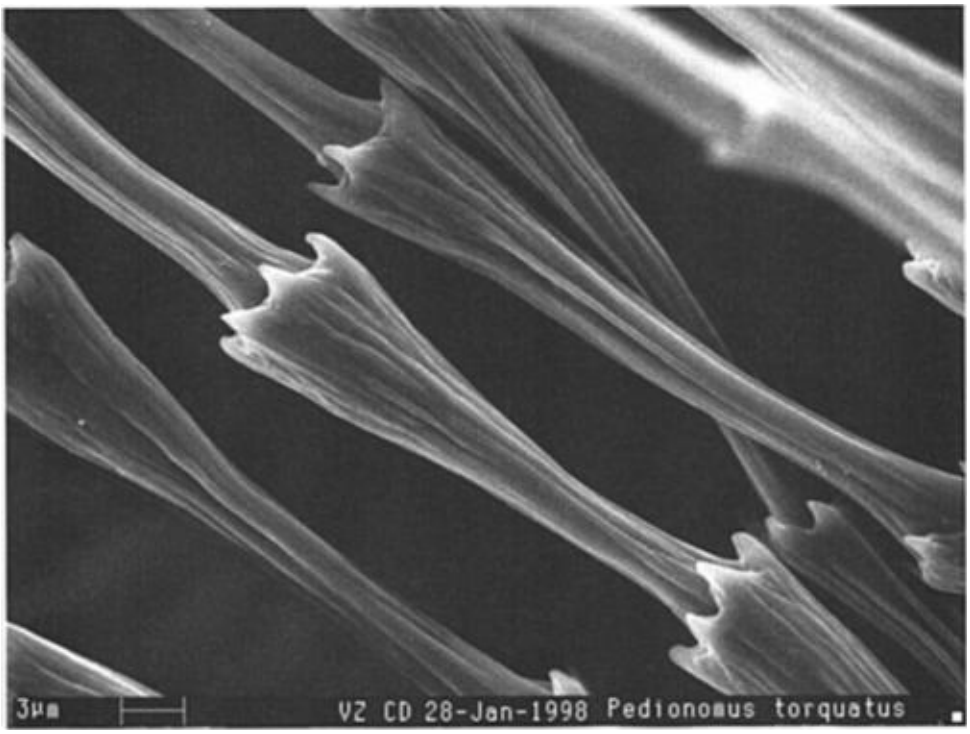


FIG. 79. Nodes of *Pedionomus torquatus* are expanded and spined.

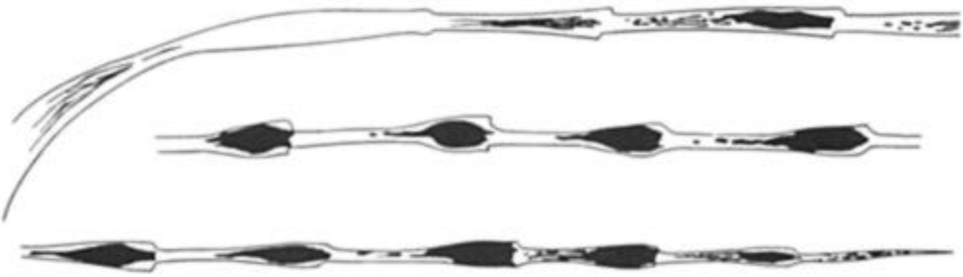


FIG. 80. Contour feather down of *Pedionomus torquatus*.

Chionididae

Chionis alba (Snowy Sheathbill)

Sheathbills are plump, dovelike birds that are confined to Antarctic regions. An outstanding characteristic of this group is that the true down is pigmented much more heavily than other down types. Contour feather down and afterfeather down are unpigmented.

Contour feather down.—At first glance, the plumulaceous barbules of the contour feather appear totally unpigmented but observation at high power (400×) shows single rows of tiny light-brown to reddish pigment granules (Fig. 82) at or just below some basal and midsection nodes. Spines are present at basal nodes,

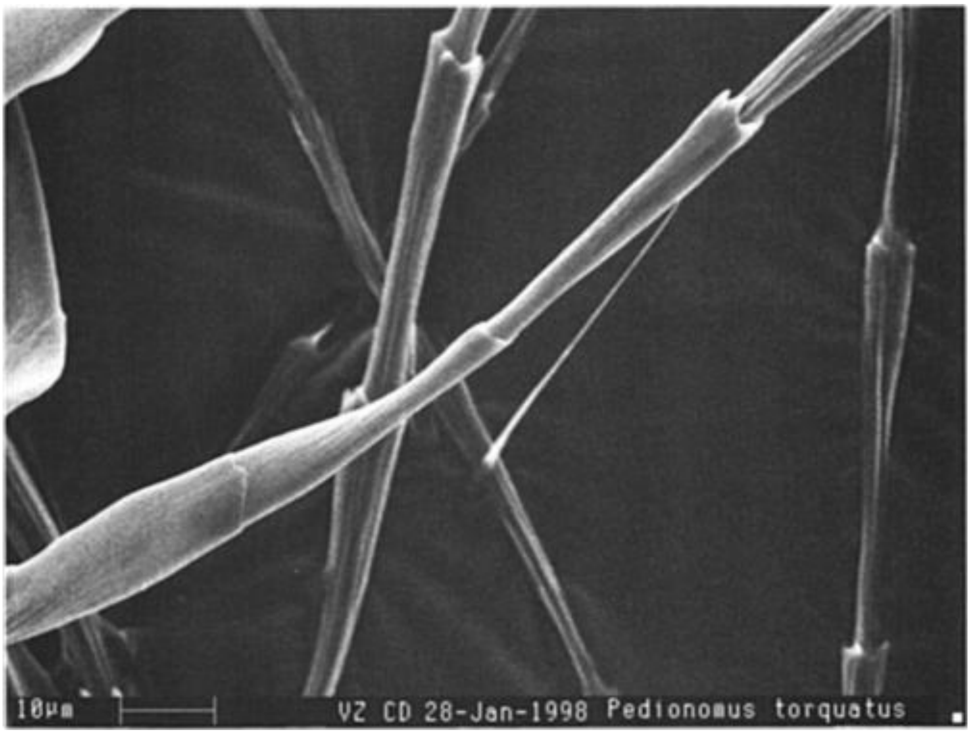


FIG. 81. The base of the barbule is typically composed of more than one cell and the first node is often reduced in size in *Pedionomus torquatus*.

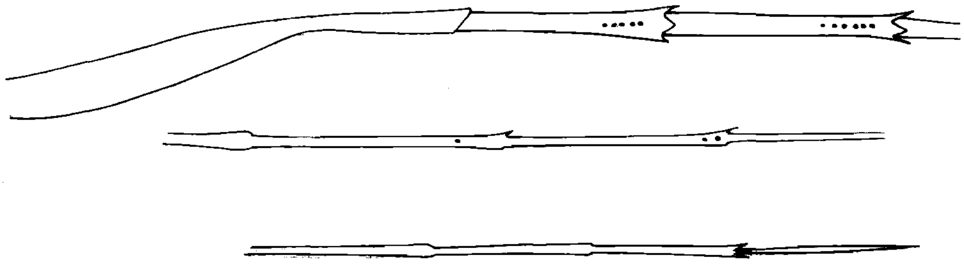


FIG. 82. Contour feather down of *Chionis alba.*

and barbules are medium length (Fig. 83). Mid-nodes usually lack visible spines (Fig. 84). The subpennaceous region is unpigmented.

Afterfeather and true down.—The afterfeather down shows similar patterns to contour feather down. No subpennaceous regions are present on these feather types.

True down is heavily pigmented (Fig. 85), often more so on the midsection of the barb. Nodes have diamond-shaped pigment, and barbules are pigmented throughout the length of the barbules.

Stercorariidae

Catharacta skua (Great Skua), *Stercorarius longicaudus* (Long-tailed Jaeger)

Skuas and jaegers are strong flying, largely pelagic, gull-like birds of high latitudes. Microscopic feather characters of both species examined in this study are similar. *Catharacta* has somewhat longer prongs at the distal nodes than does *Stercorarius.*

Contour feather down.—Barbules are short to medium in length with slightly expanded nodes that become less distinct toward the distal end of the barbule. Spines are present at nodes all along the barbule (Fig. 86a) and become longer, forming prongs at nodes on the distal portion of the barbule (Fig. 86b). This is similar to the prongs on the distal nodes of alcids. The nodes are not usually heavily pigmented throughout the barbule's length. Pigment is somewhat concentrated at basal nodes but is also diffuse or sparsely stippled throughout the internodes of basal and midsection nodes (Fig. 87). Diamond-shaped pigment is observed only at basal nodes of barbules. Base cells of barbules are stippled with pigment and some have multiple base cell divisions (Fig. 88). Subpennaceous regions are well-defined and long.

Afterfeather and true down.—True down and afterfeather down are similar in pigmentation patterns to contour feather down. Like the gulls, if contour feather down is pigmented, it is only at the umbilical or very basal barbs. No subpennaceous regions are observed in these feather types.

Laridae

Pagophila eburnea (Ivory Gull), *Larus pacificus* (Pacific Gull), *Larus scoresbii* (Dolphin Gull), *Larus belcheri* (Band-tailed Gull), *Larus crassirostris* (Black-tailed Gull), *Larus delawarensis* (Ring-billed Gull), *Larus canus* (Mew Gull), *Larus argentatus* (Herring Gull), *Larus fuscus* (Lesser Black-backed Gull), *Larus californicus* (California Gull), *Larus occidentalis* (Western Gull), *Larus*

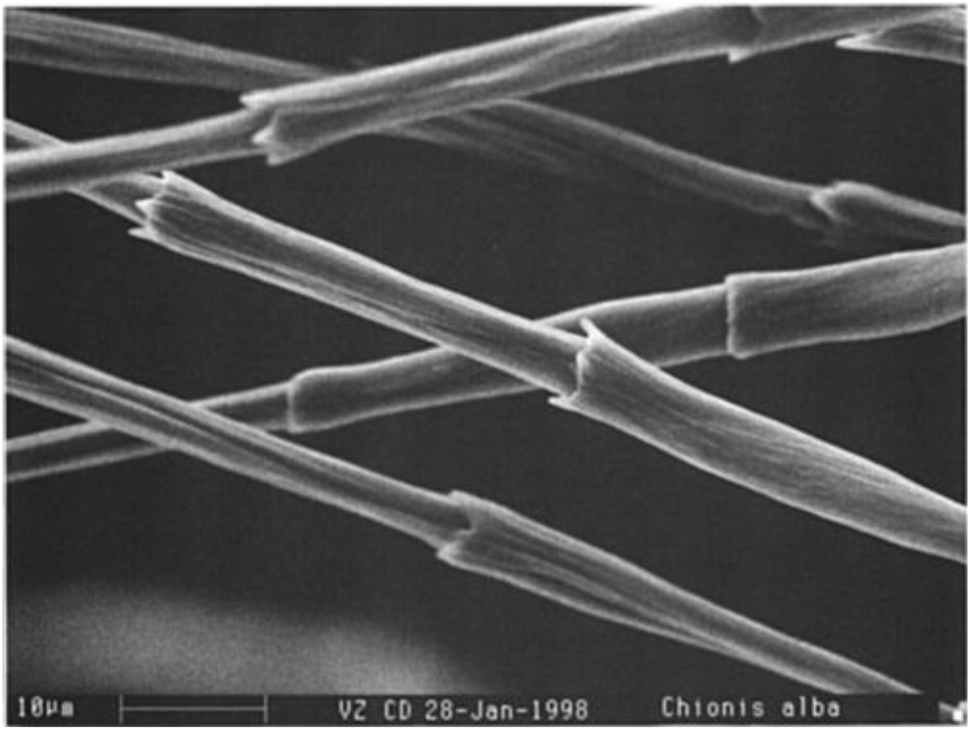


FIG. 83. Short spines are present at slightly expanded basal nodes of *Chionis alba*.

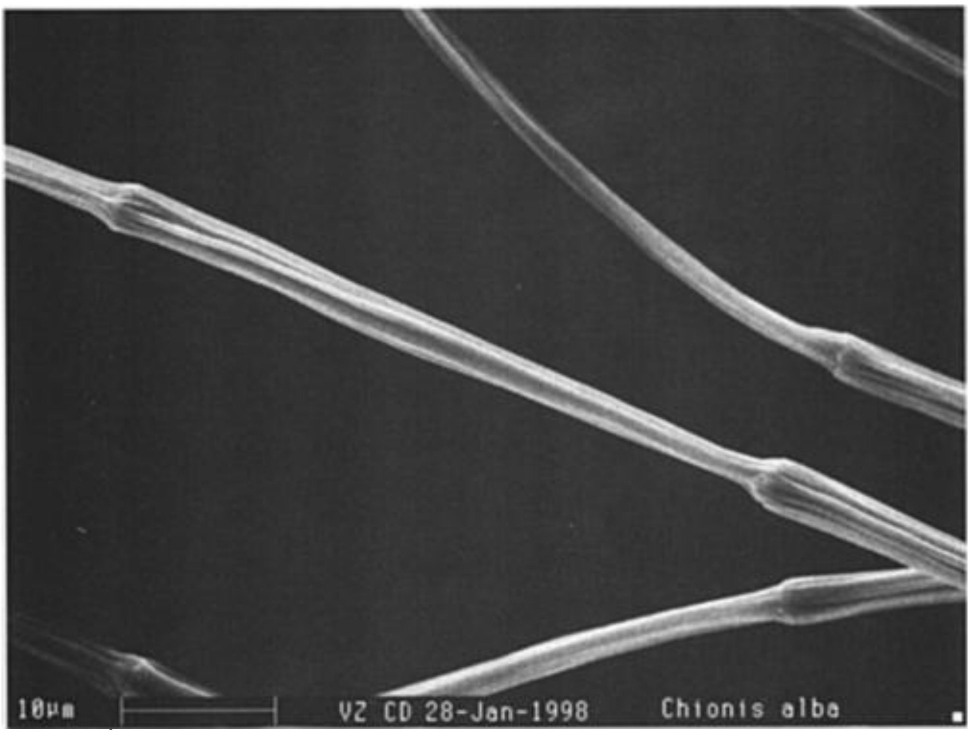


FIG. 84. Mid-nodes of *Chionis alba* usually lack visible spines.

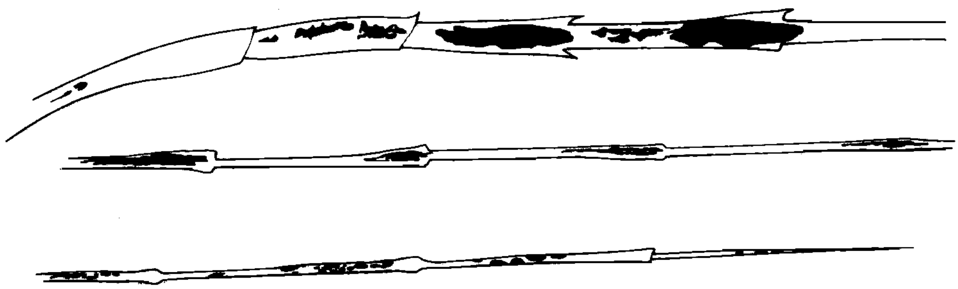


FIG. 85. True down of *Chionis alba*.

dominicanus (Kelp Gull), *Larus marinus* (Great Black-backed Gull), *Larus glaucescens* (Glaucous-winged Gull), *Larus hyperboreus* (Glaucous Gull), *Larus atricilla* (Laughing Gull), *Larus brunnicephalus* (Brown-headed Gull), *Larus pipixcan* (Franklin's Gull), *Larus novaehollandiae* (Silver Gull), *Larus maculipennis* (Brown-hooded Gull), *Larus ridibundus* (Common Black-headed Gull), *Larus philadelphia* (Bonaparte's Gull), *Rhodostethia rosea* (Ross's Gull), *Rissa tridactyla* (Black-legged Kittiwake), *Creagrus furcatus* (Swallow-tailed Gull), *Xema sabini* (Sabine's Gull), *Chlidonias nigra* (Black Tern), *Phaetusa simplex* (Large-billed Tern), *Gelochelidon nilotica* (Gull-billed Tern), *Hydroprogne caspia* (Caspian Tern), *Sterna hirundo* (Common Tern), *Sterna forsteri* (Forster's Tern), *Sterna fuscata* (Sooty Tern), *Sterna sandvicensis* (Sandwich Tern), *Larosterna inca* (Inca Tern), *Procelsterna cerulea* (Blue Noddy), *Anous stolidus* (Brown Noddy), *Gygis alba* (Common White Tern)

The Laridae comprises a large group of long-winged, web-footed, water birds that are divided into two subfamilies, the Larinae (gulls) and the Sterninae (terns). These birds are typically found on seashores and coastal waters but may also occur inland. They are cosmopolitan in geographic distribution except for deserts and permanently frozen parts of the polar regions. The family includes approximately 47 species of gulls and 43 species of terns.

Larinae

Gulls are a distinct group in their microscopic feather characters because they consistently have both pigmented and unpigmented down types on the same individual, and have distinct true down barbule nodal morphology.

Contour feather down.—Usually, contour feather down is unpigmented and does not have any distinguishing features, whereas the afterfeather and true down have pigmented nodes and contain the diagnostic microscopic characters for identifying this subfamily. Although Chandler (1916) and Brom (1991) mentioned prongs at nodes in some species of gulls, this character was found only on nodes of the distal portion of barbules from barbs of the distal plumulaceous region of the contour feather. In this study, coding focused on the barbs of the basal plumulaceous regions because these barbs have the most distinguishable barbule features. Therefore, prongs were not considered a character here. However, it should be noted that these prongs may be similar to those found in skuas.

FIG. 86a. Skuas and jaegers have long spines on nodes along the pennulum (a) that become long prongs on the distal part of the pennulum (Fig. 86b).

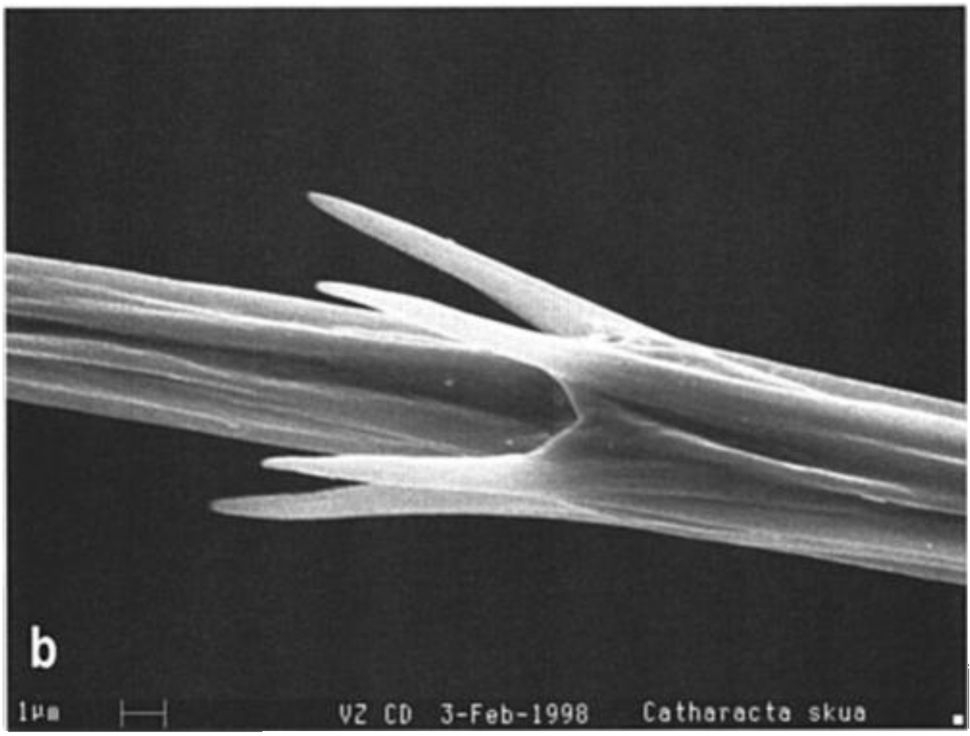


FIG. 86b.

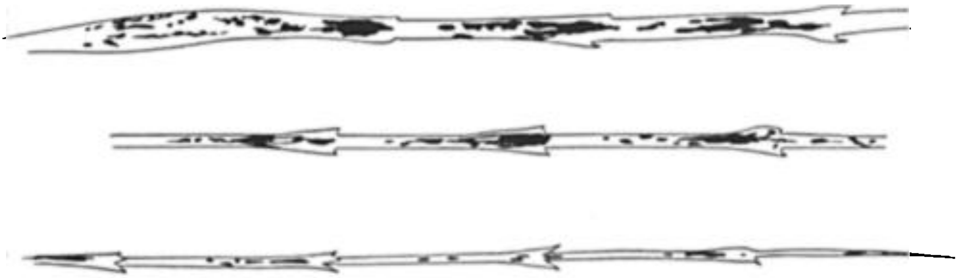


FIG. 87. Contour feather down of *Stercorarius longicaudus*.

Contour feather down in gulls is typically unpigmented. However, in some species the most umbilical barbs (located at the base of the contour feather) may be pigmented in the same manner as the afterfeather and true down. Contour feather plumulaceous barbules are short to medium in length and usually have only slightly expanded nodes (unpigmented) at the basal portion that gently taper to unexpanded nodes at the distal portion of the barbule (Fig. 89). This is in sharp contrast to the elaborately expanded basal nodes of the barbules of true down (Figs. 90–92). Spines (not prongs) occur at nodes all along the contour feather barbules (Fig. 89) and sometimes are longer and more pronglike near the distal portion of the barbule. The distal portion of the barbules is generally not filamentous in contour feather down, as it is in true down types. In some samples,

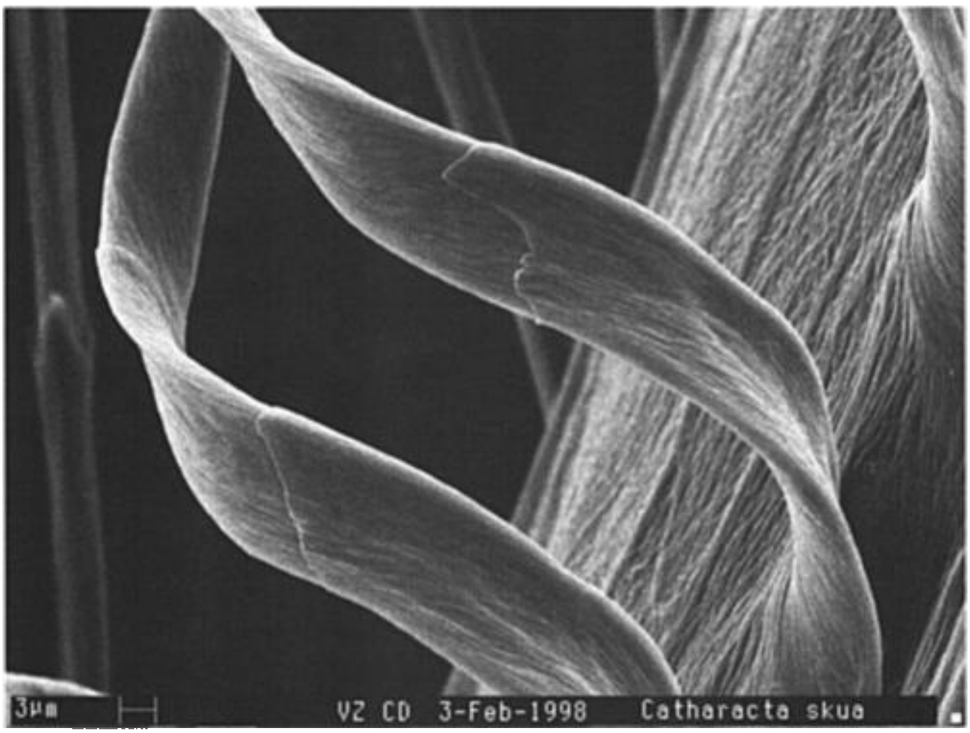


FIG. 88. Some barbule bases of *Catharacta skua* have multiple cell divisions.

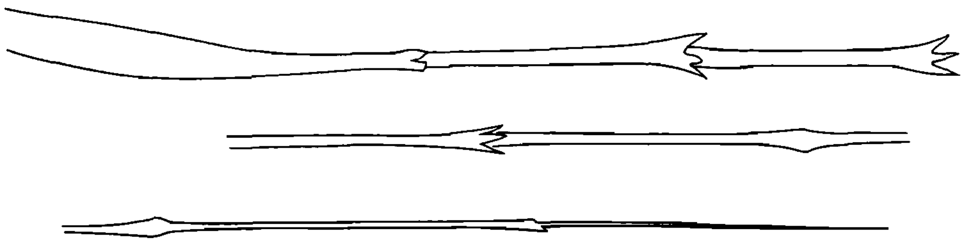


FIG. 89. Contour feather down of *Larus argentatus.*

the downy barbules of the contour feather resemble the overall morphology of the barbules of the true and afterfeather down types but lack any pigment (e.g., barbules are long with very expanded basal nodes with a threadlike distal portion of barbule). Subpennaceous regions are present on contour feather down. No striking microscopic features based only on contour feather down distinguish this group.

Afterfeather and true down.—True down and afterfeather down of every species examined in this study had some degree of nodal pigmentation. Sometimes the pigmented nodes are only on the basal barbules and the barb is not pigmented fully. Occasionally only the most basal barbules of barbs show diagnostic characters. The microscopic characters of these down types are so unique that they are immediately recognizable to subfamily level. Although the afterfeather down usually exhibits some diagnostic characters (Fig. 93), the true down is the most heavily pigmented type and most consistently contains diagnostic characters. The barbules of true down are usually short to medium in length but can be long in some species. The general pattern of barbule morphology consists of very wide expanded transparent processes around distinctly pigmented basal nodes. The first three to five nodes are always expanded (Fig. 91), but the midsection nodes are unexpanded and elongate (Fig. 94) and only contain spots of pigment. The distal portion of the barbule is filamentous or threadlike and can be long in some species. The node shape undergoes a striking morphological change from the base of the barbule to the tip (Fig. 90). The most diagnostic features of feather ultrastructure of gulls is that the basal nodes quickly become elongated and unexpanded at mid- and distal portions on the barbule (Fig. 94). This feature allows for quick identification of this group. All species examined follow this general pattern except *Larus novaehollandiae,* which generally has shorter barbules and has many more expanded nodes than any other gull species studied. Afterfeather down of *L.*

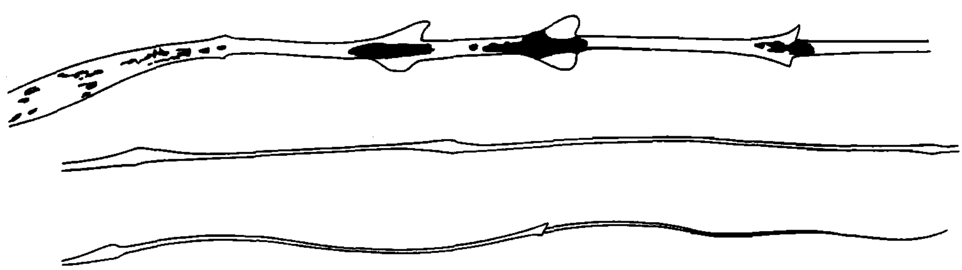


FIG. 90. True down of *Larus argentatus.*

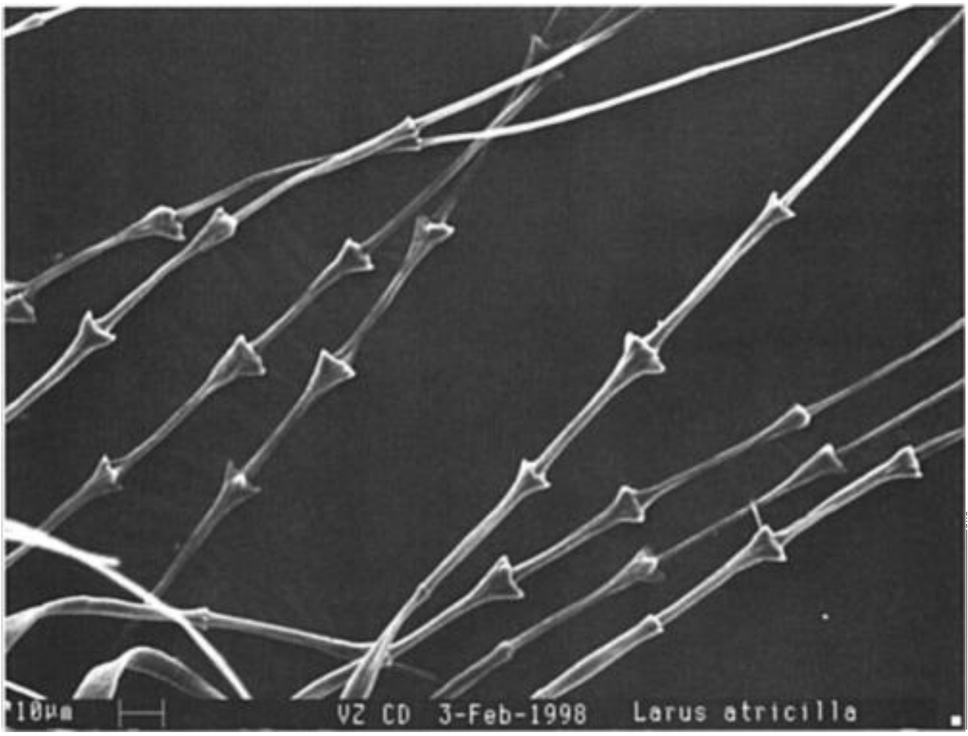


FIG. 91. True down barbule morphology of gulls has elaborately expanded basal nodes that taper to unexpanded nodes at the distal portion of the barbule.

atricilla was studied at higher magnification with SEM and found to be more similar to contour feather down than to true down in general nodal morphology (Fig. 95a, b). Differences may exist among groups of gulls in the number of expanded nodes, number of pigmented nodes, and distance between nodes in pigmented down types. More research on the variation in this family is needed to confirm this suggestion. The first node is often reduced and has a spot of pigment. Pigment is more diamond-shaped at basal nodes of barbules and becomes smaller or more constricted at midsection nodes. Pigment sometimes extends into the internode or is stippled just below the node. Distal nodes of diagnostic barbules are typically not pigmented.

The most difficult down type to identify in this subfamily is the down of the contour feather because these barbules usually do not contain pigmentation or typical barbule morphology. The unique feather features of the gull group are the diagnostic node shape and barbule morphology of the true and some afterfeather down, but the fact that true down, and to some degree, afterfeather down, is pigmented, whereas the plumulaceous region of the contour feather is usually unpigmented is also a characteristic that is not shared with many other groups in this order (in this study: stilts, Ibisbill, American Oystercatcher, Southern Lapwing, and Pied Lapwing).

Sterninae

Terns and noddies do not exhibit the unique suite of characters that unites the gull group. Although some species do have pigmented true down and unpig-

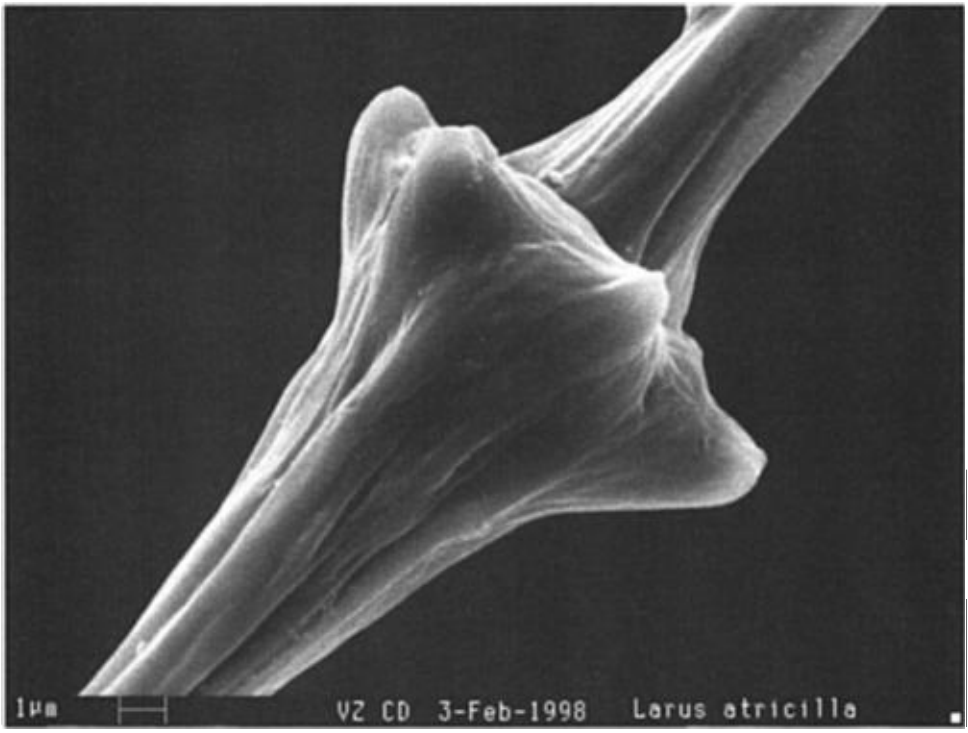


FIG. 92. Greatly expanded basal node of barbule of *Larus atricilla* true down.

mented contour feather down, they do not have the distinct flared nodes that are typical of gulls and are not easily identified by microscopic characters alone.

Contour feather down.—Of the two noddies sampled (*Procelsterna cerulea* and *Anous stolidus*), both exhibit some degree of pigmentation in all down types. The pigmentation of contour feather down in *P. cerulea* is distinctly diamond-shaped at nodes along most of the barbule, whereas *A. stolidus* has very little pigmentation that is stippled just below basal nodes of barbules. The dark gray morph of *P. cerulea* was sampled for this study. *Anous stolidus* is brown plumaged. Both species have spines at the nodes along the barbule that become longer on the distal portion of the barbule.

In this survey, the terns separated into three groups based on the presence of pigmented nodes in the different down types. The first group consisted of *Phae-*

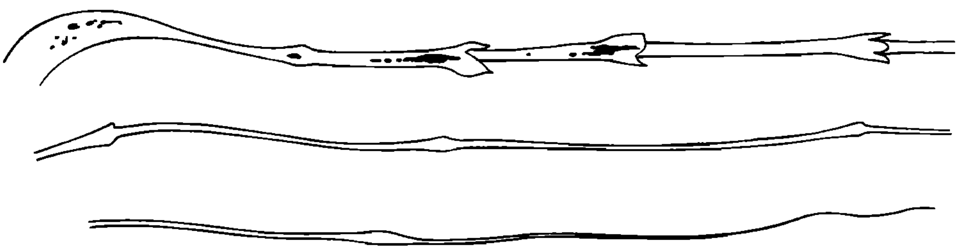


FIG. 93. Afterfeather down of *Larus argentatus*.

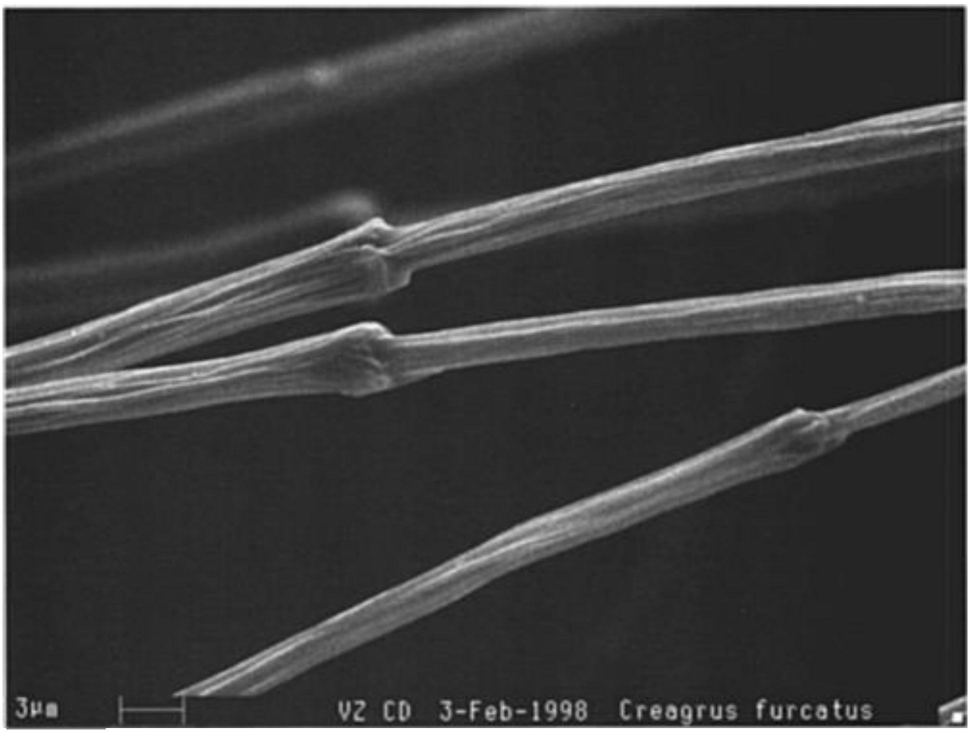


FIG. 94. Midsection nodes of the true down feathers of gulls are unexpanded and elongate.

tusa simplex, Hydroprogne caspia, Sterna sandvicensis, and *Gygis alba.* These species do not have pigmented nodes in any of the three down types studied. Microscopically, the contour feather down looks similar in all species that do not have pigmented nodes except that *Hydroprogne caspia* and *Phaetusa simplex* have longer spines at most nodes all along the barbule (Fig. 96). These spines sometimes become very elongated at the distal nodes of barbules.

The second group, *Sterna fuscata, S. forsteri,* and *Gelochelidon nilotica,* has unpigmented contour feather down and pigmented true down. Only *Sterna forsteri* has slight pigmentation at the umbilical barbs of the contour feather and afterfeather. Contour feather microcharacters are much like those of noddies, with unpigmented, slightly expanded, spined nodes. Spines of distal nodes on barbules are not as long as those observed in noddies.

The third group, *Chlidonias nigra* and *Larosterna inca,* has pigmentation in all types of down. Pigmentation is diamond-shaped at basal nodes and does not always extend to the distal portion of the barbule. *Larosterna inca* has more stippling of pigment at basal nodes and internodes than *Chlidonias nigra.*

Afterfeather and true down.—Afterfeather down of terns is typically unpigmented in the species studied except *Chlidonias nigra* and *Larosterna inca.* Afterfeather down does not have spines as prominent as contour feather down (Fig. 97). No subpennaceous regions are present on these feather types. True down nodes are pigmented throughout most umbilical and basal barbules. Pigment of true down feathers is diamond-shaped at nodes along most barbules and becomes more rounded at the distal nodes of barbules. Nodes of true down feathers are

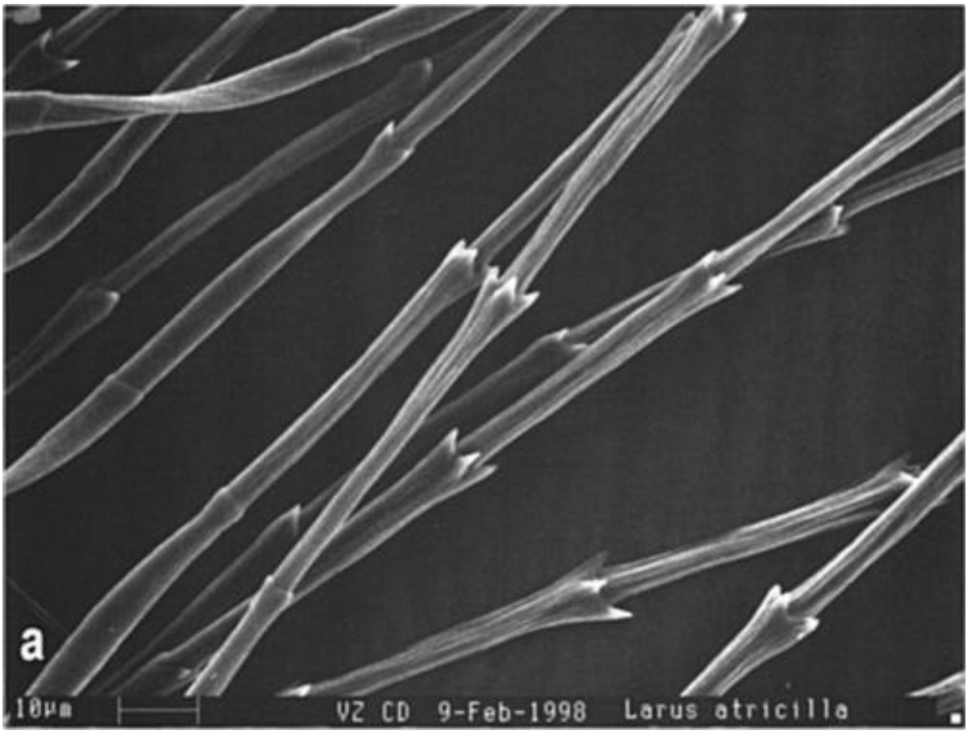


FIG. 95a. Afterfeather downy barbule morphology of *Larus atricilla* (a) is generally more similar to contour feather down (Fig. 95b) than to true down.

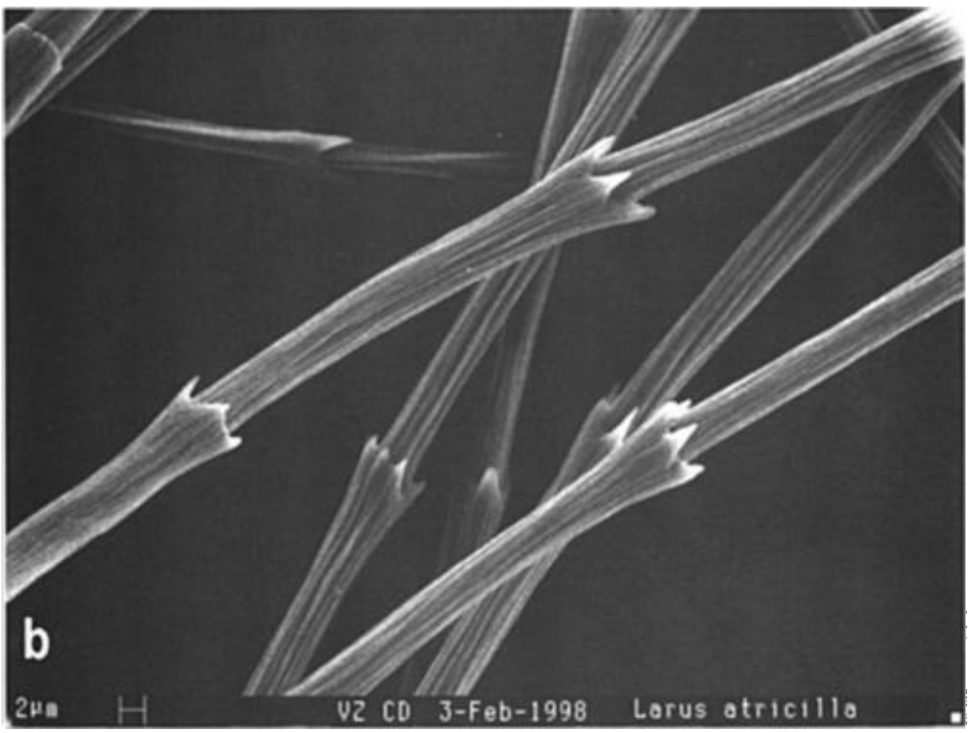


FIG. 95b.

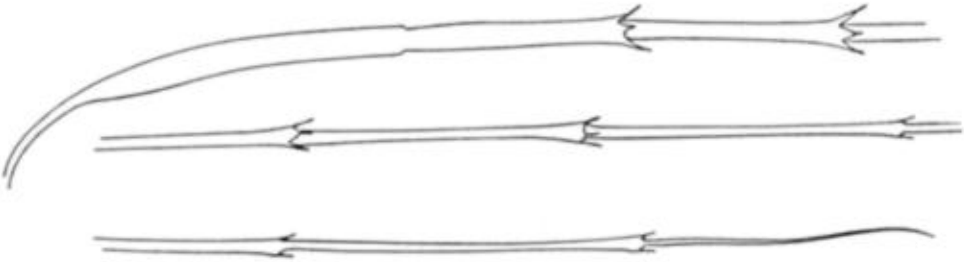


FIG. 96. Contour feather down of *Hydroprogne caspia.*

somewhat expanded with transparent projections around the pigment at basal and midsection nodes. As in all cases, the true down is finer and more filamentous in overall structure than contour feather down.

Terns are distinguished from gulls in feather microstructure because they lack the elaborately expanded basal node morphology of the true down. The overall microstructure of the contour feather down in terns is nondistinct, having unpigmented nodes, short to medium barbules, and spines at the nodes (Figs. 98, 99). In this way, contour feather down microstructure of terns is similar to contour feather microstructure of gulls.

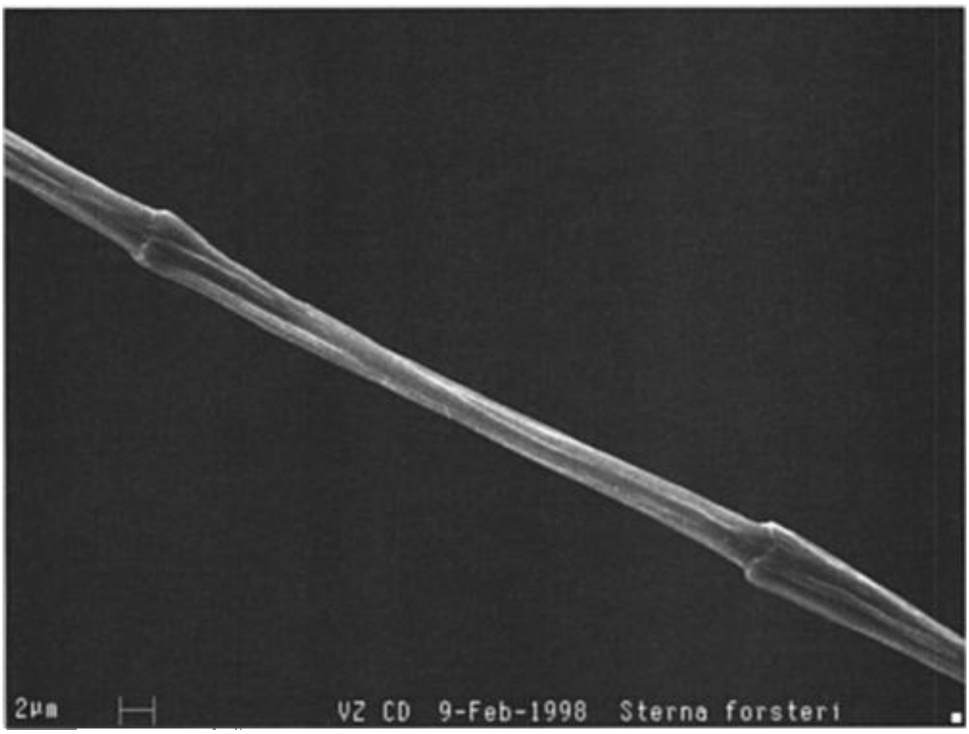


FIG. 97. Afterfeather down of terns lacks the prominent spines observed in contour feather down.

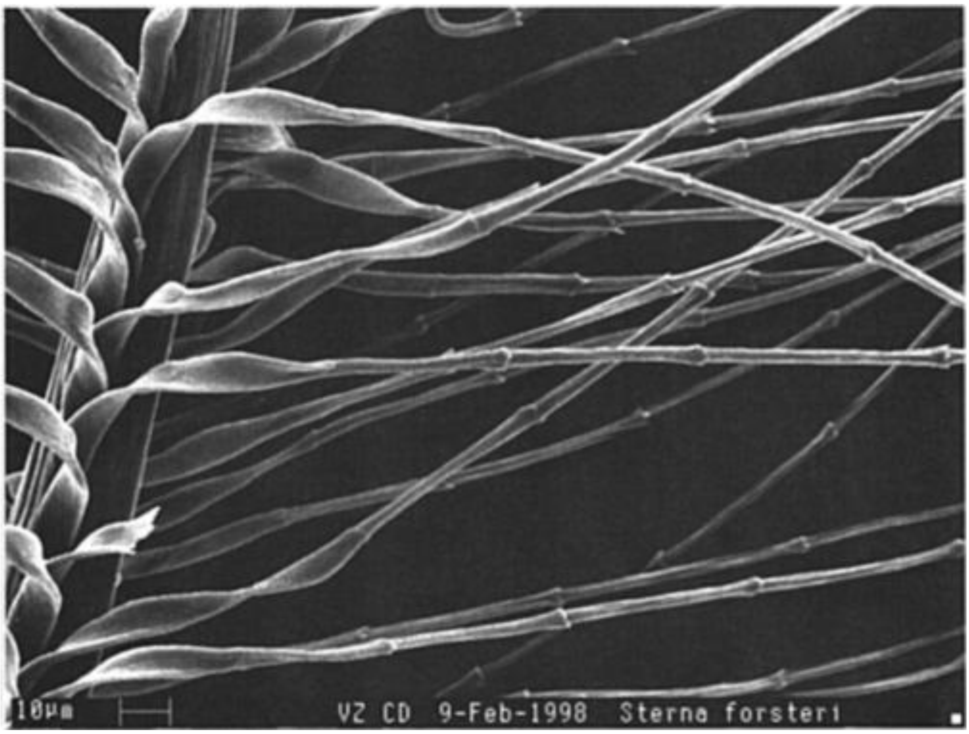


FIG. 98. Contour feather down of terns is indistinct, having slightly expanded nodes with spines at the nodes all along the pennulum.

Rynchopidae

Rynchops niger (Black Skimmer), *Rynchops flavirostris* (African Skimmer)

This family includes three species: the Black Skimmer of tropical America and inshore waters; the African Skimmer of the coasts and rivers of tropical Africa; and the Indian Skimmer (*Rynchops albicollis*), which inhabits the larger rivers of India, Burma, and Indo-China.

Microscopic pigmentation patterns differ in the two species examined here. *Rynchops flavirostris* has all down types pigmented, whereas *R. niger* has unpigmented contour and afterfeather down, and lightly pigmented (basal barbules) true down.

Contour feather down.—Both species examined have medium to long barbules that are thin and somewhat threadlike. Nodes are spined and slightly expanded (Fig. 100). The pigmentation of *R. flavirostris* is heavier on the basal portion of the barbule. Pigment is diamond-shaped and constricted into points at the basal nodes of barbules. Internodal pigmentation is heavy at the base of the barbule but more sparse and stippled at the distal portion of the barbule (Fig. 101). Subpennaceous regions are short in contour feather down.

Afterfeather and true down.—Afterfeather and true down are similar to contour feather but finer in overall structure and lack subpennaceous regions. Afterfeather down in *R. niger* is unpigmented. The true down is lightly pigmented at basal barbs.

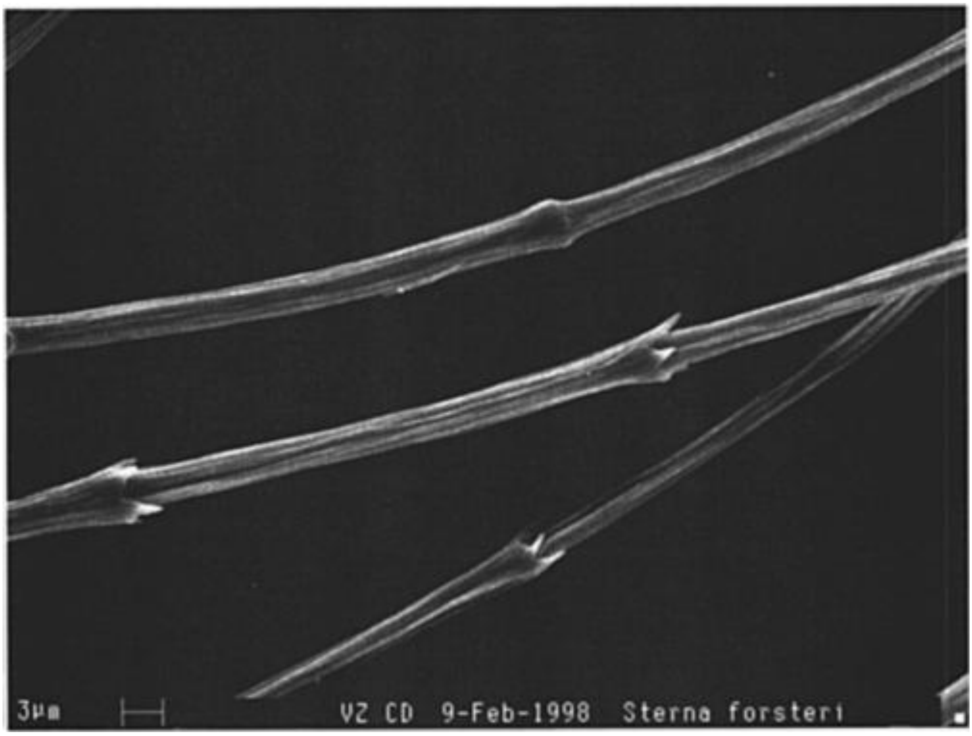


FIG. 99. Enlarged view of nodes of barbules of contour feather down of *Sterna forsteri* showing spined nodes.

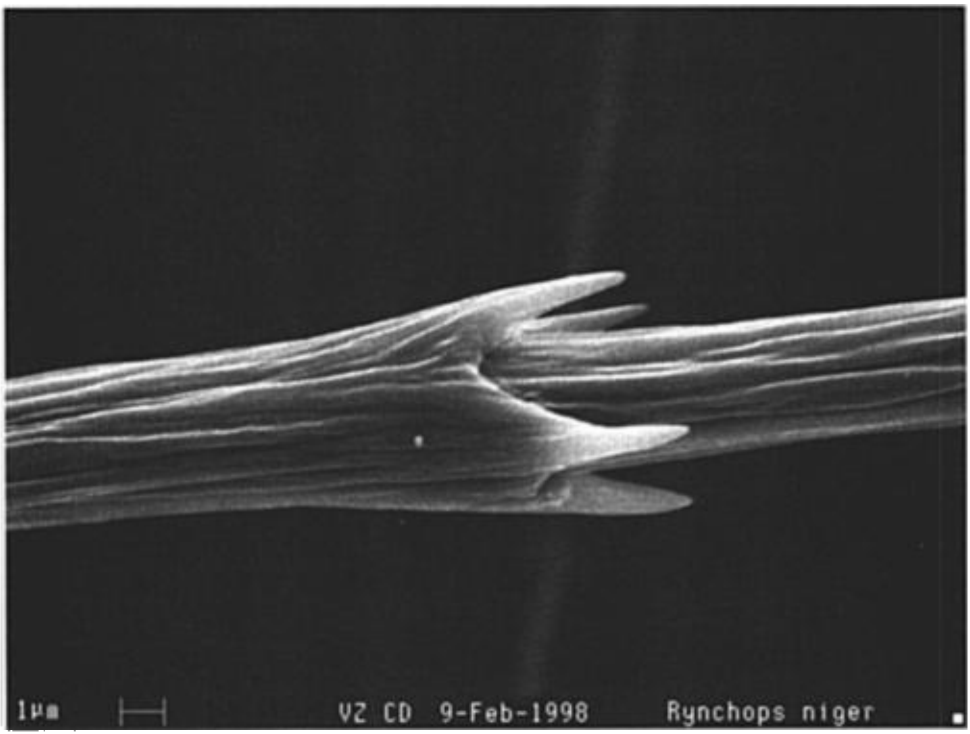


FIG. 100. Skimmers (Rynchopidae) have slightly expanded nodes with distinct spines.

FIG. 101. Contour feather down of *Rynchops flavirostris.*

Alcidae

Alle alle (Dovekie), *Alca torda* (Razorbill), *Uria aalge* (Common Murre), *Cepphus columba* (Pigeon Guillemot), *Brachyramphus marmoratus* (Marbled Murrelet), *Synthliboramphus antiquus* (Ancient Murrelet), *Ptychoramphus aleuticus* (Cassin's Auklet), *Cyclorrhynchus psittacula* (Parakeet Auklet), *Aethia pusilla* (Least Auklet), *Cerorhinca monocerata* (Rhinoceros Auklet), *Fratercula arctica* (Atlantic Puffin), *Lunda cirrhata* (Tufted Puffin)

The alcids are the northern counterparts of the penguins (Sphenisciformes) and include the auks, auklets, murres, murrelets, guillemots, Dovekie, and puffins. The 23 species are Holarctic in distribution. The microscopic characters of this family are very different from any other group in this order.

Contour feather down.—Barbules are very short with well-developed, usually long, subpennaceous regions (Fig. 102). Basal nodes of barbules are not expanded and are mostly indistinct in the species studied here. Sometimes it is difficult to see any nodal distinction at all on the basal portion of the barbules (Figs. 103, 104). In the species examined in this study, well-developed long prongs are located at the nodes on the distal portion of barbules (Figs. 105, 106). These prongs are sometimes longer on one side of the node than the other or occur only on one side. The general microstructure of the downy feathers is simple, having straight barbules without elaborately expanded nodes. Long spines on midsection nodes of the barbule are observed in most species but are most prevalent in *Lunda cirrhata* (Fig. 107). Pigment is usually diffuse and stippled all along the barbule but sometimes is loosely concentrated into a diamond-shaped point in the node in all but *Aethia,* which has the pigmentation more concentrated at the nodes. Internodal pigmentation stippling is typically heavy in alcids. Pigmentation is heaviest in *Cepphus columba* and *Aethia pusilla,* extending from the basal part of the barbule through the nodes and to the distal portion of the barbule (Figs. 108, 109). At the nodes, the pigment is sometimes interrupted briefly where it is constricted into a point, making the node appear transparent. *Ptychoramphus aleuticus, Synthliboramphus antiquus,* and *Aethia pusilla* are the species examined that have somewhat expanded nodes when viewed at high power (400×). In these three species, the basal and midsection nodes of barbules have more elongated pigment at the nodes and the slightly expanded nodes are oblong and narrow. Pigment is sometimes continuous through nodes and internodes in *A. pusilla* with slight swellings at basal and mid-nodes (Fig. 109). Long, well-developed subpennaceous regions occur in all alcids examined here.

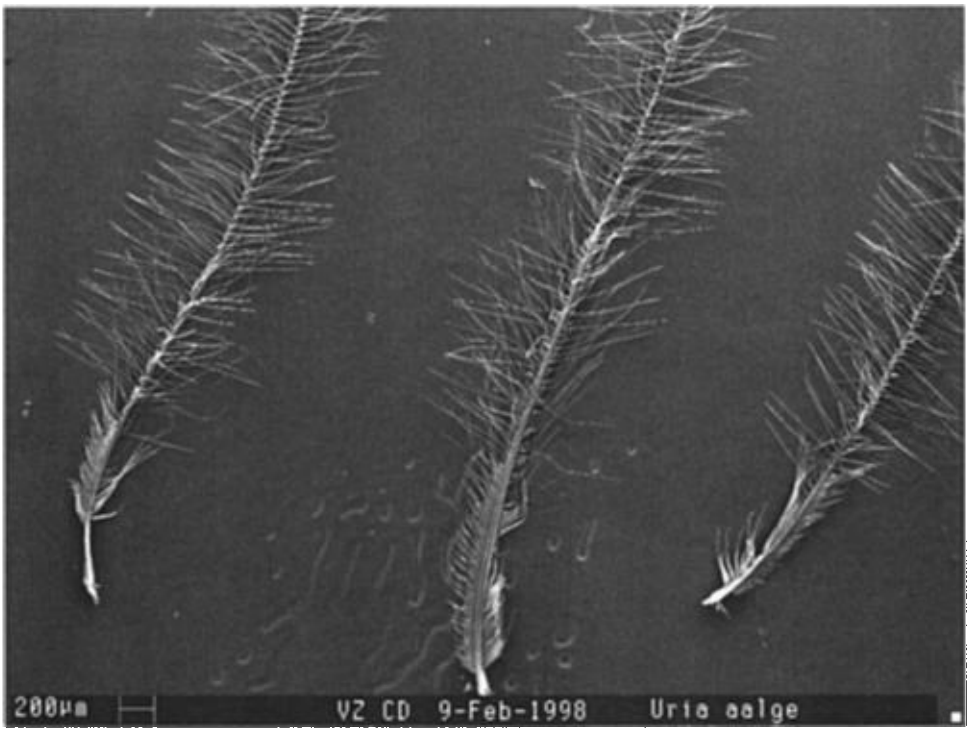


FIG. 102. Alcids have short barbules with well-developed subpennaceous regions.

Afterfeather and true down.—True and afterfeather down are similar to contour feather down but afterfeather barbs are often longer than contour feather barbs and true down is sometimes more heavily pigmented. No subpennaceous regions are present on these feather types.

OUTGROUPS

GAVIIFORMES

Loons are diving birds that live in the Holarctic seas. Although loons show no close affinities to any avian order, early researchers suggested connections to Charadriiformes (Coues 1868; Sclater 1880; Chandler 1916). This relationship was suggested again more recently by Storer (1960). The order consists of one family with four species. Chandler (1916) described the down of gaviids as being very close to that of penguins.

Gaviidae

Gavia adamsii (Yellow-billed Loon)

Contour feather down.—The microscopic feather characters of loons are simple in structure and are strikingly similar to those of the alcids in overall micromorphology. Loons have relatively long barbs with short barbules. The barb and barbules are unpigmented in the contour feather down. The barbules have a shaggy appearance due to the long prongs (Fig. 110) that are located at the nodes of the distal portion of the barbules. Basal nodes of barbules do not have prongs

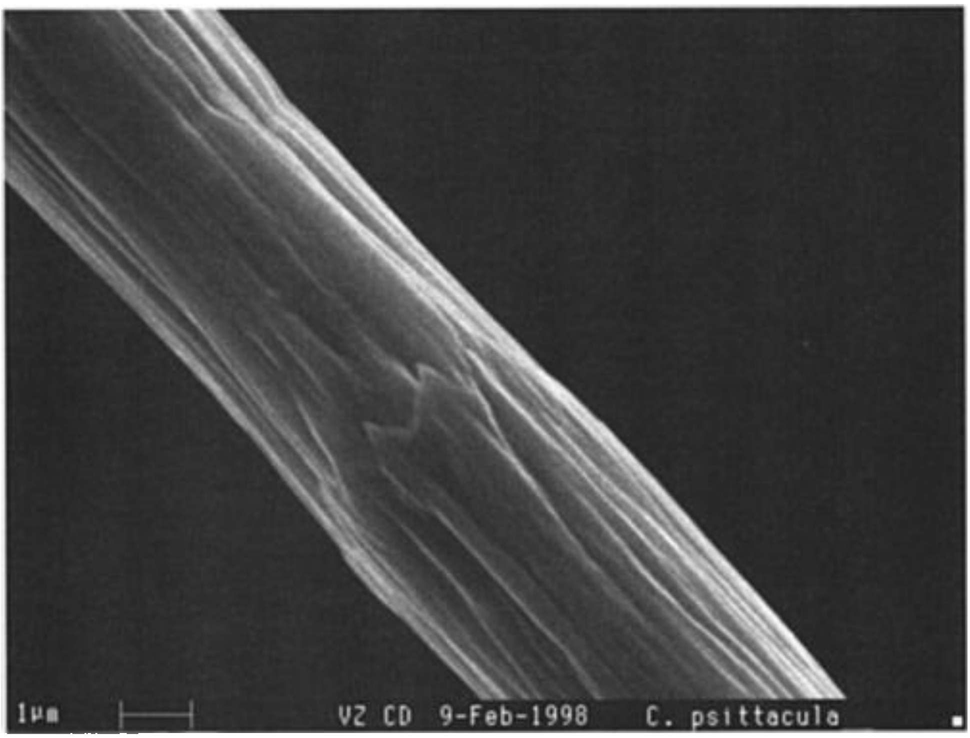


FIG. 103. Basal nodes of alcids are usually completely unexpanded and indistinct.

and are not expanded (Fig. 111). Cell divisions of the barbule are difficult to delineate because the overall barbule structure is so simple. A well-developed subpennaceous region is present.

Afterfeather and true down.—Afterfeather down is similar to contour feather down except the barbs and barbules are finer. A few barbs were found to have very light pigmentation. True down also has a finer appearance than contour feather down and pigmentation in the internode along the barbule and throughout the entire barb is light and stippled. No subpennaceous regions are found on these feather types.

GRUIFORMES

The order Gruiformes includes the cranes, rails, and allies. Three species from three families of this order were selected for outgroup comparison: *Lophotis ruficrista* (Red-crested Bustard), *Fulica americana* (American Coot), and *Grus canadensis* (Sandhill Crane). Although the Gruiformes forms a very diverse natural group, it is generally believed to be closely related to the Galliformes (fowl-like birds) and Charadriiformes and is usually placed between these two orders (Austin 1961). Cranes (Gruidae) inhabit open marshlands, wet plains, prairies, sandy flats, and seashores. Bustards (Otididae) are large cursorial upland ground birds that inhabit open grassy plains and brushy savannas of Eurasia, Australia, and Africa. Rails (Rallidae) belong to the largest and most diverse family of Gruiformes and consist of medium-sized running, wading, or swimming birds. Most species live

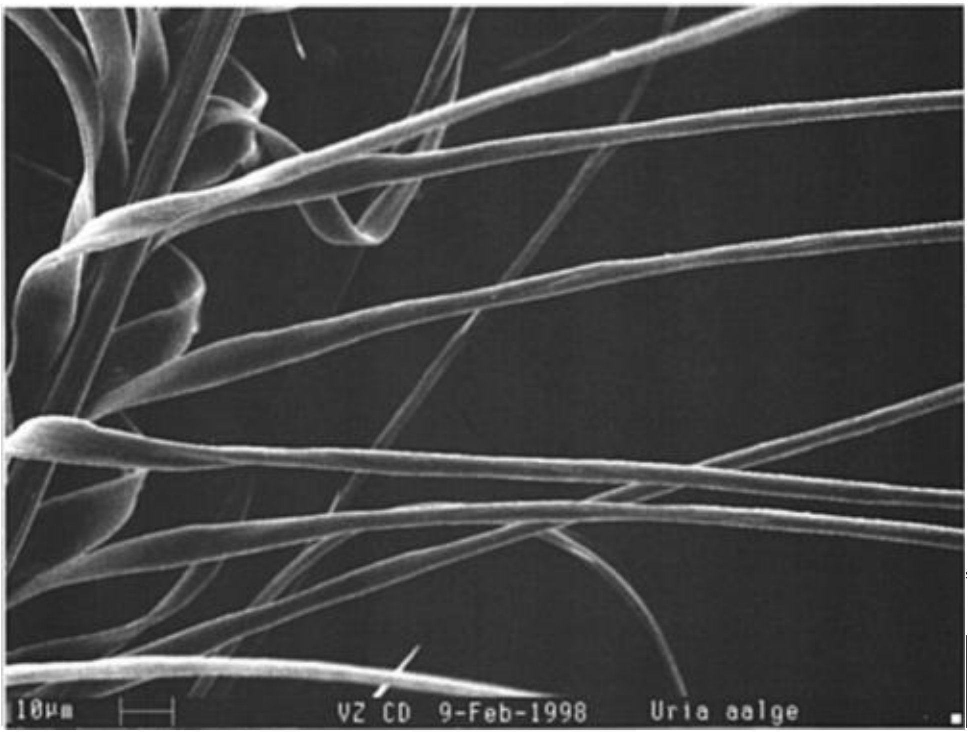


FIG. 104. Indistinct basal nodes of *Uria aalge*.

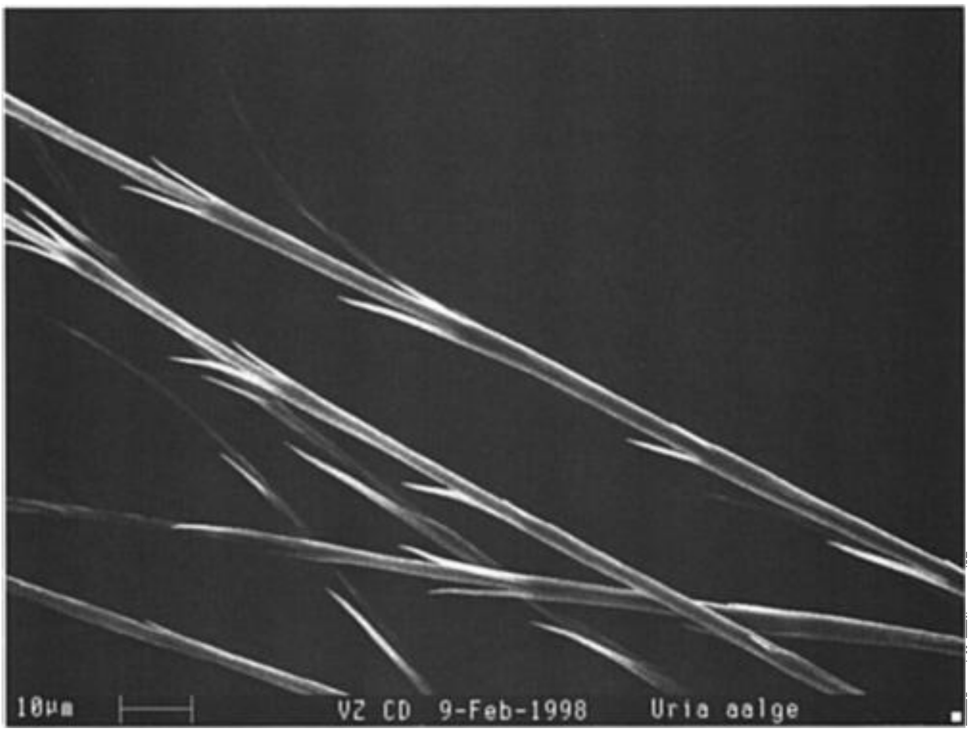


FIG. 105. Distal nodes of alcids have long, well-developed prongs.

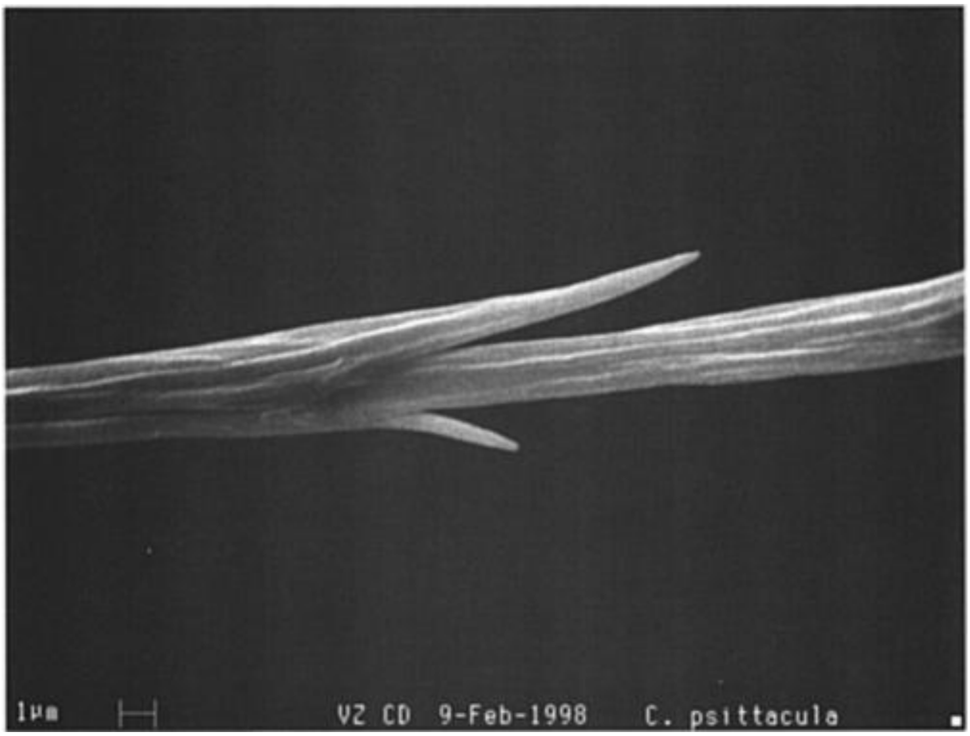


FIG. 106. Enlarged distal node of *Cyclorrhynchus psittacula* showing long prongs that are typical of alcids and loons (see Fig. 110).

FIG. 107. Contour feather down of *Lunda cirrhata*.

FIG. 108. Contour feather down of *Cepphus columba*.

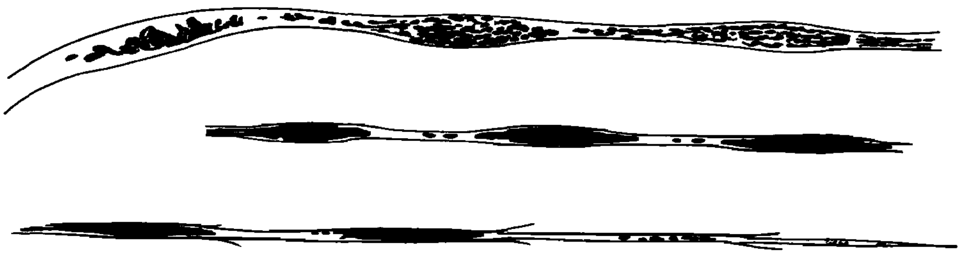


FIG. 109. Contour feather down of *Aethia pusilla.*

in marshes, and some occur on ponds and lakes and few are present in woodlands and dry plains.

Gruidae

Grus canadensis (Sandhill Crane)

Contour feather down.—Barbs are long with relatively short barbules. Barbule pigmentation is lightly stippled in the internode and the node is usually unpigmented. Pigmentation is heaviest at the base of the barbule and is less intense at the distal portion of the barbule. The barb is usually pigmented throughout its length. Because pigmentation is usually light, it is most visible with LM at higher powers (200–400×). The general appearance of the barbules is short and sticklike when viewed at low magnification. Prongs are present at unexpanded nodes all along the barbule but are most visible at the basal nodes. Although the prongs appear paired when viewed with LM, SEM photomicrographs show that the prongs actually surround the nodes (Fig. 112). Sometimes these prongs are of unequal length (Fig. 113). A well-developed subpennaceous region is present (Fig. 114).

Afterfeather and true down.—Afterfeather down is identical to contour feather down. True down is similar but the rachilla is more flexible and finer with the barbules being less pigmented and finer than those of the contour feather down. No subpennaceous region was observed on any barbs of the afterfeather or true down.

Rallidae

Fulica americana (American Coot), *Porzana fusca* (Ruddy-breasted Crake), *Gallicrex cinerea* (Watercock), *Ortygonax sanguinolentus* (Plumbeous Rail), *Gallinula melanops* (Spot-flanked Gallinule), *Gallinula chloropus* (Common Moorhen), *Atlantisia rogersi* (Inaccessible Rail), *Rallus longirostris* (Clapper Rail), *Rallus elegans* (King Rail), *Porphyrio porphyrio* (Purple Swamphen)

Contour feather down.—Barbs and barbules are relatively short. Many rails have a unique microstructural character of asymmetry in nodal morphology (Figs. 115, 116). The asymmetry is apparent because the first few basal nodes on barbules of the distal vanule are largely expanded, whereas adjacent nodes of the proximal vanule are not expanded. This character has been observed in hummingbirds (Trochilidae) and to a lesser degree in pigeons (Columbidae) (Laybourne, pers. comm.; Dove, pers. obs.). A general microscopic survey of eight species of rails showed that vanule asymmetry is characteristic of many species

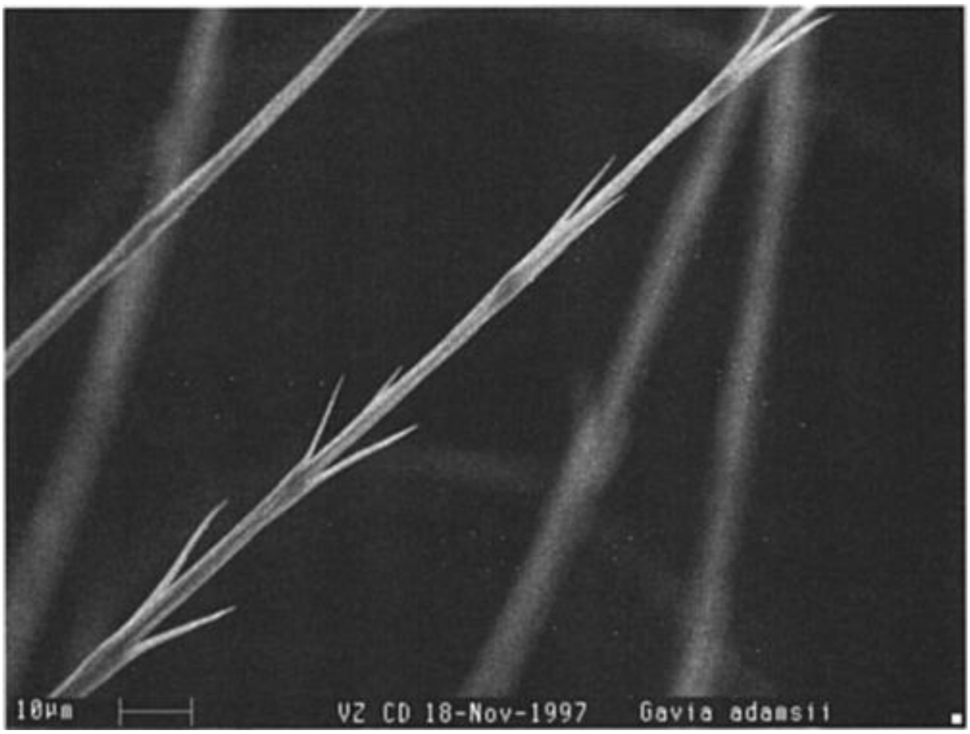


FIG. 110. Loons (Gaviiformes) have short barbules with long prongs at distal nodes.

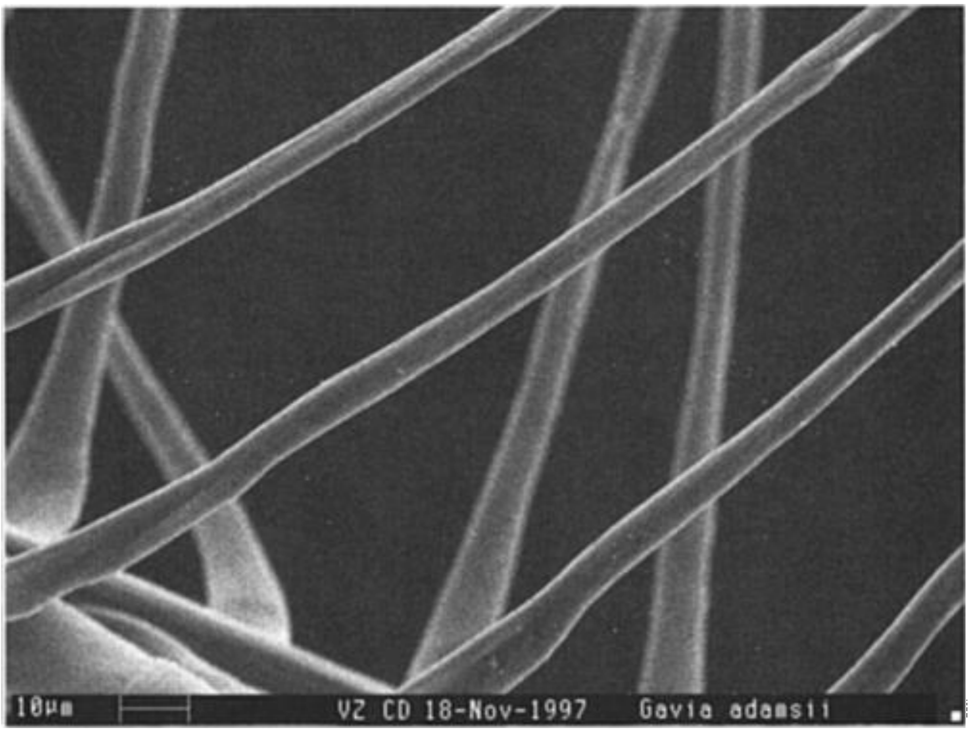


FIG. 111. Enlarged proximal portion of barbule showing indistinct basal nodes of *Gavia adamsii* that are similar to barbule morphology of alcids.

FIG. 112. *Grus canadensis* has distinct prongs that surround nodes all along the barbule.

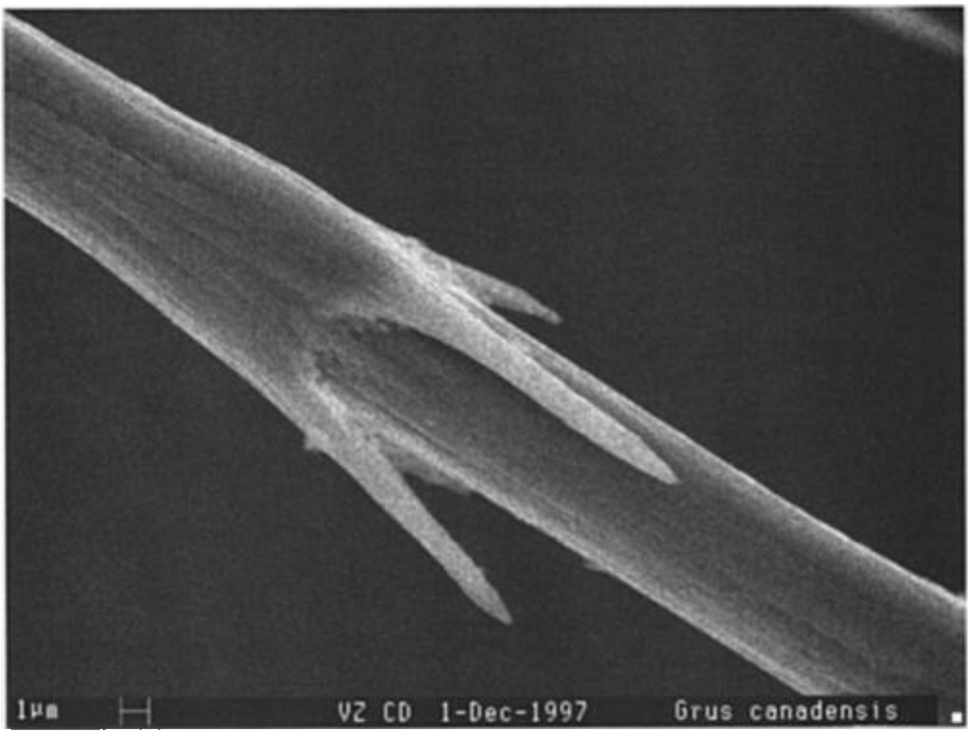


FIG. 113. Prongs at nodes are sometimes of unequal lengths in *Grus canadensis*.

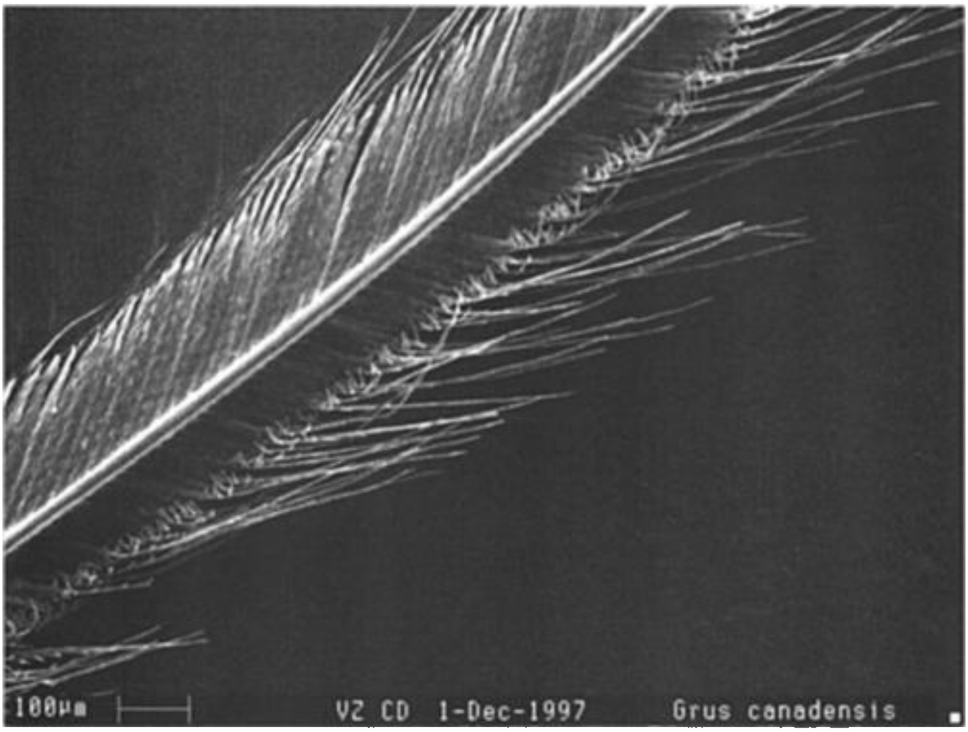


FIG. 114. Well-developed subpennaceous region of contour feather down in *Grus canadensis*.

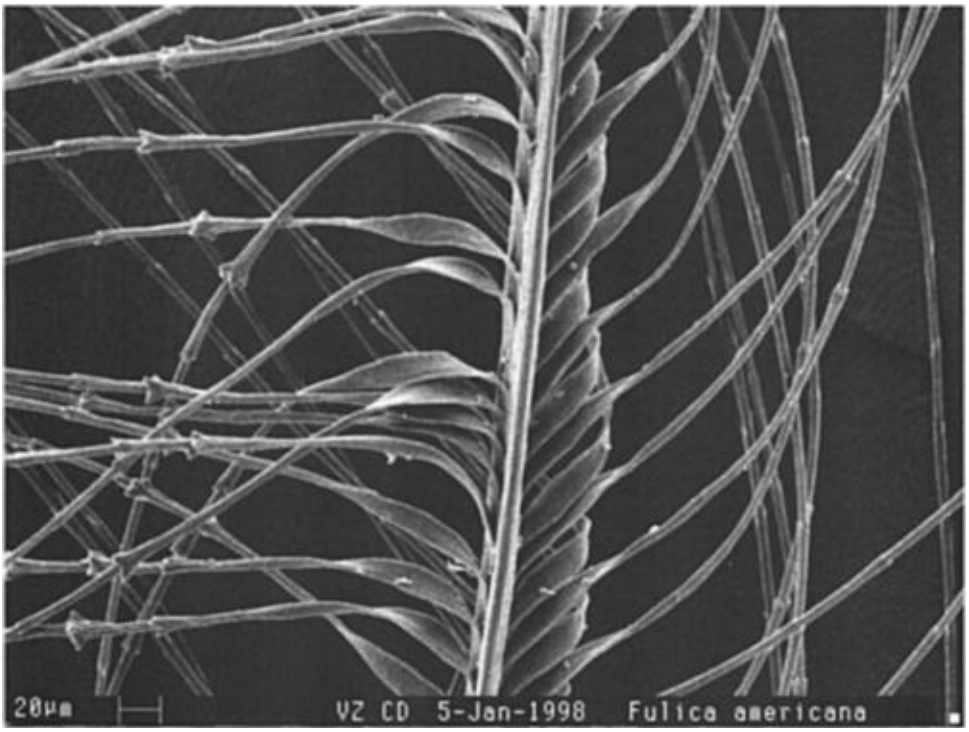


FIG. 115. Many members of the family Rallidae have the unique microscopic feature of barbule asymmetry. Nodes of one vanule (distal) are very expanded, whereas nodes on the opposite vanule (proximal) are unexpanded and indistinct.

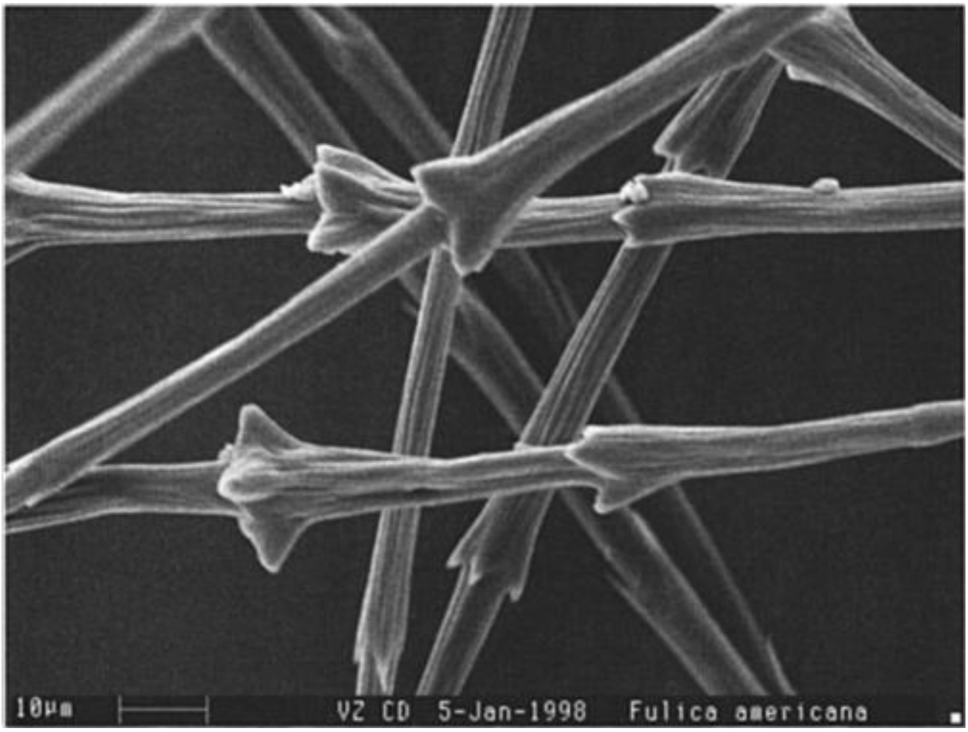


FIG. 116. Expanded nodes of *Fulica americana.*

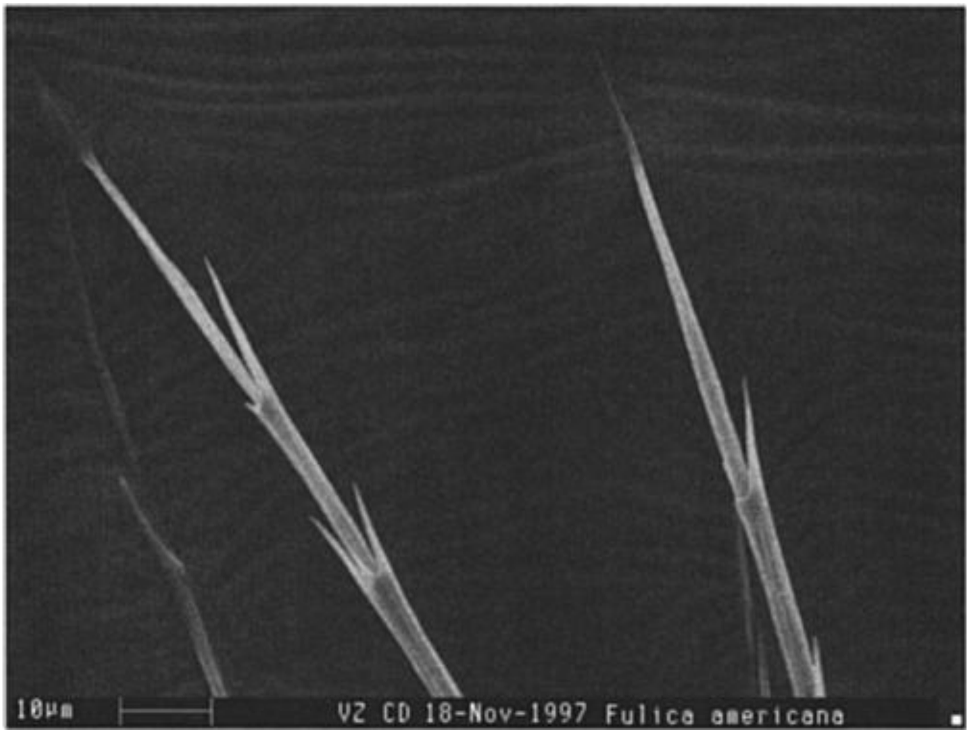


FIG. 117. Distal nodes of members of the family Rallidae typically have prongs.

in this family (*Porzana fusca, Gallicrex cinerea, Ortygonax sanguinolentus, Gallinula melanops,* and *G. chloropus*), but not others (*Antlantisia rogersi, Rallus longirostris,* or *R. elegans*). Both vanules of *Porphyrio porphyrio* had very expanded nodes on basal portions of barbules. This character needs to be further investigated in this family on all down types to assess consistencies among natural groups of rails.

Barbs and barbules are heavily pigmented in *Fulica americana.* Pigmentation is so heavy that it extends from the node through the internode and is continuous throughout the barbule. Transparent areas around the pigment are observed at some nodes where pigment constricts into a point. Mid-nodes of barbules are not expanded; distal nodes have prongs (Fig. 117). The subpennaceous region is absent or very difficult to find on most barbs of the contour feather plumulaceous region examined in this study.

Afterfeather and true down.—Afterfeather and true down pigmentation is similar to that of contour feather down except that these feather types are not as heavily pigmented. Pigment is less intense in the internodes. No expanded nodes or asymmetry are observed on these down types and prongs are more pronounced at distal nodes on the barbules. No subpennaceous regions are present on these feather types.

Otididae

Lophotis ruficrista (Red-crested Bustard), *Eupodotis senegalensis* (White-bellied Bustard), *Afrotis atra* (Black Bustard), *Choriotis kori* (Kori Bustard), *Chlamydotis undulata* (Houbara Bustard)

Contour feather down.—Bustards typically have relatively long barbs and barbules and most species have brownish-red pigment throughout the entire length of the barb and barbules. The barbule pigmentation in *Lophotis ruficrista* is heaviest in the internodal region and is distinctly absent at the node. Basal nodes of barbules are slightly expanded with very short spines (Fig. 118); distal nodes are unexpanded with no spines. The subpennaceous region is relatively short and pigmented.

Pigmentation patterns in this family are not consistent among all taxa. Brom (1991) reported that the three species used in his study (*Otis tarda, Chlamydotis undulata, Tetrax tetrax*) were all unpigmented. Qualitative analysis of reference microslides in the current study reveals that *Eupodotis senegalensis* and *Afrotis atra* have similar pigmentation to *Lophotis ruficrista,* whereas *Choriotis kori* is only lightly pigmented. Microslides of *Chlamydotis undulata* examined in this study show light pigment stippled throughout the internodes of barbules. Long barbules and slightly expanded nodes are characteristic of all species examined.

Afterfeather and true down.—Afterfeather and true down have pigmentation patterns like contour feather down. No subpennaceous region is present in either afterfeather or true down and barbs and barbules are finer and more flexible. Barbules of the afterfeather are generally shorter than either of the other down types.

COLUMBIFORMES

This order contains the pigeons and sandgrouse (Morony et al. 1975). The sandgrouse (Pteroclidae) were selected for outgroup comparison because of a long-standing classification problem that places them with either shorebirds or

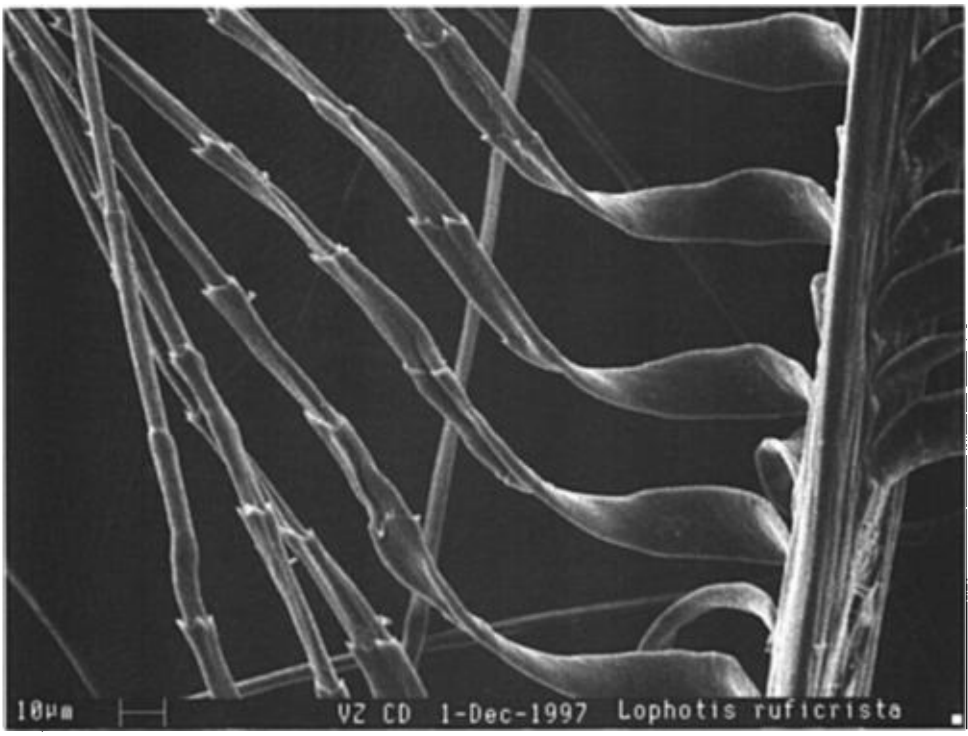


FIG. 118. *Lophotis ruficrista* has long barbules with slightly expanded, short-spined basal nodes.

pigeons. Sandgrouse inhabit the sandy, open, treeless habitats of Africa, Madagascar, southern Europe, and central and southern Asia.

Pteroclidae

Syrrhaptes paradoxus (Pallas's Sandgrouse), *Pterocles namaqua* (Namaqua Sandgrouse), *Pterocles orientalis* (Black-bellied Sandgrouse)

Contour feather down.—All three species examined here are similar to each other in the microscopic characters of the plumulaceous feathers. Barbules are very long and become very fine and filamentous at the distal half of the barbule. Pigmentation patterns of barbules are very similar in pigmentation color and stippling to those of some bustards (*Lophotis*) except that the sandgrouse generally have nodes that are more heavily pigmented than internodes. Pigment color is brownish-red and uniform throughout the barb and barbule (Figs. 119, 120). Only the first few basal nodes on barbules are expanded (Fig. 121), midsection nodes are not expanded, and distal nodes are indistinct. Internodal length is long. Spines occur on basal nodes and some distal nodes. *Syrrhaptes paradoxus* differs in having long prongs on many of the most distal nodes (Fig. 122). No extensive subpennaceous region was observed on any species examined.

The length of the barbules and the more expanded basal nodes that taper into indistinguishable distal nodes are more similar to the patterns observed in Columbiformes than those in Charadriiformes. Brom (1991) did not report pigment

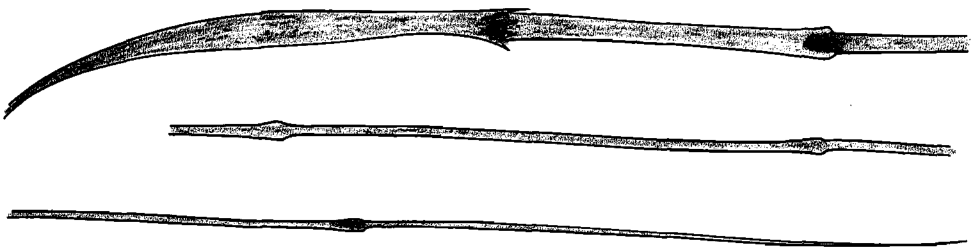


FIG. 119. Contour feather down of *Pterocles namaqua.*

in Pteroclidae even though he examined two of the same species that were studied here.

Afterfeather and true down.—Afterfeathers are rudimentary or absent in this group and true down is similar to contour feather down on the species examined here.

RESULTS

The results of the descriptive study are presented primarily in the summations of the microcharacters presented in each of the preceding family sections. However, while seeking to describe the variation in feather ultrastructure of this order of birds, some unique feather features were noted for the first time and these warranted further investigation. The pigmentation of downy barbules was found to differ among down types (contour, afterfeather, true) of the same species; villi were discovered on some charadriiforms; and the base, or base cell, of the barbule was studied to determine if it was composed of more than one cell. The results of these three separate studies are presented here. These studies were necessary to clarify or document these previously unstudied feather features.

DOWN PIGMENTATION

One of the first new discoveries made in this study of the downy barbs of Charadriiformes came during the preparation of microslides. While sampling plumulaceous barbs of contour feathers, the different types of downy barbs were discovered to be pigmented differently in some species. For example, in some species only the true down and afterfeather down are pigmented, whereas the downy barbules of contour feathers lack pigmentation. The presence or absence of pigment in downy barbs is usually visible to the naked eye.

Pigmented downy barbules are most important in identifying unknown samples

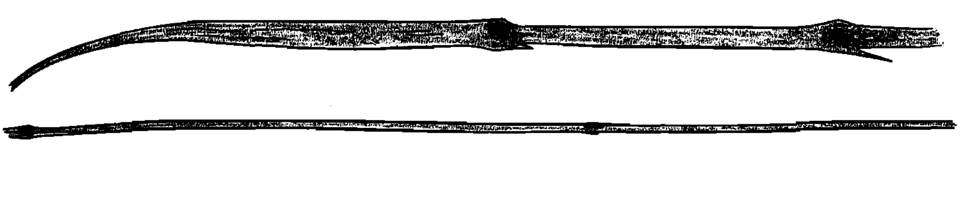


FIG. 120. Contour feather down of *Pterocles orientalis.*

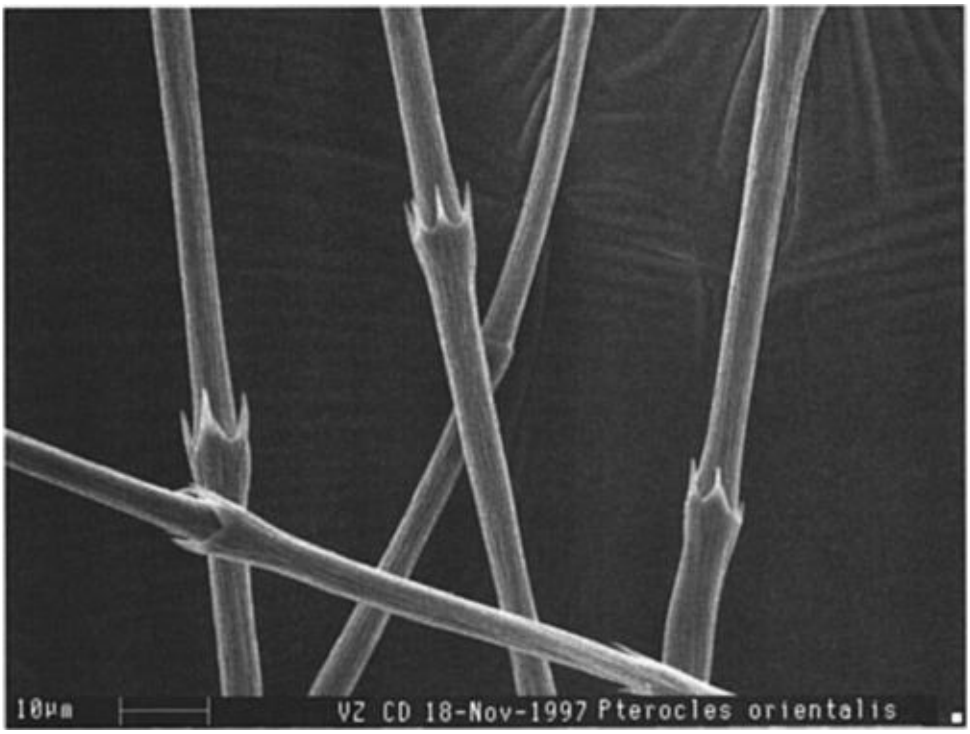


FIG. 121. Sandgrouse typically have long barbules with only the most basal nodes of barbules expanded.

because pigmentation patterns usually provide diagnostic clues that aid in group designation. From previous observations made during bird strike identifications, gulls were known to have two types of downy barbs—pigmented and unpigmented (Dove, pers. obs.). Also, designating the unknown sample to the gull family (Laridae) was known to be easier if the pigmented type of down was present in the unknown sample. However, because each bird strike sample is different, and most samples include at least some of the pigmented down types, this difference in plumulaceous pigmentation was never fully investigated. Thus, after discovering that some individuals in Charadriiformes may exhibit differences in pigmentation of different downy types (true, contour, and afterfeather), examining this variation within the entire charadriiform order became necessary. Be-

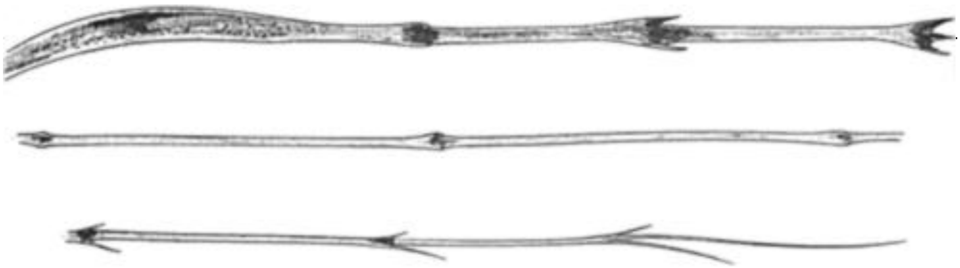


FIG. 122. Long prongs on distal nodes of *Syrrhaptes paradoxus* contour feather down.

cause these down types may be pigmented differently, the question of a possible correlation between the external coloration of the feather and the coloration of the down is evident.

In each of the taxa examined in the descriptive part of this study, one slide was made of true down, one of afterfeather down, and five of contour feather down. All samples were taken from feathers of the upper left breast of museum specimens. Multiple specimens were selected for contour feather down study to determine if individual variation existed in feather structures. For this investigation, observations were made on each type of down pertaining to the presence of pigment, and the color (dark vs. white) of the pennaceous contour breast feather from which the down was taken. In species with a dark band across the breast, samples were taken from just below the band.

Most charadriiforms observed in this study (72% of species) had all down types pigmented; only 7.6% of the species studied here had all down types unpigmented. Of the totally unpigmented species, all but one species (*Pluvianus aegyptius*) had pure white pennaceous breast feathers. Two species (*Anous stolidus, Xenus cinereus*) in this study (1.9%) had the unique feature of having both the contour and afterfeather down pigmented, whereas the true down was unpigmented. Only afterfeather down and true down were pigmented in 4.8% of the species studied (*Himantopus himantopus, Cladorhynchus leucocephalus, Recurvirostra americana, Haematopus palliatus, Vanellus cayanus*). Three of these species are in the family Recurvirostridae. Only the true down was pigmented in 13% of the species examined in this study. This pattern appears in the Snowy Sheathbill (*Chionis alba*), gulls (*Larus delawarensis, L. pacificus, L. argentatus, L. atricilla, Rissa tridactyla, Xema sabini, Rhodostethia rosea, Pagophila eburnea, Cregrus furcatus*), one skimmer (*Rhynchops niger*), and two species of terns (*Sterna forsteri, Sterna fuscata*). As stated earlier, the true down of gulls contains the most diagnostic microscopic characters for that group.

Of the 72% of species that had all types of down pigmented, about half (43%) had pure white breast feathers. Species with dark pennaceous feathers had all down pigmented in 56% of the species examined. So, even though it seems logical that dark pennaceous feathers should also have dark downy types, this is not necessarily the case. Examples of species having pure black pennaceous feathers with pure white plumulaceous down also occurs in other families of birds (e.g., *Psarocolius wagleri* [Icteridae], *Corvus leucognaphalus* [Corvidae]).

After conducting this general survey, plumage color obviously does not affect the amount of pigmentation in the various down types in this group of birds. More in-depth analysis is needed to verify these results, but large differences in the proportion of pigmentation were not noted in pigmented down of birds with colored breast feathers when compared to those with white breast feathers. A general review of the birds that breed in northern latitudes compared to those that breed in southern latitudes also did not show correlations with pigment color (Dove 1998b).

This survey satisfies concerns over feather color correlations to pigmentation of different down types and allows us to proceed with the assumption that the microscopic feather pigmentation patterns are independent of other contour feather features such as color.

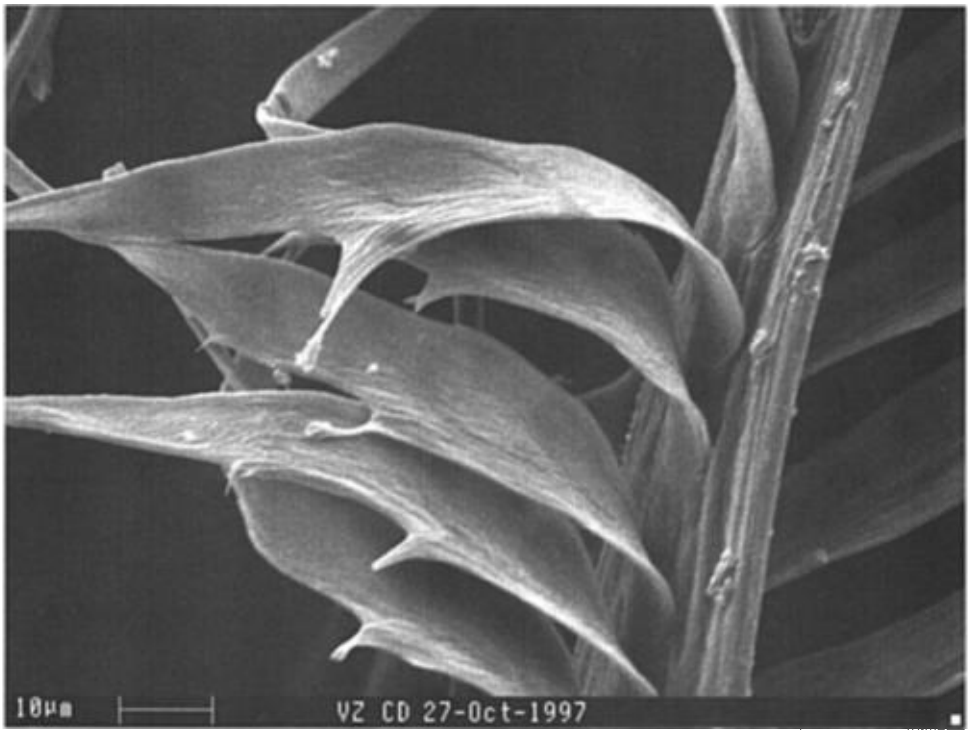


FIG. 123. Scanning electron microscopy provides a three-dimensional surface view of villi morphology of *Eremophila alpestris*.

VILLI

Villi were first described in the downy barbules of passerines by Chandler (1916:382) as "... a constant and peculiar character in the presence of lobate or finger like villi on the ventral edge or on the side of the base [of plumulaceous barbules]." These tiny structures appear as transparent projections on the basal cells of downy barbules when viewed with high-power (400×) LM and are visible in much more detail with SEM (Fig. 123). Villi were first noted as occurring in the Trochilidae, all of the suborder Pici (Capitonidae, Rhamphastidae, Picidae) except the Galbulidae, and passerines (Chandler 1916) and are most commonly found in passerines. Chandler (1916) found villi present in more than 100 species of passerines representing many diverse families. Furthermore, he found that these diagnostic characters usually occur on the barbules of the basal part of the barb. Although Reaney et al. (1978) described the exact same structure using SEM, they did not acknowledge Chandler's (1916) priority in terminology because they observed "knobbed" projections, which they claimed Chandler did not describe. However, these knobs were clearly illustrated in Chandler's (1916) figure F (p. 253) and in plates 37, 114b, and 115b and were defined by him as being "lobate." Although the function of villi remains unknown, Reaney et al. (1978) speculated that they serve to associate adjacent barbule bases. Other studies have also shown villi to vary morphologically among some groups of birds (Reaney et al. 1978; Brom 1991; Farquhar et al. 1996). In an attempt to assess the value of villi for

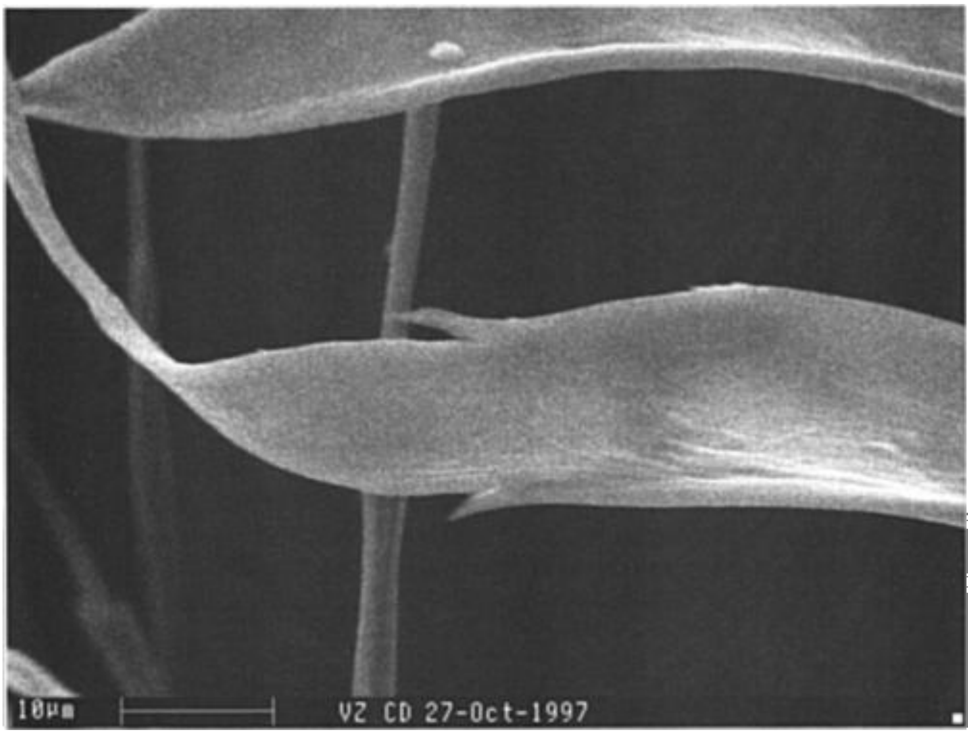


FIG. 124. Simple, pointed villi are observed in *Cursorius cursor.*

the determination of the phylogenetic relationships among some groups of birds, Brom (1991) examined villi in 105 species of passerines, six families of Piciformes, and 20 other outgroup families representing more than 270 species, and found villi only in Trochilidae, Passeriformes, and four families of Piciformes (Capitonidae, Indicatoridae, Ramphastidae, and Picidae). He did not use any charadriiform taxa in the villi study. However, he did examine 68 species in nine shorebird families in another comprehensive study of the microscopic variation of plumulaceous feathers and did not find villi on basal cells of any species of Charadriiformes (Brom 1991:46). In contrast to Chandler (1916), Brom (1991) did find villi on downy barbules of the afterfeather, although they were observed in much lower numbers than on the contour feather down. Hence, the presence of villi has long been a curious feature of downy barbules and is known to be important in the identification of certain groups of birds.

Downy barbules from the umbilical and basal regions of contour breast feathers of more than 100 species of shorebirds have been examined in this study using LM and SEM to search for feather characters that might prove useful for phylogenetic study. During this preliminary search for feather character variation in Charadriiformes, villi-like projections were observed for the first time in at least six families of this order, which warranted study of this character at higher levels of magnification. Therefore, the purpose of studying this newly discovered feather feature here is to analyze and document the occurrence and morphology of these villi projections and to determine if they are morphologically similar to the villi that have been observed in other unrelated groups of birds. SEM villi comparisons

TABLE 1. List of charadriiform taxa that were found to have villi on base of barbules. Table lists presence of subpennaceous region, the vanule of the barb where villi most often occur, relative density of villi throughout the whole barb, number of villi per base cell, and whether the villi occur on most barbs.

Taxon	Subpennaceous region	Vanule	Density	Number/base	Occur on most barbs
Haematopodidae					
Haematopus bachmani	Present	Distal	Few	Single	Yes
Ibidorhynchidae					
Ibidorhyncha struthersii	Present	Proximal	Very few	Single	No
Recurvirostridae					
Recurvirostris americana	Present	Both	Few	Single	Yes
Charadriidae					
Vanellus indicus	Present	Proximal	Few	Single	No
Vanellus lugubris	Present	Proximal	Very few	Single	No
Charadrius tricollaris	Absent	Both	Moderate	Single	Yes
Charadrius mongolus	Intermediate	Proximal	Few	Single	Yes
Charadrius montanus	Present	Proximal	Few	Single	Yes
Charadrius vociferus	Present	Proximal	Few	Single	Yes
Anarhynchus frontalis	Present	Proximal	Few	Single	Yes
Pluvialis squatarola	Present	Proximal	Few	Single	Yes
Eudromias morinellus	Absent	Both	Moderate	Single/multiple	Yes
Scolopacidae					
Tringa flavipes	Present	Proximal	Few	Single	Yes
Arenaria interpres	Intermediate	Proximal	Few	Single	No
Lymnocryptes minimus	Absent	Both	Moderate	Single	Yes
Calidris bairdii	Absent	Both	Moderate	Single	Yes
Calidris pusilla	Absent	Both	Moderate	Single	Yes
Eurynorhynchus pygmeus	Absent	Both	Moderate	Single	Yes
Micropalama himantopus	Intermediate	Proximal	Moderate	Single	No
Tryngites subruficollis	Present	Proximal	Few	Single	No
Philomachus pugnax	Present	Proximal	Few	Single	Yes
Phalaropus tricolor	Absent	Both	Moderate	Single/multiple	Yes
Phalaropus lobatus	Absent	Both	Moderate	Single/multiple	Yes
Glareolidae					
Cursorius cursor	Absent	Both	Moderate	Single	Yes
Stiltia isabella	Absent	Both	Few	Single	No

were made on Trochilidae (*Archilochus colubris* [Ruby-throated Hummingbird]), Picidae (*Sphyrapicus varius* [Yellow-bellied Sapsucker]), Alaudidae (*Eremophila alpestris* [Horned Lark]), Nectariniidae (*Nectarinia senegalensis* [Scarlet-chested Sunbird]), and three species of shorebirds (*Charadrius vociferus* [Killdeer], *Cursorius cursor* [Cream-colored Courser], and *Phalaropus lobatus* [Red-necked Phalarope]). LM examination was first conducted on umbilical and basal barbs of 105 shorebird taxa to determine the presence or absence of villi. SEM was then used on select species to allow a detailed view of the three-dimensional morphology and origin point of the villi.

In this study, villi varied morphologically from a few, simple, pointed villi per base cell (Fig. 124), as in *Cursorius cursor,* to many knobbed and pointed villi that occur all around the base (Fig. 125), as in hummingbirds. The general shapes of villi found in this study conform to previous descriptions by Brom (1991) and

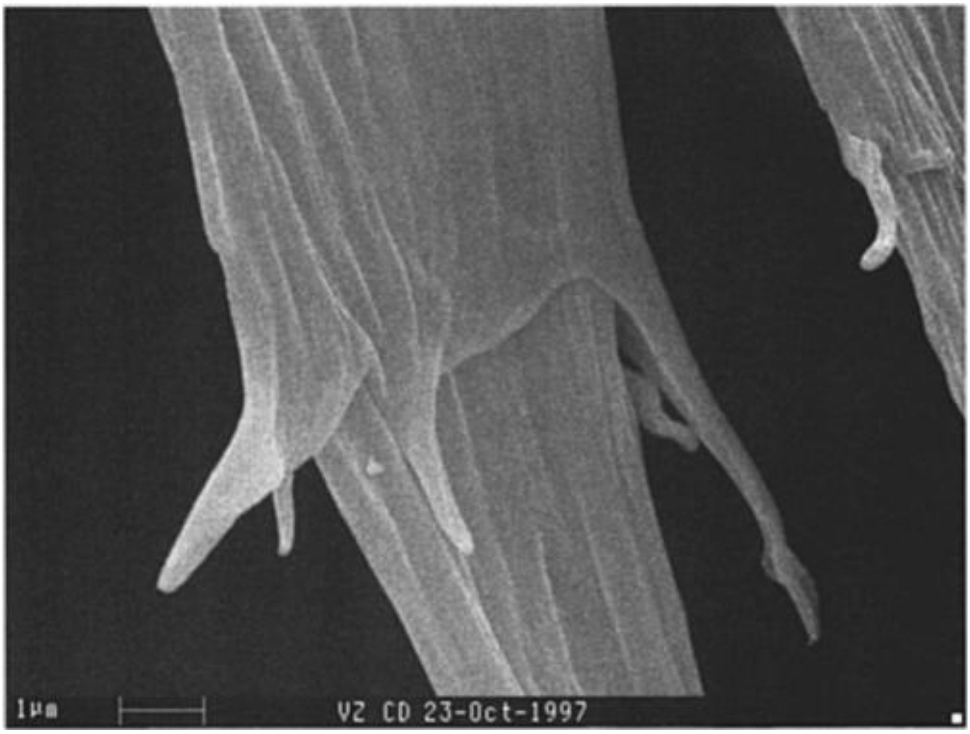


FIG. 125. Hummingbirds usually have many knobbed and pointed villi that occur all around the base of the barbule.

others: curved or scimitar-shaped with the axis usually pointing backwards in the direction of the barb in Piciformes; blunt, knobbed, or fingerlike in Passeriformes; knobbed, or fingerlike and sometimes sharply bifurcated in Trochilidae; and pointed and knobbed, and sharply knobbed in Nectarinidae (Farquhar et al. 1996). Because previous studies have thoroughly documented the comparative morphologies of villi among noncharadriiform groups, the results of this study focus on shorebird villi and compare the shapes and distributions to the villi of other known groups.

Charadriiform villi.—Villi were observed in six families (25 species) of shorebirds with LM (Table 1). As in other groups, shorebird villi are confined to cell borders of the base region of the barbule and are direct outgrowths from the cell's edge (phalarope, Figs. 126, 127). The villi observed in shorebirds are consistent in origin (cell border) and location (base of the barbule) with the villi observed in other orders. Charadriiform villi (Fig. 127) are thicker and sometimes shorter than those observed in other groups and do not have the stem with a distinct knob most typical of passerines. In Charadriiformes, villi are usually less frequent in number than in other species, are located only on the very basal region of the barb, and always point in the direction of the pennulum. In charadriiform species that have a subpennaceous region, the villi, if present, are always found directly above that region (e.g., Killdeer).

SEM examination of villi.—The following descriptions and SEM photomicro-

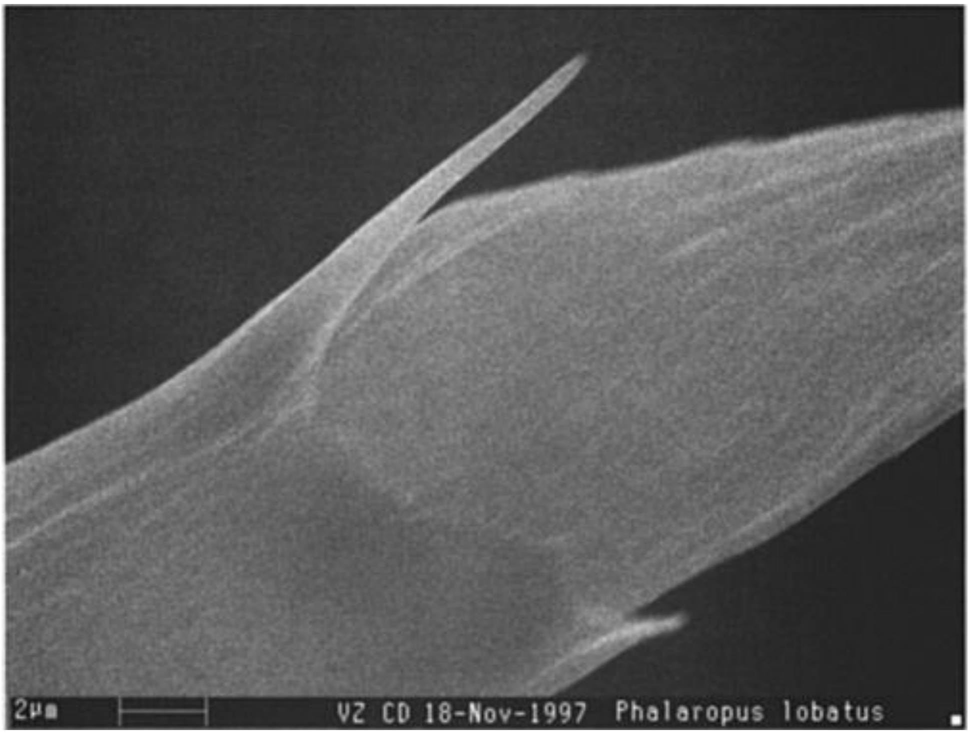


FIG. 126. Villi of shorebirds are similar to those found in other groups by being confined to cell borders of the base region of the barbule.

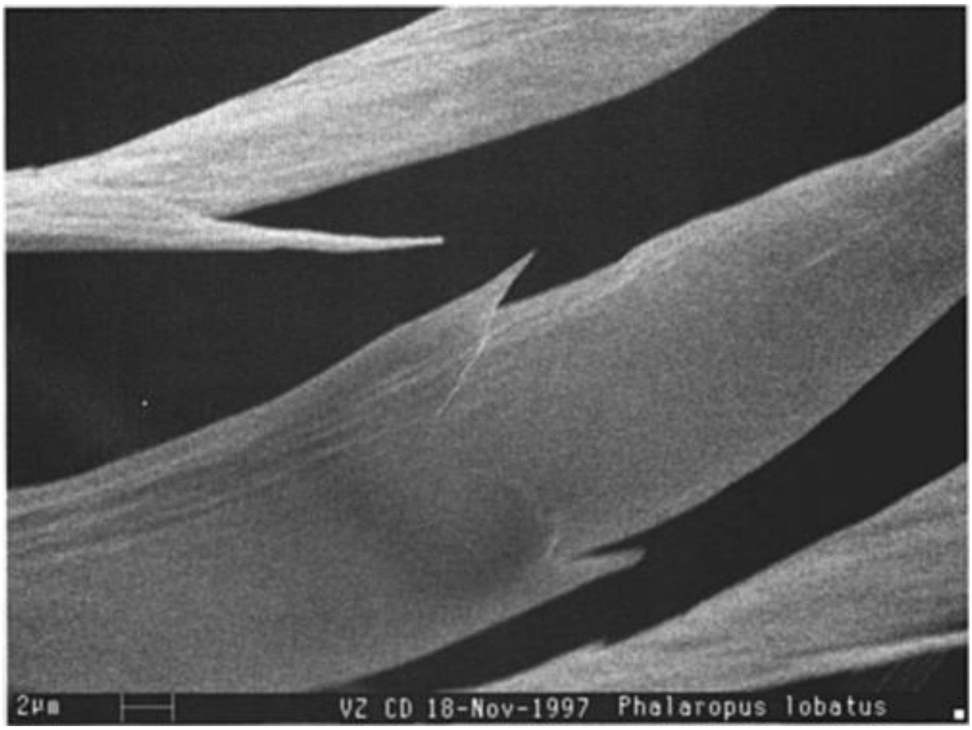


FIG. 127. Charadriiform villi are short, straight, and do not have knobs that are typical of passerine villi.

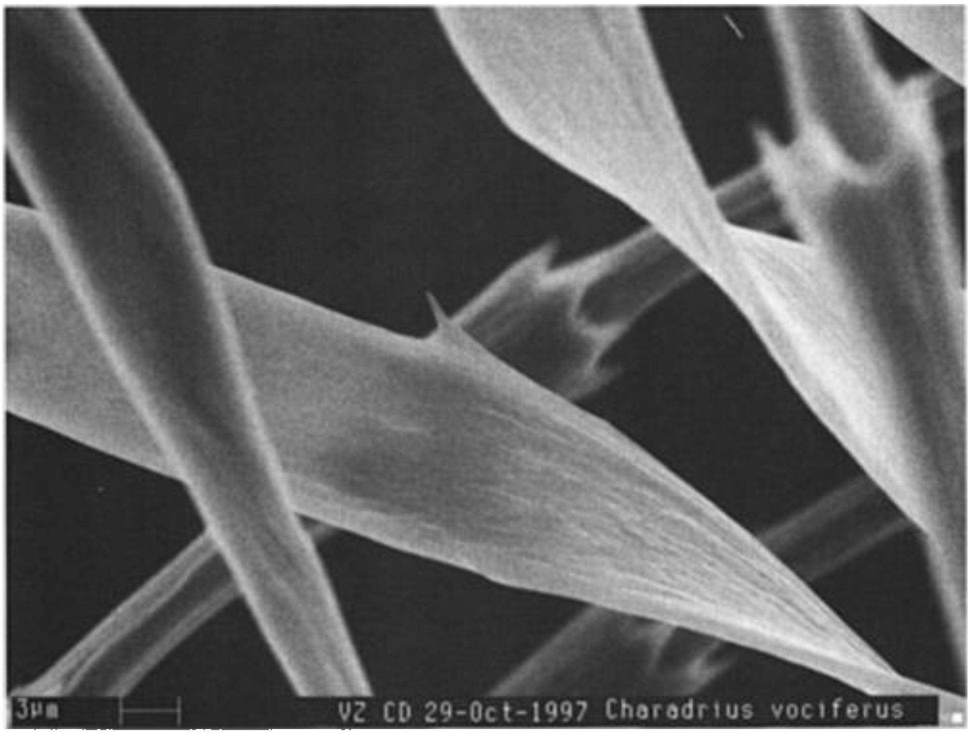


FIG. 128. The Killdeer has small villi that are few in number and difficult to locate.

graphs explain the morphological and distributional similarities and differences between villi of Charadriiformes and other species examined in this study. Villi are most commonly found on proximal barbules of umbilical and basal barbs.

Charadriidae

Charadrius vociferus (Killdeer)

Villi on this species are very few and difficult to find. The villi are only found just above the subpennaceous region of the barb. The shape is pointed; no knobs or bifurcated villi were observed. Figure 128 (proximal vanule) shows a typical villus. At least one villus was found on all umbilical or basal barbs examined in this study.

Scolopacidae

Phalaropus lobatus (Red-necked Phalarope)

This species has the most numerous villi of any shorebird examined. Villi occur only on the most proximal barbules of the barb but are easily observed with LM. Two or more villi per base is the common condition (Fig. 129). These villi are pointed and originate from the cell border. This species does not have a well-developed subpennaceous region. Villi were observed on both vanules.

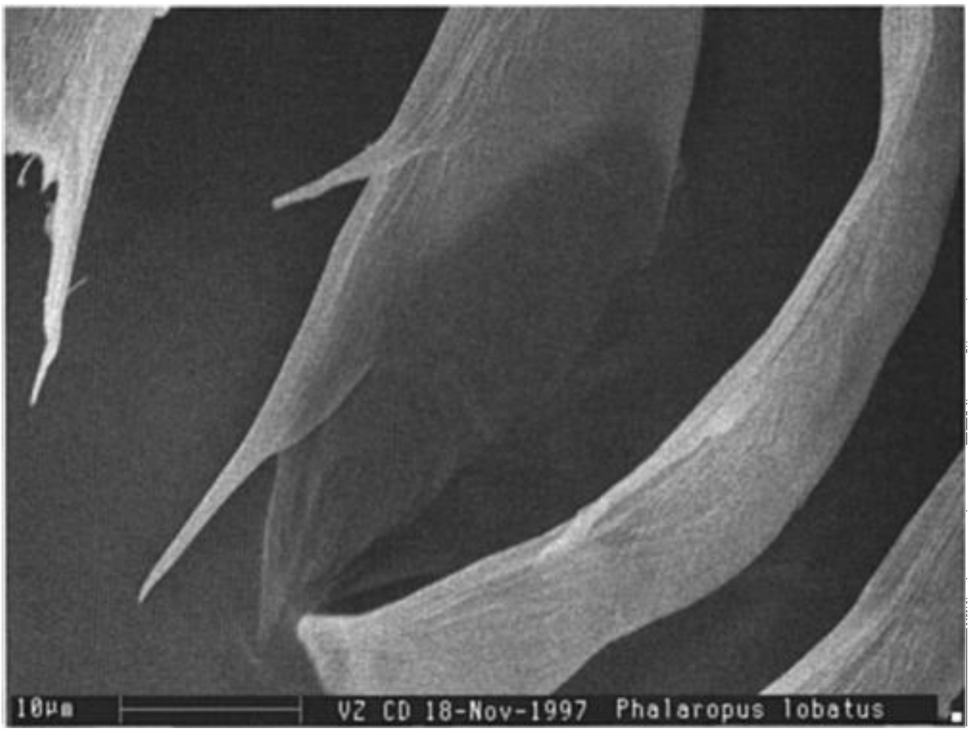


FIG. 129. Phalaropes may have numerous villi on the same base.

Glareolidae

Cursorius cursor (Cream-colored Courser)

Villi are located on the bases of the most proximal barbules of most barbs because this species does not have an extensive subpennaceous region. Villi occur on both vanules in this species and are more numerous than those found on the Killdeer.

Picidae

Sphyrapicus varius (Yellow-bellied Sapsucker)

Villi are typical in shape when compared to those described in other Picidae by Brom (1991) but can also be split (Fig. 130a) or anvil-shaped (Fig. 130b). Villi are located mainly on barbules of the proximal half of the barb but can rarely be found on midsection barbules of the barb. The villi usually occur on the lower edge of the base cell and when viewed with LM and seem to hold on to the next barbule base. Villi occur on both vanules in this species and are more often observed in higher numbers on barbules that are located on the most proximal portion of the barb (Fig. 131). SEM examination also revealed hairlike structures on the rachilla of this species (Fig. 132).

Trochilidae

Archilochus colubris (Ruby-throated Hummingbird)

Villi are knobbed and pointed and occur on the barbules of the proximal to midsection of the barb. These villi can also be split and paired (Fig. 133a, b) and

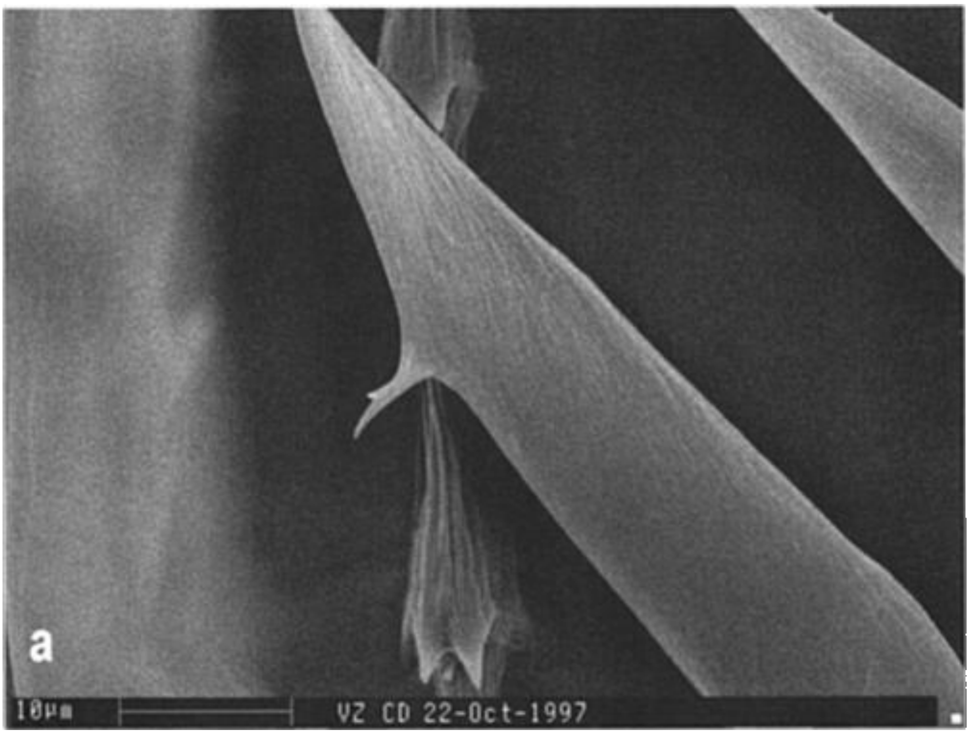


FIG. 130a. Villi of *Sphyrapicus varius* (a picid) are usually scimitar-shaped but can also be split (a) or anvil-shaped (Fig. 130b).

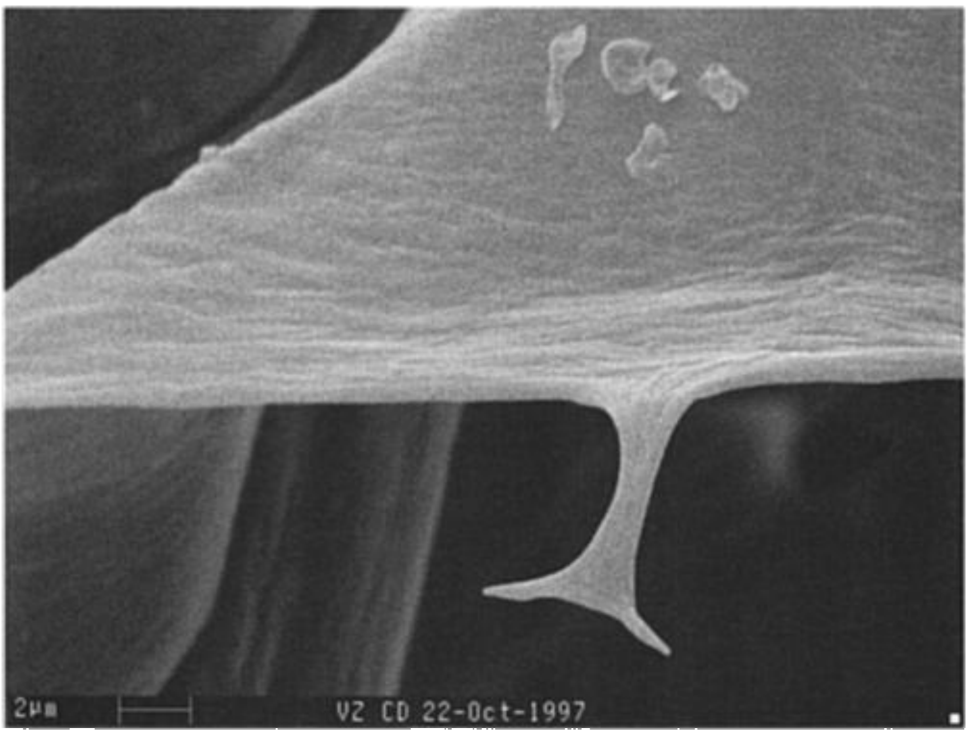


FIG. 130b.

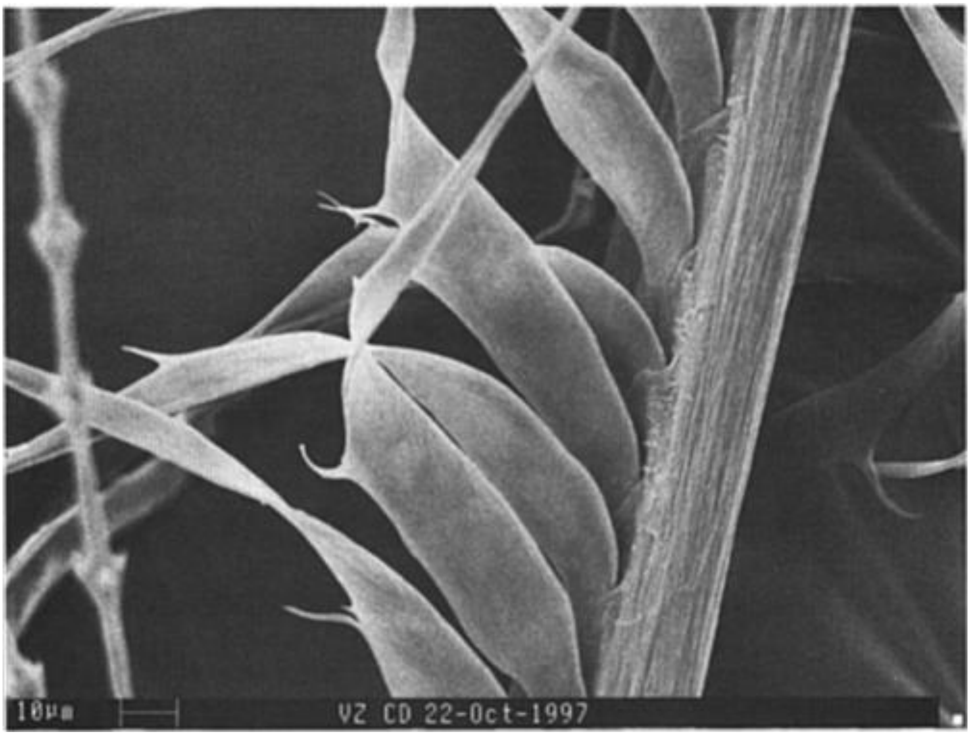


FIG. 131. Villi are observed in higher density on barbules near the base of the barb in picids (villi of *Sphyrapicus varius* are shown).

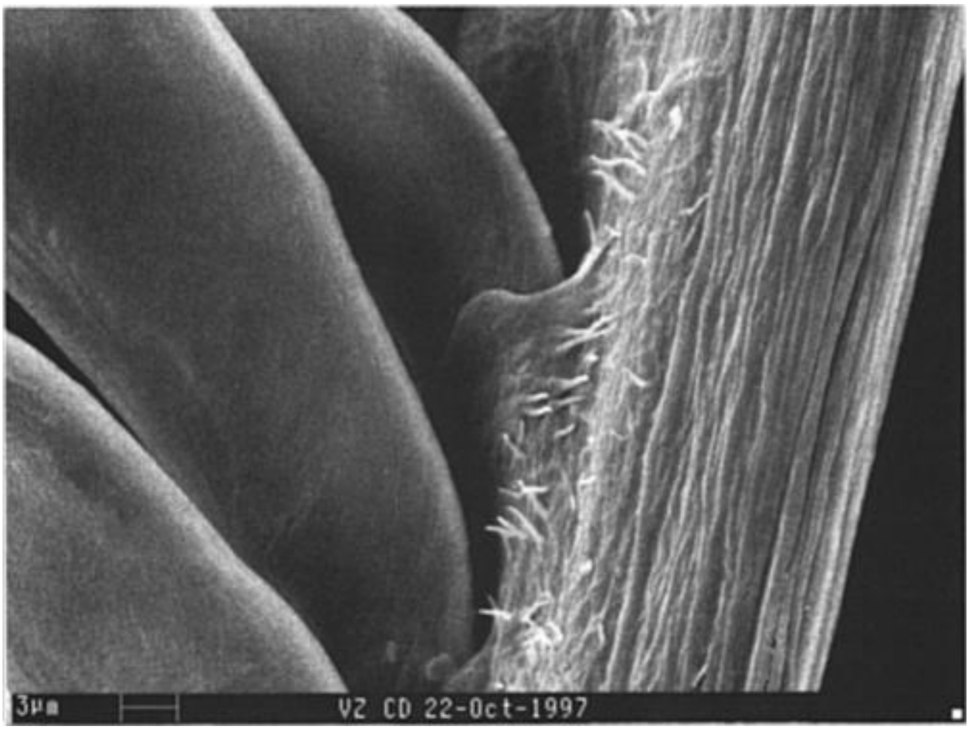


FIG. 132. Rachilla of *Sphyrapicus varius* showing many hairlike structures.

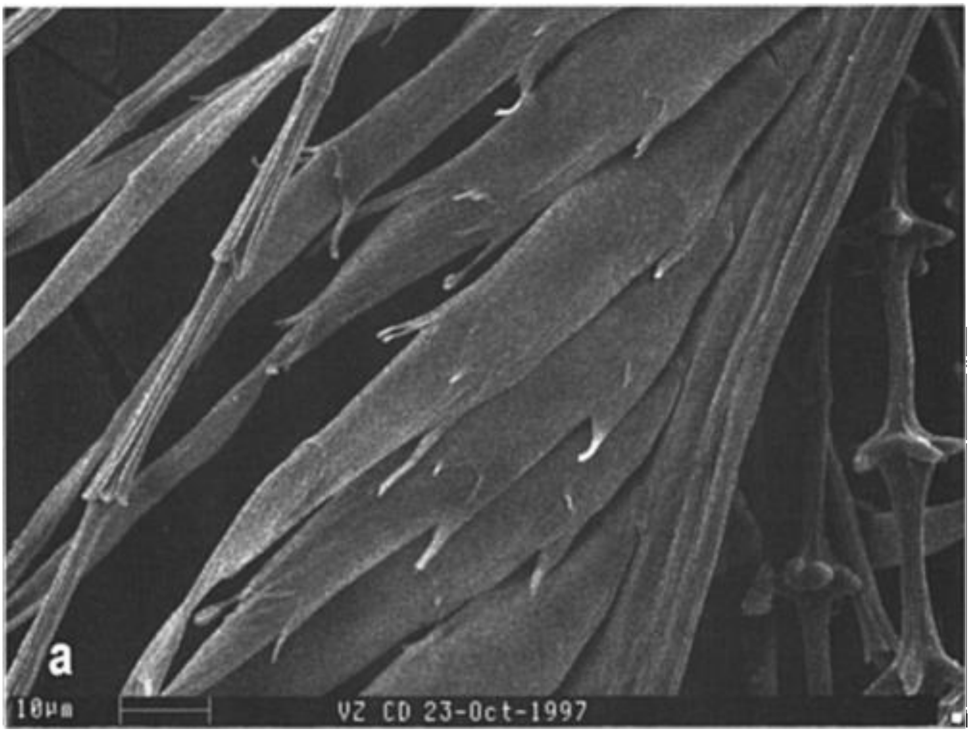


FIG. 133a. Villi of hummingbirds (*Archilochus colubris* are shown) are very numerous and typically have knobs (a), but some villi were observed to be split or double-knobbed (Fig. 133b).

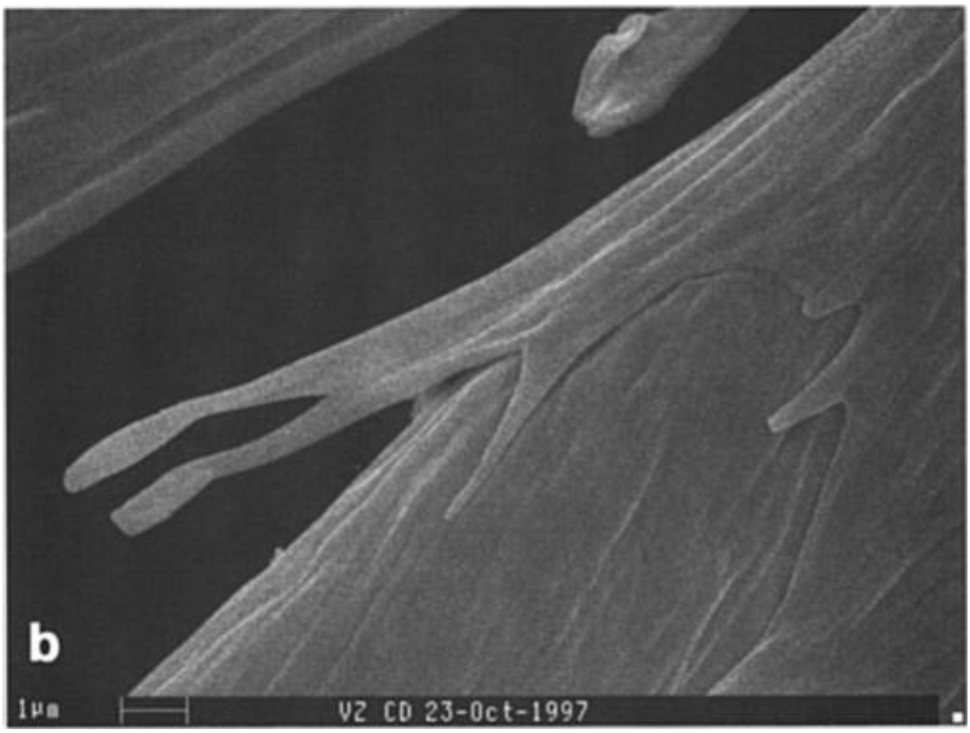


FIG. 133b.

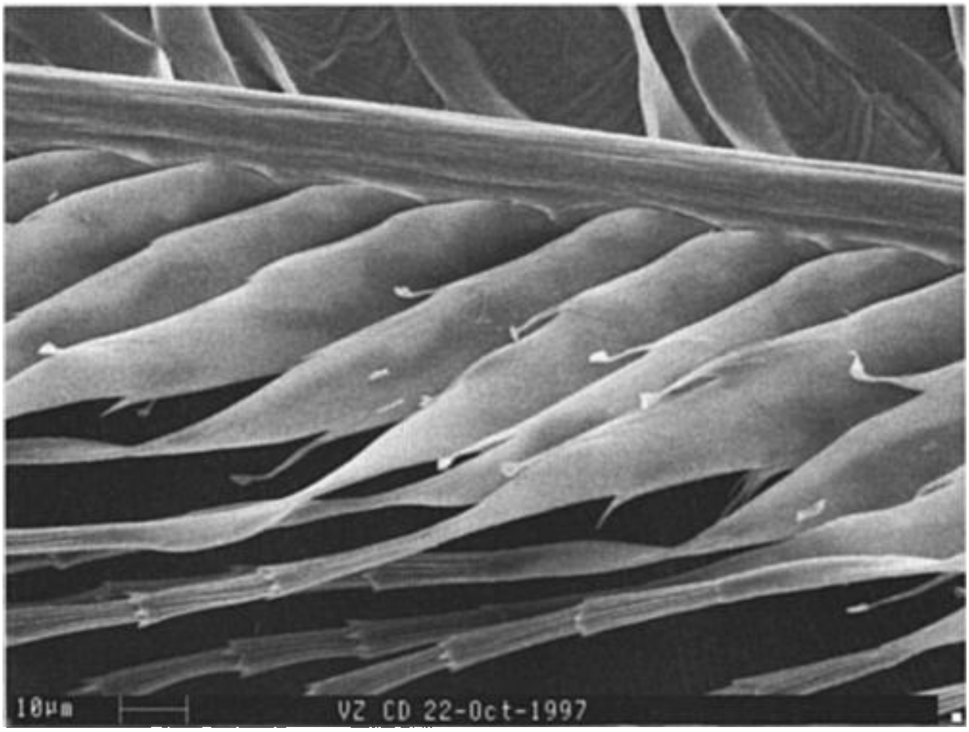


FIG. 134. Villi of *Nectarina senegalensis* (Scarlet-chested Sunbird) are similar to those of hummingbirds and passerines with multiple-knobbed types.

often occur all around the base cell. Villi on this species are very numerous and multiple villi are often observed on the same base cell.

Nectariniidae

Nectarina senegalensis (Scarlet-chested Sunbird)

As in other passerines and hummingbirds, the villi are very numerous with many knobbed and pointed types present (Fig. 134). Split villi were observed in low numbers. Villi in this species are usually located bilaterally along the base and not all around the base cell as in hummingbirds. They occur on proximal to midsection barbules of both vanules of the barb but sometimes are more heavily distributed on one vanule.

Alaudidae

Eremophila alpestris (Horned Lark)

Many knobbed, pointed, paired, and split villi are present on both vanules (Fig. 135). Knobs are larger than those of other species examined in this study and often overlap with adjacent villi (Fig. 136). In this species, villi are mostly found on the proximal half of the barb but also can be found on barbules throughout the barb. These villi are typical of passerine villi because they are very numerous, easy to find, and diagnostic of the order by having large knobs, and villi often number two or more per base.

FIG. 135. *Eremophila alpestris* (Horned Lark) has many large-knobbed villi.

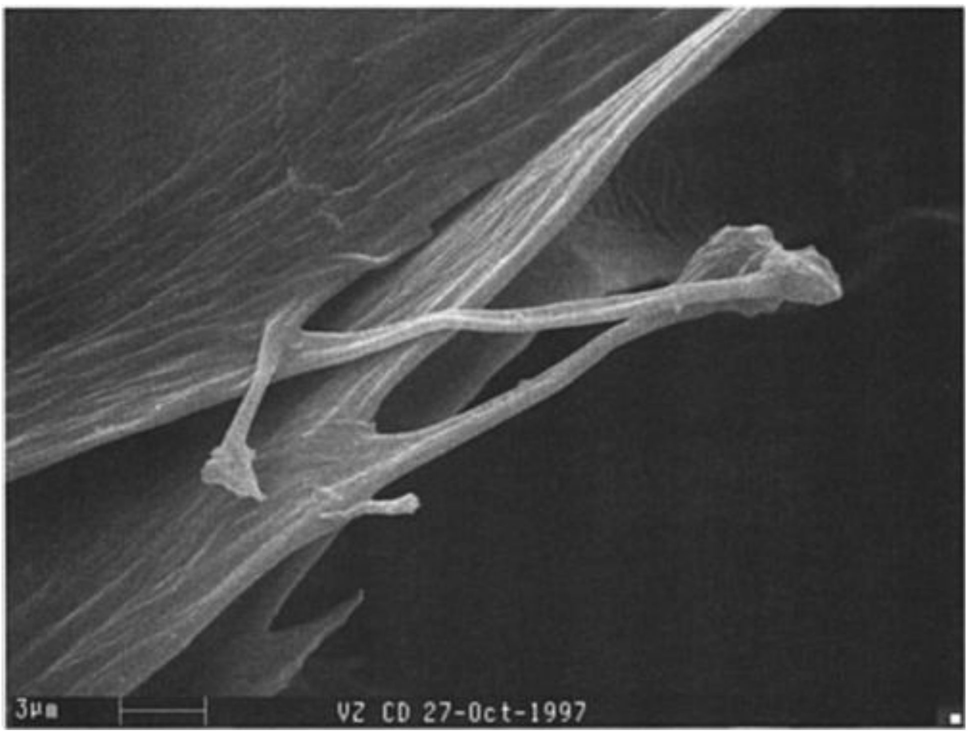


FIG. 136. Overlapping villi in a Horned Lark.

LM examination of villi.—High-power (400×) LM was sufficient to assess the distribution, density, and occurrence of villi in shorebirds. Table 1 shows that species that have no subpennaceous region, or species with a less extensive or intermediate subpennaceous region, usually have villi on both vanules. Additionally, villi in species with little or no subpennaceous regions are denser, or easier to find on individual base cells when compared to those species with a subpennaceous region. A complete analysis of the subpennaceous region in other groups of birds that have villi has not been done, but all noncharadriiform species examined in this study did not have subpennaceous regions on the barbs of feathers examined. Most shorebirds have a single villus per base; only the Eurasian Dotterel (*Eudromias morinellus*) and phalaropes (*Phalaropus tricolor, Phalaropus lobatus*) were observed having more than one villus on some base cells. Villi were found on most of the 6–10 umbilical and basal barbs of the species examined in the LM study. Charadriiform villi structures originate on the borders of base cell divisions just as they do in other groups of birds. Shorebird villi are almost always found on proximal vanules but sometimes can also occur on both vanules of the barb. Only the Black Oystercatcher (*Haematopus bachmani*) was observed to have villi on the distal vanule. Vanule orientation is determined by searching for the hooklet-like structures of the subpennaceous region; distal vanules have hooklets.

Because this is the first study to document villi in shorebirds, care was taken to examine as many species as possible for these structures. LM proved sufficient for observation of these structures, but SEM was utilized for further study of the morphology and origin of the villi. This study only examined the umbilical and basal barbs of the breast feathers of representative species in this order. Because these structures can be difficult to find by the untrained eye, a more complete SEM study of the entire order would better document the occurrence and significance of villi in this group of birds.

Because villi in shorebirds are clearly visible with LM and may vary among species and families, this character was coded and included in the phylogenetic study of feather characters of Charadriiformes to determine if it was of phylogenetic importance in this order. Because the morphology of shorebird villi is somewhat simpler than in other groups, the villi are fewer in number, and the location is limited to downy barbules that are located at the very base of the barb, these villi can be used to aid in feather identifications.

The findings of this study weaken Brom's (1991) phylogenetic hypothesis of piciform relationships to passerines and hummingbirds based on the presence of villi and underscores the danger of placing too much emphasis on single characters in phylogenetic studies. More analysis is needed to determine if this structure is homologous or convergent with that of passerines and other groups. These findings also raise the possibility that villi could occur in other groups of birds and should be searched for with greater care in future studies.

Base of Barbule

The base of the downy barbule is the part of the barbule that attaches to the rachilla and is proximal to the pennulum (Fig. 4). The base of the barbule is flat

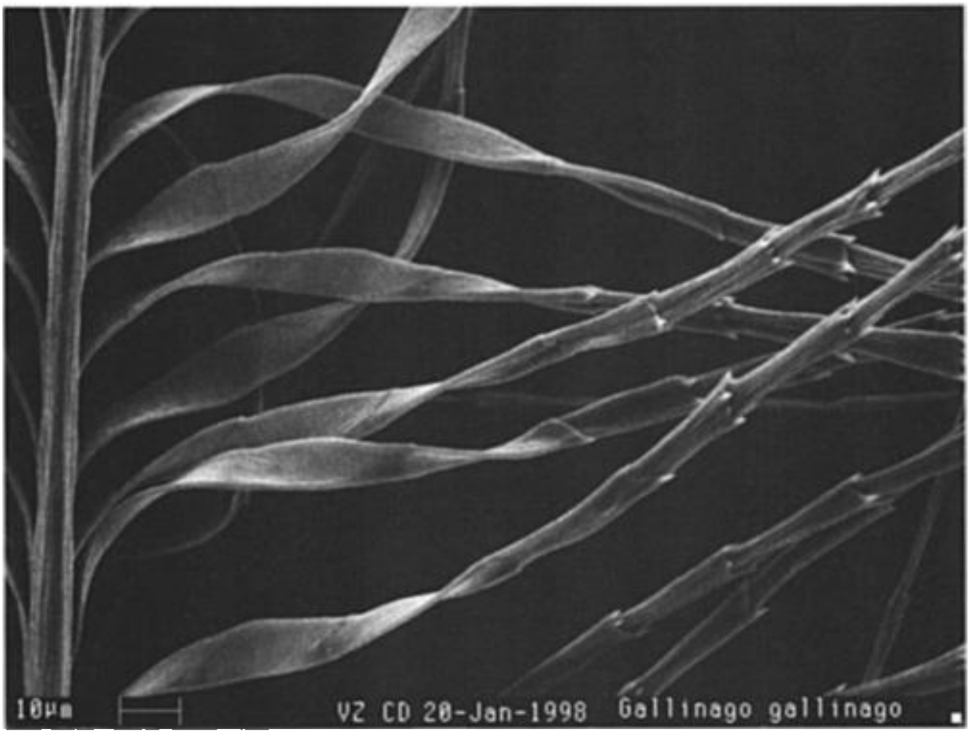


FIG. 137. Base of barbule of *Gallinago gallinago* showing straplike, flattened base.

or straplike in appearance when viewed with LM or SEM (Fig. 137). In describing a plumulaceous barbule, Lucas and Stettenheim (1972) specifically defined the base as being divisible into a laterally compressed base of fused cells and a slender pennulum. The "base of fused cells" is what makes up the flattened base of the downy barbule. The simple flat shape of the base that projects almost perpendicularly from the rachilla acts to stiffen the barbule and allows flexibility (Lucas and Stettenheim 1972). Lucas and Stettenheim (1972) reported that the base is much wider than the pennulum in the Wild Turkey (*Meleagris gallopavo*) but almost the same width as the pennulum in other species (gulls, cormorants). The base of the barbule has been referred to as the base region, basal cell, base of pennulum, ventral lamella, and ventral flange.

The base region of the barbule was investigated in further detail because some variation has been observed in the number of cells that compose this region. The base cell sometimes has more than one distinct divisional cell border (Fig. 138) that may be visible with LM. Gilroy (1987) refers to this division as a basal scar in her study of the Rock Dove (*Columba livia*) and Dove (1994) observed it in a study of plovers (Charadriidae). To determine if this scar or division is indeed a character on the base region of the barbule that is consistent within individuals but varies among species, this part of SEM analysis focused on the base of the barbule.

In Charadriiformes, the barbule base consists of a single cell or multiple cells (two or three) in a series of flattened or straplike cells, or the base is indistinguishable from the rest of the pennulum. Barbules commonly are found that have

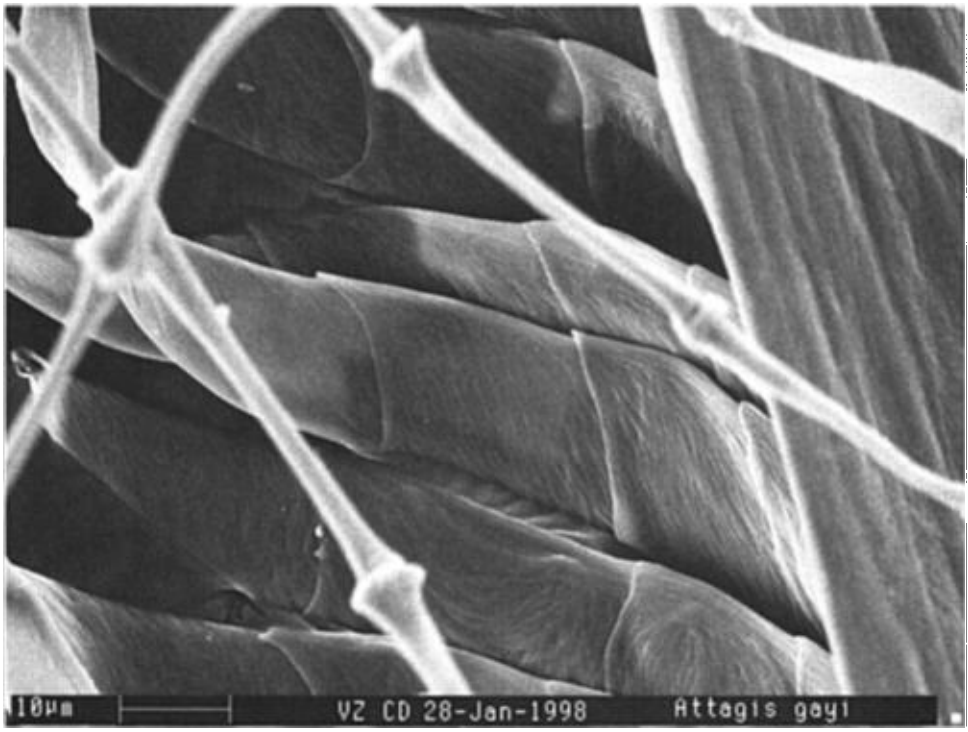


FIG. 138. In some species the base is composed of multiple cells (base cells of *Attagis gayi* are shown).

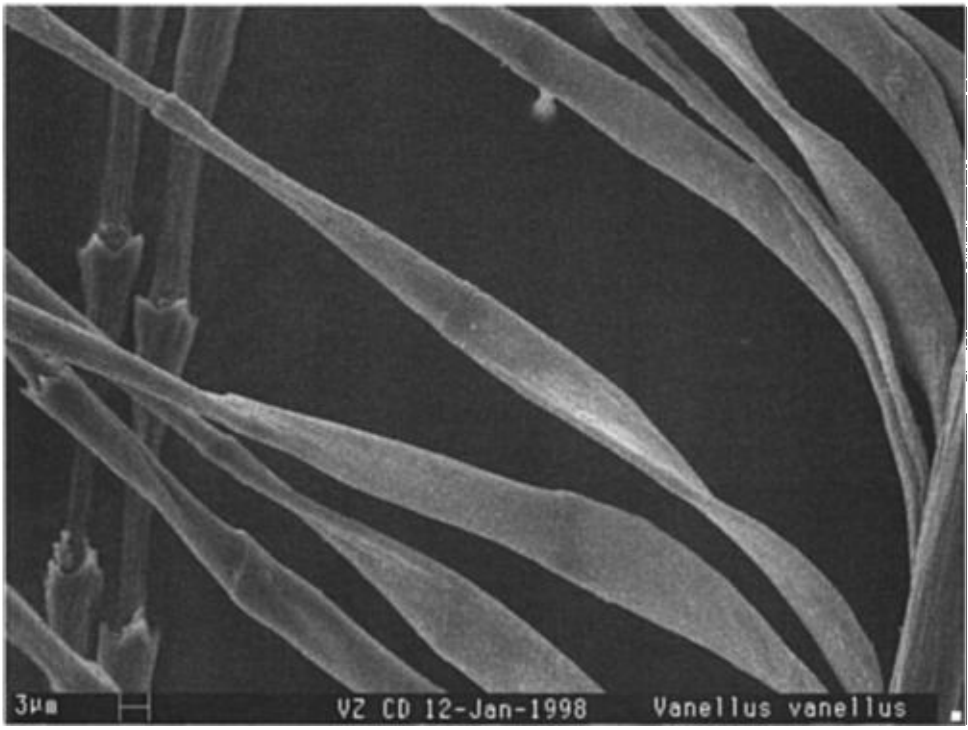


FIG. 139. Lapwings (e.g., *Vanellus vanellus*) typically have bases with only one visible cell.

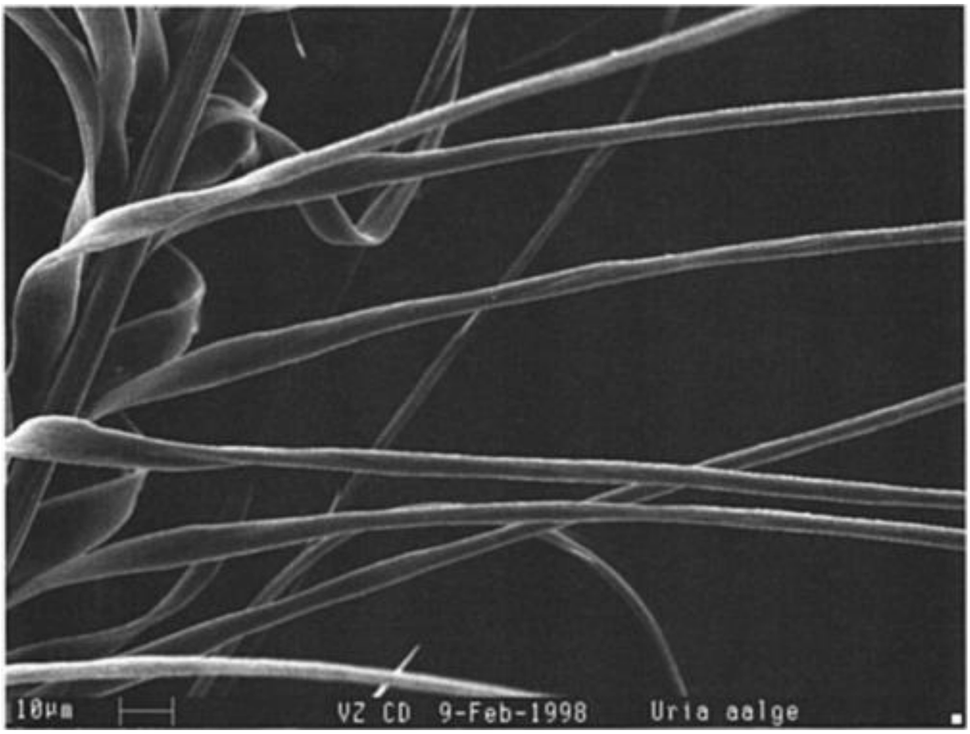


FIG. 140. Alcids have bases that are indistinguishable from the pennulum.

single-celled bases on the same barb with barbules that have multiple-celled bases. Single and multiple cells occur in species throughout the charadriiform order. All species of *Vanellus* examined in this study had single-celled bases (Fig. 139). Single-celled bases were observed in 25% of the species studied and were distributed throughout most of the major groups in this order. Multiple-celled bases were noted in 40% of the species but were most commonly observed in the Scolopacidae. Both multiple- and single-celled bases of barbules on the same barb were noted in 22% of the species scattered throughout the order. The most consistent observation of base cell composition was in the Alcidae, where the base cells of every species examined were determined to be indistinguishable from the rest of the pennulum (Fig. 140). In the alcids, no distinct cell division between the base and the pennulum could be observed with LM.

The cell composition of the base region of the barbule is variable within and between groups in this order. Because the base is unique in at least one family of Charadriiformes (alcids), the base will be included in the character data matrix for a phylogenetic analysis of this order. Ideally, this character should be coded using SEM photomicrographs because the cell divisions are not always visible with LM.

DISCUSSION

In this descriptive study more than one third of the species in the charadriiform order have been examined with LM. Select species from each family or subgroup were used for illustrations, SEM study, and character coding. Large differences exist among the microscopic characters of some families within this order, making simplified characterizations pertaining to feather structure difficult and statements regarding relationships impossible. However, some generalizations can be made. In general, charadriiform birds have relatively short barbules that are usually pigmented at the nodes. Nodes are typically expanded more at the base of the barbule and spines are often present at nodes all along the barbule. The nodal pigment shape is usually distinctly diamond-shaped and constricted into a point at the node, with pigment sometimes extending or trailing into the internode. Pigment at the nodes is sometimes surrounded by a transparent process that flares away from the pennulum and forms rounded or pointed projection-like processes at the node.

Scolopacids are more similar to charadriids than to other families of this order in feather characters of barbule length (except *Scolopax*), pigmentation patterns and shape, and general nodal morphology, but much variation exists in this family. Pigment is usually confined to nodes with pigment extending below the nodes in the Tringinae, but in some groups (Calidrinae) the pigment is more confined to the nodes and rounded in shape. Internodal pigmentation, when present, is usually heavier than in the Charadriidae. Scolopacids rarely have partially unpigmented barbules as is frequently seen in charadriids. Only *Xenus cinereus* has unpigmented true down.

Gulls are easily diagnosed to family level based on nodal morphology of true down. Pigment patterns of gull down are unique in that the true down is most often pigmented whereas other down types lack pigment or are only sparsely pigmented.

Seedsnipes also have a unique suite of characters that separates them from other members of the order. Long barbules with large expanded pigmented nodes all along the barbule are typical of every species examined.

Alcids exhibit a unique combination of microcharacters that easily distinguish this group from other members of Charadriiformes. They are more similar in microcharacters to loons, grebes, and other diving birds than to shorebirds because they share the features of a simple, short pennulum with long prongs that are located on the distal portion of the barbule. This combination of characters makes the overall microstructure appear shaggy. The alcids differ from loons in pigmentation patterns.

Enigmatic taxa such as *Dromas, Chionis, Pedionomus,* and *Pluvianellus* do not have unique feather microcharacters.

Afterfeather down and true down examined in this study usually have similar characteristics to contour feather down but some groups (e.g., gulls, stilts, and avocets) show marked differences between the microcharacters of these down types. Afterfeather and true down barbs always have finer structures and are more threadlike or delicate in appearance when compared to plumulaceous barbs of the contour feather. True down and afterfeather down studied here did not have subpennaceous regions on the bases of barbs.

A descriptive study of as many species as possible is imperative in understanding the amount of variation in feather characters before attempting to estimate relationships based on those characters. In this study, LM proved sufficient for this type of character assessment. Although SEM allowed a more detailed three-dimensional view of the feather, it did not prove to be a resource for many additional feather characters. SEM scans the surface of the barbule and presents a better view of nodal morphology, barbule texture, and other anatomical features than is possible with LM. However, not one single character was discovered in the SEM study that was not observed with LM. Rather, SEM helped to clarify what was seen with LM. A few observations such as furrowed internodes (*Bartramia*) and multiple-spined distalmost cells of barbules (*Bartramia* and *Prosobonia*) were noted here but these features must be investigated further to determine if they are due to specimen age, individual age, or barbule wear. Because the multispined distalmost cells occur in relative high frequency among multiple specimens (five), these cells probably are a real feature, but again, this is not an observation that was not already known from LM study. After conducting this survey, previous speculation about the use of SEM for feather identification is confirmed: it is best to use LM to search for identifiable microscopic feather characters and SEM for detailed research questions that arise from an LM investigation. In this study, SEM was most valuable in documenting the presence of villi on some species and investigating base cell composition. These characters are visible with LM but were never before thoroughly described or known to occur in this group of birds and warranted a more detailed study. SEM preparation is extremely laborious and costly, and the examination of specimens is time consuming. Further, this type of microscopy only gives a view of the surface features of the feather and cannot provide any information on the pigmentation patterns that are so important in the identification methods.

The next section of this study devotes special attention to the microscopic feather characters selected from the descriptive survey for phylogenetic analysis. Testing these characters against other data sets is necessary in order to learn more about the evolution of the microscopic feather characters and determine if these characters are indeed phylogenetically informative.

PART 2

A PHYLOGENETIC ANALYSIS OF DOWNY FEATHER CHARACTERS IN CHARADRIIFORMES

Recent trends in the study of evolutionary systematics in birds have focused on the reproducibility of the data or characters that are used to hypothesize relationships. Traditionally, scientists relied on their expert opinions (traditional taxonomy) and later on morphometric measurements of a wide variety of characters (numerical taxonomy/phenetics) to infer systematic relationships. Some of the criticisms of these methods include difficulties in quantifying characters and inherent differences in expert opinions. A popular current application to systematic biology is that of phylogenetic systematics, which follows the principles of Hennig (1950, 1966) under the criterion of global parsimony (Wiley 1981), and seeks to hypothesize relationships of organisms based on character states of derived polarity. The resulting hierarchical cladogram of the phylogenetic relationships of organisms is based on shared derived characters (synapomorphies). This method receives enthusiastic support because it allows a posteriori assessment of character homology and avoids intuitive suggestions of evolution. Parsimony methods of inferring phylogenies search for trees that minimize the amount of evolutionary change (tree length) needed to explain the distributions of the characters that are being studied. Tree length is calculated by summing the number of character changes along each branch of the tree. Each character is a trait, judged to be homologous across taxa, that comprises a primitive (plesiomorphic) state and one or more derived (apomorphic) states. This type of analysis provides an ideal tool for assessing the value and performance of microscopic feather characters in a phylogenetic framework. In this study, parsimony analysis has a twofold purpose. First, it is used to compare tree statistics (e.g., consistency indices) between minimum-length trees generated by feather characters, osteological characters, and a combination of all characters. Secondly, this analysis is used to attempt to identify informative and homoplasious feather characters and to seek ecological or functional bases for correlation of sets of characters with those of previous phylogenies.

Thirty-eight microscopic feather characters were deemed potentially significant and independent for phylogenetic analysis. These characters may or may not be valid for other groups. Because other unrelated groups may have similar characters to shorebirds, it is important to limit feather analysis to specific groups or closely related outgroups when conducting parsimony analysis based on these characters alone.

METHODS

DERIVATION OF TREES

Analyses were conducted using the phylogenetic software PAUP*, version 4.0.0d61 (Swofford 2000). Printing of trees and character matrix coding were performed on MacClade 3.01 (Maddison and Maddison 1992). Binary characters were coded using numbers and include microscopic features such as presence or absence of pigment, nodal spines, and others, whereas multistate characters such as pigment shape and nodal morphology were coded using letters. Multistate characters were treated as unordered because the path of character evolution in these feather characters is unknown. Also, according to Hauser and Presch (1991) cladograms should be used to determine order much in the same manner as they are used to identify homoplasy. Character states were coded as missing if the character was unavailable or not applicable for a specific taxon. All characters were unweighted and outgroup rooting was specified.

Three separate sets of analyses were conducted using various forms of the original data matrix. The first analysis consisted of a matrix of 38 feather characters and 111 taxa (including seven outgroup species, Appendix 3). Outgroups for all analyses consisted of loon (Gaviiformes); crane, coot, and bustard (Gruiformes); and sandgrouse (Columbiformes). Sandgrouse were considered an outgroup to Charadriiformes following Morony et al. (1975) and contra Sibley and Ahlquist (1990). The second analysis used only the taxa from the original list that matched Strauch's 1978 taxa list (see Appendix 3) and included 68 of his osteological characters. The third set of analyses consisted of the taxa that matched Chu's 1995 reduced-taxa list (see Appendix 3) and was conducted using feather characters alone, osteological characters alone, and a combination of both data sets according to the principle of total evidence (Kluge 1989; Kluge and Wolf 1993). The matrices of Chu and Strauch are not printed here because they can be reproduced from Strauch's matrix following the procedures described in Chu (1995, appendix 2). Because Strauch did not code outgroups and Chu (1995) used a hypothetical ancestor, osteological characters were coded for six outgroup species used in this study (Appendix 4). Osteological character number 11 was coded according to Strauch's (1978) description because Chu (1995) split this character into two separate types that could not be distinguished on the outgroups. Strauch's characters 51 and 59 were rejected according to Chu's (1995) recommendation. All other skeletal characters were coded according to Chu (1995).

The relationships between tree topologies and data matrices were examined using the summary tree statistics of consistency index (CI), retention index (RI), and rescaled consistency index (RC). Individual characters were compared on trees using RIs. The RI was chosen as the best measure of character quality because it is a modification of the CI that accounts for the number of steps needed to explain evolution within the transformation series under the worst possible conditions (Wiley et al. 1991). Basically, transformation series with no homoplasy have high index values (e.g., 1.00). Definitions of the indices are provided by Wiley et al. (1991). Tree comparisons using osteological, feather, and combined data were based on strict consensus results that contain only those monophyletic groups that are common to all competing trees. Final results are based on a data matrix of 53 species that matches the original taxa of this study with Chu's (1995) reduced-taxa list. The osteological data matrix of Chu's reduced-taxa list had to be reanalyzed in this study because the taxa list used to compare feather characters was slightly different from his (1995) list, and the exact same osteological character list was not used here because Chu's (1995) character number 11 was deleted from this analysis. Additionally, this study used real outgroups for feather analysis and those species had to be coded for osteological characters.

This study involved too many taxa to permit the use of exact methods that guarantee optimal solutions, so PAUP*'s heuristic approach was employed. Heuristic methods build an initial tree (or set of trees) by the random addition of taxa, and attempt to find shorter trees by carrying out trial rearrangements of the tree (branch swapping). The algorithm may get trapped in local optima, so different approaches were utilized to search for shortest trees. Shortest trees were searched for by carrying out tree bisection and reconnection (TBR) branch swapping on trees constructed with the random addition sequence; completing 100 replications under the random addition sequences, setting the branch-swapping options to save no more than 250 trees per replication; and continuing TBR swapping on the minimum-length trees found during a given replication until all trees had been swapped or the number of trees saved reached the maximum number (MAXTREE) limit of 10,000.

The maximum of 10,000 trees was reached using these constraints in the first analysis of 111 taxa and 38 feather characters. The 100 replications produced 500 trees (two sets of 250); shortest trees were obtained on 2 of the 100 replications. Then, TBR swapping (MAXTREES set to 5,000) was performed on each set of the 250 most-parsimonious trees. Because no overlap occurred between the two sets of trees, all 10,000 trees were used to compute consensus trees. Due to the large number of taxa and the small number of characters, it was expected that numerous equally parsimonious trees would be found. The probability of discovering a single most-parsimonious tree is small with less than two or three characters per taxon (McCracken and Sheldon 1998). Also, exhaustive search strategies that evaluate every possible tree are not useful beyond 11 taxa (Swofford 1991).

FEATHER CHARACTERS

Because of the complexity involved in coding characters, and the fact that microscopic feather characters have never before been used in this type of analysis, conducting the detailed descriptive study of Part 1 was necessary. Observations of characters were made from a population of barbules to assess the range of character variation. All observations were made using LM (100–430×) and coded on contour feather plumulaceous barbs (unless otherwise noted) because these typically show the most diagnostic characters for identification. Plumulaceous feather topography is shown in Figure 4. In cases where species have both pigmented and unpigmented barbs, only pigmented barbs are coded for pigment characters. Microslide preparation is given in the methods section of Part 1. Because some barbs are too long to fit within the ocular micrometer's range and some barbules are difficult to measure accurately on species that have medium-length or long filamentous barbules, a generalized method using the field of view of the microscope was employed here to code barb lengths.

This is the first attempt to utilize multiple microscopic feather characters in a phylogenetic analysis; therefore, characters are selected in a liberal fashion in order to include all possible characters. However, characters are coded conservatively to avoid violating assumptions of character independence and homology.

The following feather characters are used in this phylogenetic analysis:

1. *Subpennaceous region.* The region or area at the very base of some plumulaceous barbs of some contour feathers that is composed of pennaceous-like flattened barbules with hooklet structures on the distal vanule (see extensive definition in Appendix 1 and Fig. 6). If the subpennaceous region is extensive enough to be easily observed at 50×, it is coded as present. If typical plumulaceous barbules are observed all the way to the base of the complete barb, then the subpennaceous region character is absent.

Some variation has been observed in charadriiform birds in the downy barbs of contour feathers that have subpennaceous regions. A somewhat intermediate condition exists between a purely subpennaceous region with flattened, pennaceous-like barbules and the normal plumulaceous types of barbules that have a base and a cylindrical pennulum. The subpennaceous region is coded as intermediate if the very base of the barb has barbules with hooklets on the distal vanule and plumulaceouslike barbules with distinct nodes on the proximal vanule (Fig. 141B). In the intermediate condition, the plumulaceous-like barbules (proximal vanule) are very similar in appearance to the type found elsewhere in the plumulaceous region except they are reduced in size and length. The normal condition that is observed (Fig. 141A) does not have expanded nodes on the proximal barbules of the subpennaceous region. The intermediate appearance of this region is obvious when viewed at 100× because one vanule (proximal) has barbules that appear as reduced plumulaceous types, whereas the other vanule (distal) has distinct hooklets. a = absent; b = present; c = intermediate.

2. *Subpennaceous region pigmentation.* The barbules that make up the subpennaceous region of some contour feathers are pigmented heavily enough to be

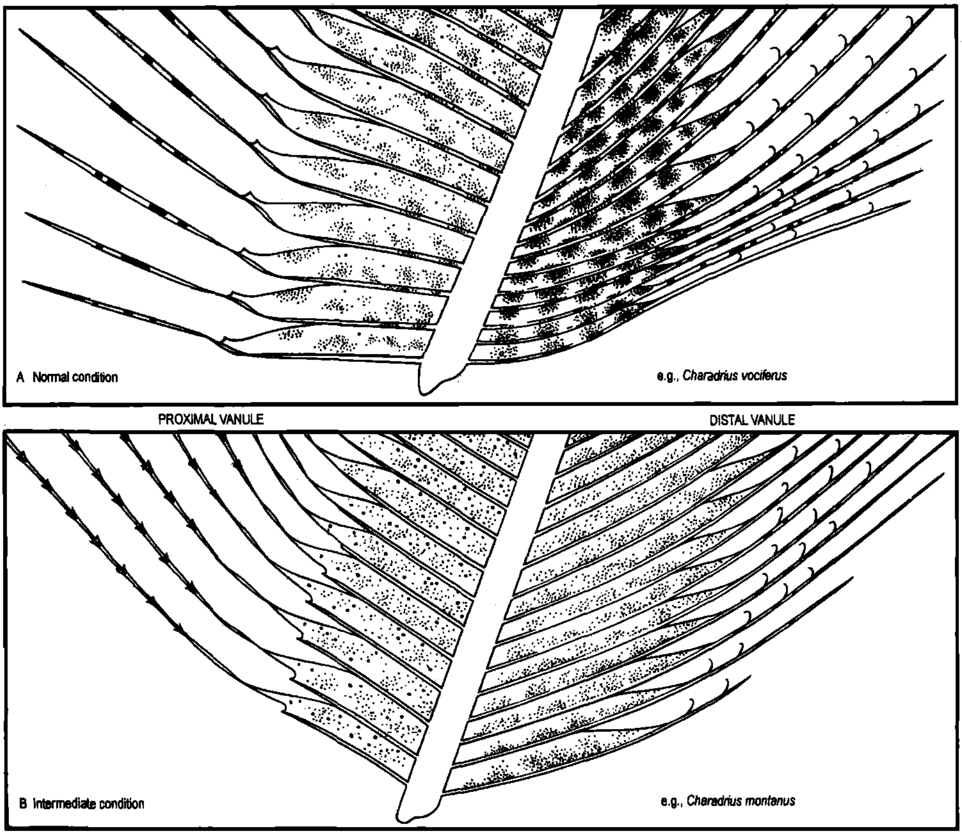


FIG. 141. Subpennaceous region showing (*A*) normal and (*B*) intermediate coding conditions. Note distinct nodes on proximal vanule of *B*. For location of this region, see Figure 6C.

readily observed at 100×. Because slight variation in pigment intensity may be observed between proximal and distal vanules of the subpennaceous region, only extreme or striking differences in vanule pigmentation were coded for a. In species that do not have subpennaceous regions, this character is coded as missing. a = distal vanule more pigmented; b = both vanules equally pigmented; c = both vanules unpigmented.

3. *Subpennaceous length.* The general length of the entire subpennaceous region, from the base of the barb to the point where normal downy barbules are encountered when viewed at 50×. a = short, approximately equal to 25% or less the length of the barb; b = long, considerably more than 25% of the length of the barb; c = very long, at least one half of the length of the barb.

4. *Barbule base pigmentation.* Pigmentation of the straplike base cell(s) of plumulaceous barbules (430×). Sometimes when a subpennaceous region is present and heavily pigmented on a barb, some of the pigment granules may carry over into the base cells of the normal plumulaceous barbules just above that region. In order to avoid confusion of plumulaceous base cell pigmentation with the subpennaceous pigmentation, this character was scored on the plumulaceous

barbules somewhat above the subpennaceous region. This character was scored on the same location of the barb regardless of the presence or absence of subpennaceous regions. 0 = pigment absent; 1 = pigment present.

5. *Barbule base length.* Length of the cell(s) that make up the base or straplike portion of the barbule. Base length is relative to total length of the pennulum when viewed at 100×. Sometimes determining where the base ends and the first nodal cell begins is difficult. However, the flattened, straplike appearance of the base region is usually apparent on plumulaceous barbules and can be used as a guide to where the base ends. The base usually ends just before the first node. This area of the barbule appears straplike because the base is wider and thinner than the more rounded pennulum and twists and flattens during microslide preparation. Base length was not correlated with barbule length in a study of *Charadrius* (Dove 1997). a = short, less than 10% of total pennulum length; b = long, greater than 10% of total pennulum length; c = continuous with pennulum.

6. *Barbule base composition.* The base region of the barbule terminates where the straplike portion of the cell meets elongated cells with swollen or expanded nodes. The base cell(s) is distinguished by a definite cell division that is clearly visible at 430×. However, sometimes another less distinct base scar (Gilroy 1987, and Fig. 138) is located nearer the rachilla on the base that is more difficult to see. Even though this scar needs to be studied further to determine whether it is indeed a true cell wall, it is a character that exhibits variation within Charadriiformes. Because these divisions are visible with LM, the basal cell composition is coded as being either single, multiple, or not visible. On some individuals, barbs had both single-celled and multiple-celled barbule bases, whereas other individuals of the same species showed only one of these characters. Bases of several barbules were examined for this character. a = most bases composed of a single cell; b = most bases composed of multiple cells; c = both single and multiple celled bases on barbules of the same barb; d = not visible.

7. *Barb length.* Length of barb relative to microscopic field of view at 50×. Absolute length of basal barbs of the plumulaceous region is generally not affected by the size of the bird (pers. obs.). Although some large birds in this study are coded as having long barbs (crane), other small birds (Eurasian Woodcock, Buff-breasted Sandpiper) also are coded as having long barbs. The greatest concern in coding this character is to be certain that barbs from the exact same plumulaceous region are being coded across taxa. In a study of North American plovers, Dove (1997) noted increased barb lengths from the umbilical to the distal portion of the plumulaceous feather. a = short, length of barb is less than three times the field of view; b = long, length of barb is more than three times the field of view; c = both short and long barbs.

8. *Barb pigmentation.* Amount of pigmentation or pigmented barbules of the whole barb when viewed at 50×. The basal and some umbilical barbs are examined in this study. a = no pigmentation; b = pigmented throughout or mostly throughout the length of the barb (base to tip); c = pigmented mainly on the proximal part of barb with most of the distal portion of the barb unpigmented; d = both fully pigmented and fully unpigmented plumulaceous barbs; e = both fully pigmented and only half pigmented barbs.

9. *Barbule symmetry.* Nodes on barbules of both vanules appear symmetrical and morphologically similar when viewed at 100× and 430×. 0 = asymmetrical; 1 = symmetrical.

10. *Barbule length.* Length of barbule relative to microscopic field of view at 100×. Barbule lengths are not dependent on the size of the bird; some large birds can have very short barbules (crane) and small birds such as woodcock can have long barbules. Dove (1997) did not find barbule length to be correlated with overall bird size. a = short, barbule length is within, or nearly within, the field of view; b = long, barbule length is well beyond the field of view; c = barbules at base of barb are extremely long whereas barbules at the tip of the barb are extremely short.

11. *Barbule pigmentation.* Amount and location of pigmentation along pennulum of basal barbules (430×). In species that lack pigmented barbs, the barbules must also be unpigmented, so this character must be coded as missing. a = no pigmented nodes or internodes on basal barbules (note: refers only to basal barbules, pigment could be present on barbules of other regions on the barb); b = pigmentation mainly or more heavily at nodes or internodes of the proximal portion of the barbule; c = pigmentation mainly at nodes or internodes throughout the entire length of the barbule.

12. *Node location.* This character refers to the position on the barbule where the majority of expanded nodes are located. Some groups (e.g., ducks) are distinct in having expanded nodes only on the most distal portion of the barbule, whereas others (e.g., gulls) may have expanded nodes only at the proximal portion of the barbule. a = uniform, expanded nodes distinct and visible, similar in appearance, and located along most or all of the barbule's length from proximal to distal portion of the barbule; b = proximal, expanded nodes only on basal part of barbule, nodes are less distinct distally on the barbule; c = unexpanded, nodes unexpanded but visible and uniformly located along the barbule.

13. *Density of nodes per barbule.* Average number of nodes per 0.0025 mm of barbule. Measured using a 1-mm ocular micrometer at basal nodes of barbules (400×). This character allows use of a micrometer because only a small portion of the barbule is measured. Measurements on larger parts of barbs and barbules are extremely tedious and sometimes impossible with LM. 0 = sparse, fewer than 7 nodes per 0.0025 mm; 1 = dense, more than or equal to 7 nodes per 0.0025 mm.

14. *Proximal node shape* (Fig. 142). This character refers to the shape of the nodes only at the proximal portion of barbules. This does not refer to the shape of nodes all along the barbule. Sometimes nodes at the proximal portion of barbules can be unexpanded and nondistinct, whereas distal nodes have elaborate shapes. Because the shape of the node is not always consistent along the length of the barbule each section is coded separately. a = normal, node is slightly wider than internode or intermediately expanded; b = flared or expanded, node is significantly wider than the internode, flares greatly from the pennulum, especially at basal nodes; c = oblong, node is much longer than wide and gently tapers from pennulum; d = straight, node is unexpanded with little distinction between

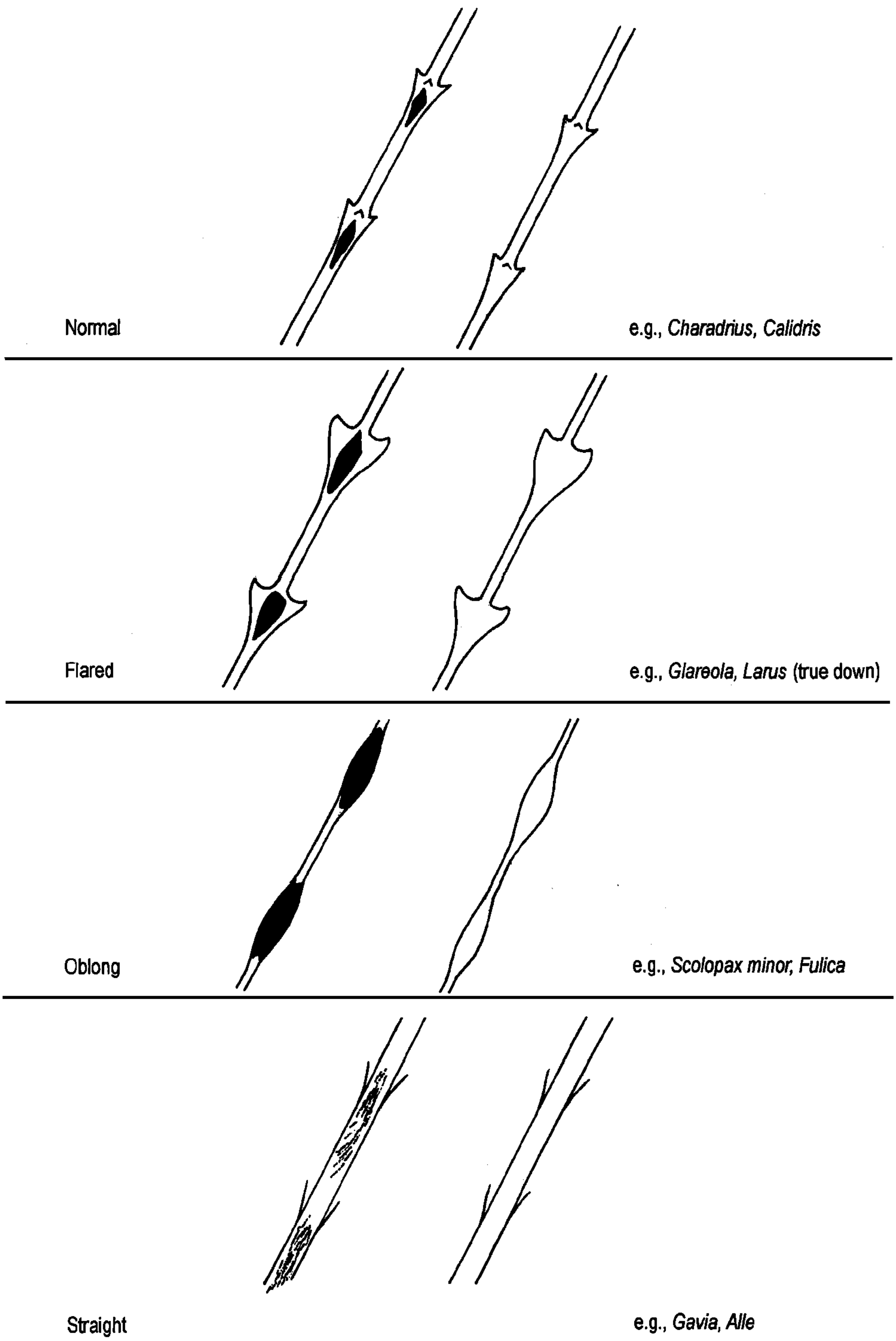


FIG. 142. Node shape: basal node, mid-node, and distal node shapes. Node drawn without pigment (right) to emphasize shape. Reference for scoring character numbers 14, 15, 16, and 31.

node and internode along pennulum, node usually determined by presence of long spines.

15. *Midsection node shape* (Fig. 142). Shape of nodes at midsection of barbules. a = node indistinct, cannot distinguish cell divisions or determine where nodes are located; b = normal, node is slightly wider than internode; c = flared, node is significantly wider than internode; d = oblong, node is much longer than wide; e = straight, node is unexpanded but cell divisions can be distinguished along barbule section.

16. *Distal node shape* (Fig. 142). Shape of nodes at distal section (tip) of barbules. a = node indistinct, cannot distinguish cell division or determine where nodes are located; b = normal, node is slightly wider than internode; c = oblong; node is much longer than wide.

17. *Nodal spines* (Fig. 143). Short to medium-length spines present at nodes when viewed 430×. a = absent; b = present at nodes all along the barbule; c = present mainly at basal to mid-nodes on the barbule; d = some nodes with spines and some nodes on other barbules at the same location without spines.

18. *Nodal prongs* (Fig. 143). Much longer pronglike structures present at nodes when viewed at 430×. 0 = absent; 1 = present at distal nodes on the barbule.

19. *Nodal points* (Fig. 143). Transparent, slightly rounded points instead of prongs or spines at nodes. a = absent; b = present at nodes all along the barbule; c = present mainly at basal to mid-nodes on the barbule; d = present mainly at distal nodes on the barbule; e = some nodes with points and some nodes on other barbules at the same location without points.

20. *Proximal node pigment shape.* Shape of pigmentation at nodes that are on the proximal portion of the barbule. Pigment shapes are defined using Stearn's (1992) chart of simple symmetrical plane shapes and Figure 144. In species that lack pigmented barbs, this character is coded as missing. a = only a few pigment granules at nodes (not illustrated, e.g., *Chionis,* Fig. 82); b = long and constricted (numbers 63 or 45 from Stearn 1992, fig. 19); c = pigment loosely confined at node in diamond shape with many scattered granules at nodes and internodes; d = short and constricted (numbers 64 or 46 from Stearn 1992, fig. 19); e = round (numbers 66 or 48 from Stearn 1992, fig. 19); f = diffuse, pigment not confined to a shape at node but present throughout node and internode; g = pigment not confined to a shape at node but more pigmented at internode, node appears clear.

21. *Mid-node pigment shape.* Shape of pigmentation at nodes located at midsection of barbule. Shapes defined using Stearn's (1992) chart of simple symmetrical plane shapes and Figure 144. In species that lack pigmented barbs, this character is coded as missing. a = only a few pigment granules at nodes (not illustrated, e.g., *Chionis,* Fig. 82); b = long and constricted (numbers 63 or 45 from Stearn 1992, fig. 19); c = pigment loosely confined at node in diamond shape with many scattered granules at nodes and internodes; d = short and constricted (number 64 or 46 from Stearn 1992, fig. 19); e = round (numbers 66 or 48 from Stearn 1992, fig. 19); f = diffuse, pigment not confined to a shape at node but present throughout node and internode may be pigmented more heavily

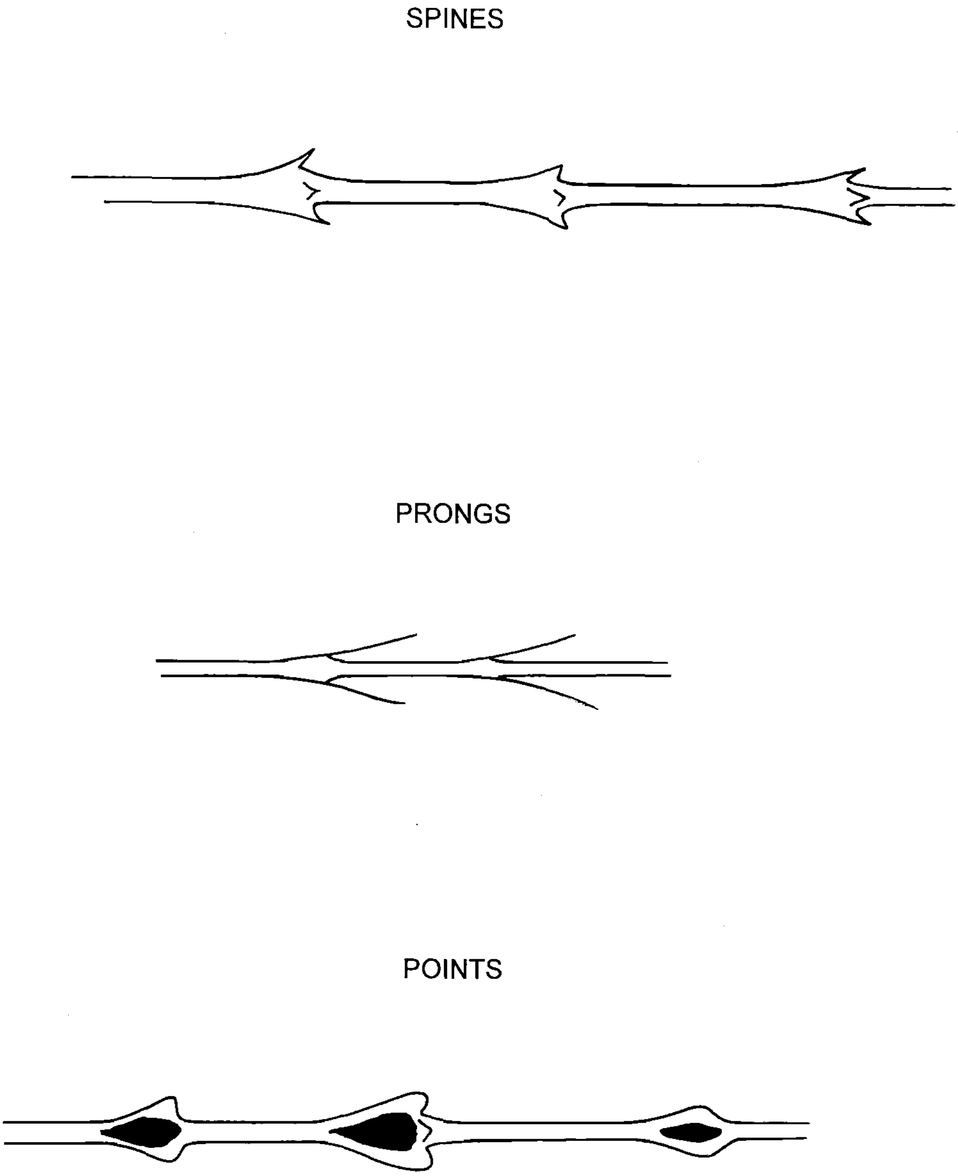


FIG. 143. Node: spines, prongs, and points at nodes. Reference for scoring character numbers 17, 18, and 19.

at node; g = pigment not confined to a shape at node but more pigmented at internode, node appears clear.

22. *Distal pigment distribution.* Pattern of pigmentation at distal nodes on the barbule. In species that lack pigmented barbs this character is coded as missing. a = unpigmented nodes; b = pigment continuous through most distal nodes; c = pigment distinctly confined at distal nodes; d = trailing pigment that nearly connects distal nodes; e = node clear, internode pigmented.

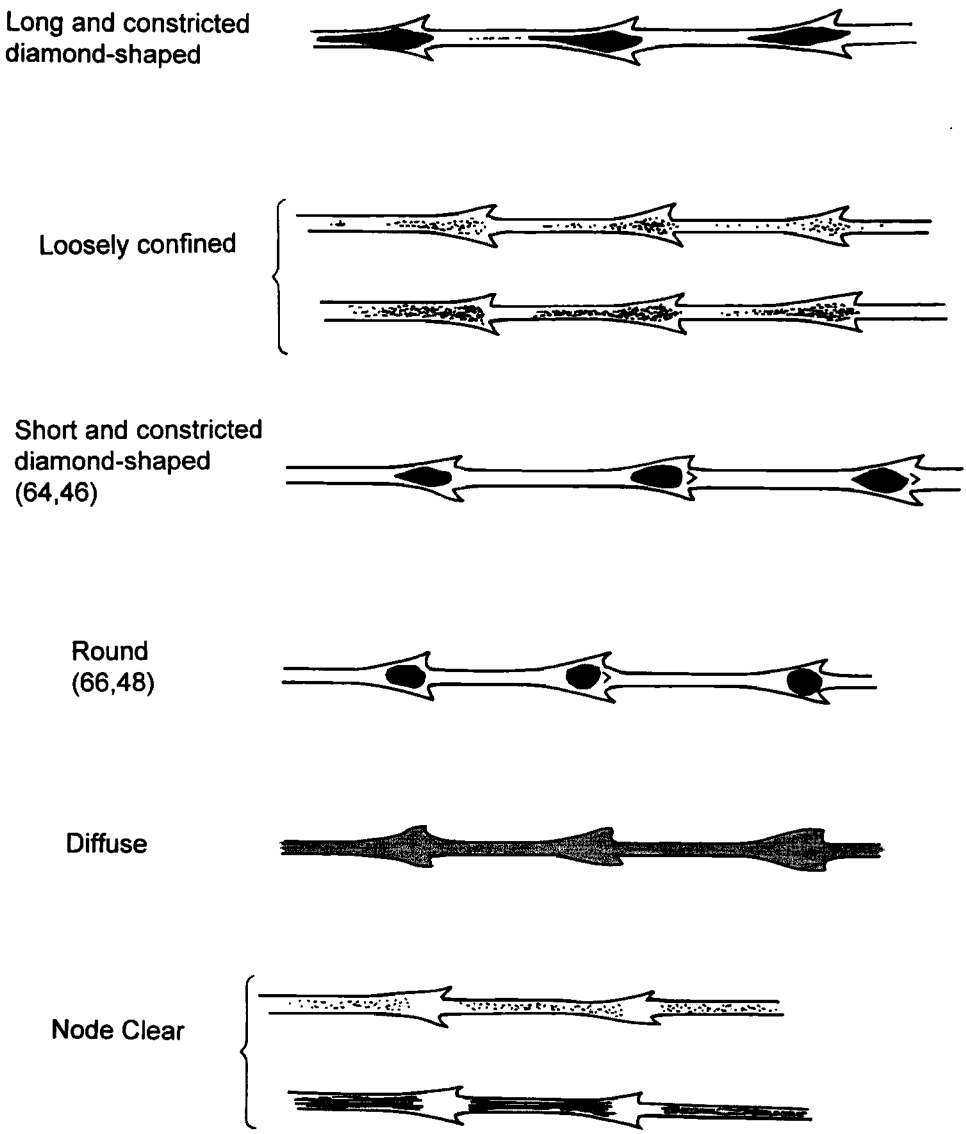


FIG. 144. Pigment: description of pigment shape of basal nodes, mid-nodes, and true down nodes. Reference for scoring character numbers 20, 21, and 32. Numbers in parentheses correspond to Stearn's (1992) chart of simple symmetrical plane shapes.

23. *Nodal pigment intensity at basal nodes.* Intensity, or amount, of pigment at basal nodes. In species that lack pigmented barbs, this character is coded as missing. 1 = lightly pigmented, or scattered granules; 2 = heavily pigmented.

24. *Nodal pigment intensity at distal nodes.* Intensity, or amount, of pigment at distal nodes. Some species may have pigmented nodes on the proximal portion of the barbule but not on the distal portion. In species that lack pigmented barbs, this character is coded as missing. a = absent at distal nodes only; b = lightly pigmented, or scattered granules; c = heavily pigmented.

25. *Pigment color.* The general color of the pigment of the barbule. In species that lack pigmented barbs, this character is coded as missing. a = brown; b = black; c = light reddish-brown.

26. *Morphology of first node.* Morphology of first distinct proximal node (not basal cell) on the barbule. Node is sometimes only slightly expanded, differing in size and appearance from the next distal node (430×). a = node much reduced; b = node similar to other nodes; c = both reduced and expanded first nodes.

27. *Internode pigmentation.* Presence and degree of internodal pigmentation along basal to midsection of the barbule. In species that lack pigmented barbs, this character is coded as missing. a = absent in most internodes or only small amount of intermittent granules; b = stippled; c = heavily pigmented or trailing from node far into internode; d = uniformly pigmented throughout but no distinct granules.

28. *Distal cell length.* Length of distalmost cell on the barbule is at least as long as the cell proximal to it on the barbule (430×). 0 = no; 1 = yes.

29. *Distal cell morphology.* Morphology of distalmost cell on the barbule. The very last cell of some contour feather downy barbules forms a single, pointed cell. However, some distal cells may terminate with many short spines at the tip. 0 = cell terminates in a single-spined point; 1 = cell terminates with multiple-spined points.

30. *True down pigmentation.* This character describes the amount of pigment on barbs of only true down feathers and is coded separately from contour feather down. Variation can exist in the amount of pigment in each downy feather type (contour, true, and afterfeather). a = absent; b = present mostly on proximal to middle part of barb; c = present throughout most of barb.

31. *True down nodes.* Morphology of proximal nodes of true down barbules (Fig. 142). a = node indistinct; b = flared; c = normal; d = both flared and normal nodes.

32. *True down pigment shape.* The shape of the pigment at proximal nodes of true down barbules. Shapes are defined using Stearn's (1992) chart of simple symmetrical plane shapes and Figure 144. In species with unpigmented true down, this character is coded as missing. a = long and constricted (numbers 63 or 45 from Stearn 1992, fig. 19); b = pigment loosely confined in diamond shape with many scattered granules at nodes and internodes; c = short and constricted (numbers 64 or 46 from Stearn 1992, fig. 19); d = round (numbers 66 or 48 from Stearn 1992, fig. 19); e = diffuse, pigment not confined to a shape at node but present throughout node and internode; f = pigment not confined to a shape at node, but present more heavily in internode, node appears clearer.

33. *True down pigmented like contour down.* This character compares nodal pigmentation patterns of true down to those of contour down. Because variation exists in which types of down have similar pigmentation patterns, each down type is compared to the other types for similarity. Characters 33, 34, and 36 are coded to determine if true and afterfeather downs are pigmented similarly to the contour feather down. 0 = no; 1 = yes.

34. *True down pigmented like afterfeather down.* In some cases the true down

may be more similar in pigmentation patterns to afterfeather down than to contour feather down. In species that lack afterfeathers, this character is coded as missing. 0 = no; 1 = yes.

35. *Afterfeather pigmentation.* Presence of pigmented nodes or internodes on barbs of afterfeather. In species that lack afterfeathers, this character is coded as missing. a = pigment absent; b = pigment present mostly on nodes or internodes of proximal barbules; c = pigment present at nodes or internodes throughout the length of barbules; d = pigment present or heaviest at nodes or internodes of distal barbules.

36. *Afterfeather down pigmented like contour feather down.* This character compares nodal pigmentation patterns of the afterfeather down to the contour feather down. In species that lack afterfeathers, this character is coded as missing. 0 = no; 1 = yes.

37. *Villi.* Presence of villi structures on the flattened, straplike base cell(s) of contour plumulaceous barbules. Villi are only located on the base regions of barbules and are morphologically distinct structures. Shorebird villi are found at the very base of the barb on barbules just above the subpennaceous region or on the most proximal barbs of those species that lack subpennaceous regions. Several barbs should be examined for this character. 0 = not found; 1 = present.

38. *Distal prong morphology.* Morphology of the prongs at the distal nodes on the barbule. In species that lack prongs, this character is coded as missing. 1 = prongs on one side of the node are longer on most barbules; 2 = prongs on each side of the node are equal in length on most barbules.

Results

Strict consensus of the 10,000 trees using 111 taxa and 38 microscopic feather characters is given in Figure 145. Although this consensus tree does not include highly resolved groups within the order, or on certain branches, many of the deeper nodes follow traditional classification. In this initial analysis, the best-resolved clade, containing the gulls and terns, depicts the skuas (Stercorariidae) as sister to the rest of that clade. The oystercatcher and avocets form a clade within the "gull" group (with the exception of *Haematopus bachmani,* which has an unresolved relationship in a more basal position on the tree). *Dromas* (Crab Plover), *Chionis* (sheathbill), and *Pluvianus* (Egyptian Plover) are also included in the "gull" clade. The inclusion of these genera in this clade is generally consistent with the results of Strauch (1978), Sibley and Ahlquist (1990), Mickevich and Parenti (1980), and Chu (1995). *Anous stolidus* (Brown Noddy), *Rynchops flavirostris* (African Skimmer), and *Procelsterna cerulea* (Blue Noddy) were not included in the "gull" clade according to feather characters. Sister to the "gull" clade was another that consisted of 12 species of alcids and one outgroup species (loon). Although the relationships of its members are unresolved (except for sister relationship of *Lunda* and *Cepphus*), all species of alcids always group together according to feather structure. The other large part of this tree consists of an assembledge of sandpipers and plovers. Seedsnipes and *Glareola* form a clade within this sandpiper/plover group but other coursers group with *Prosobonia. Pluvianellus socialis* (Magellanic Plover) grouped in a small clade with *Arenaria* (turnstone) and *Calidris bairdii* (Baird's Sandpiper). In this cladistic analysis,

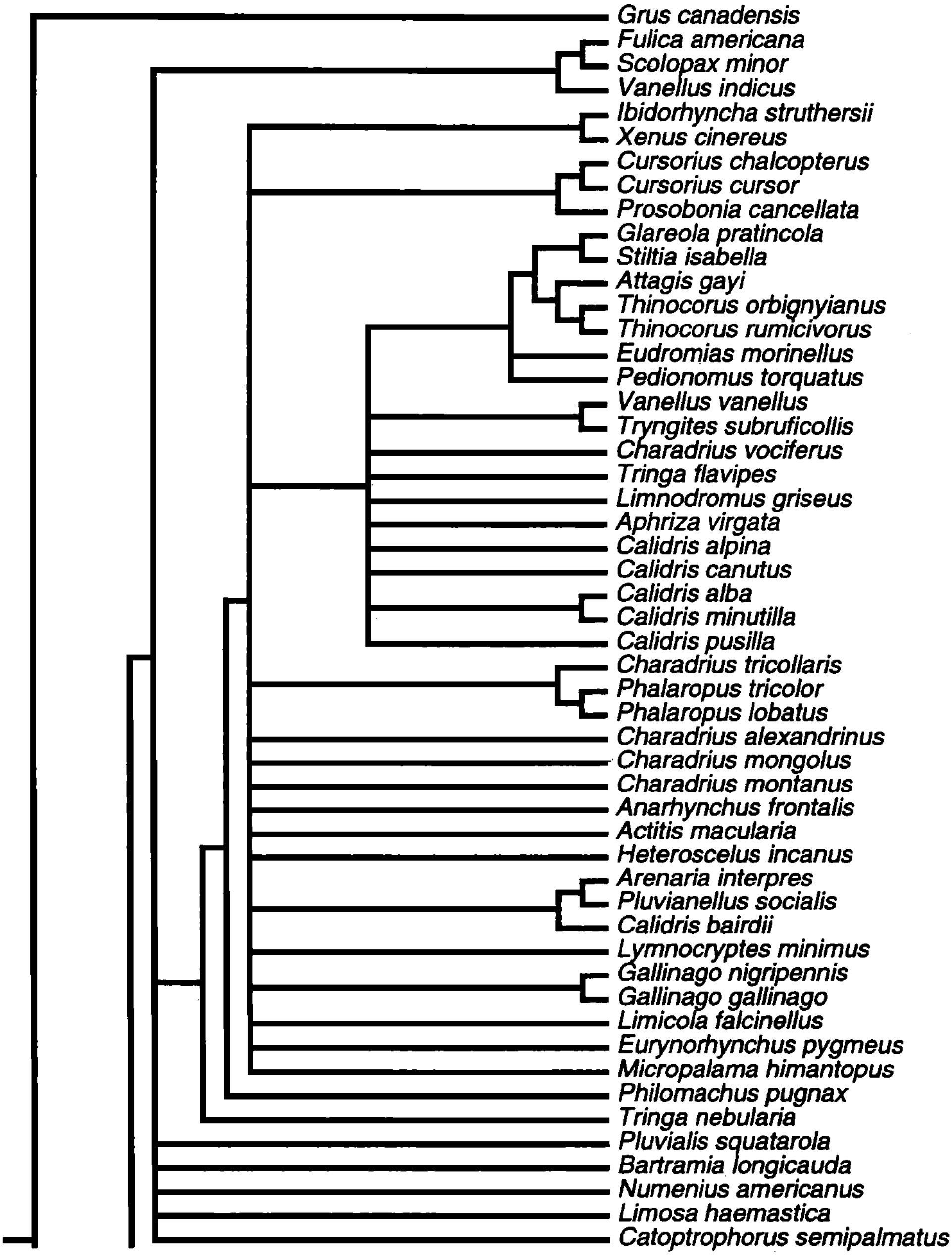


FIG. 145. Strict consensus of a sample of 10,000 trees using 111 taxa and 38 microscopic downy feather characters.

feather structure places *Pedionomus* (Plains-Wanderer) and *Eudromias* (dotterel) as sisters to seedsnipes and pratincoles. *Vanellus* (lapwings) are scattered throughout this tree as they are in the tree of Mickevich and Parenti (1980). *Grus canadensis* (Sandhill Crane) was the most basal outgroup; sandgrouse grouped with

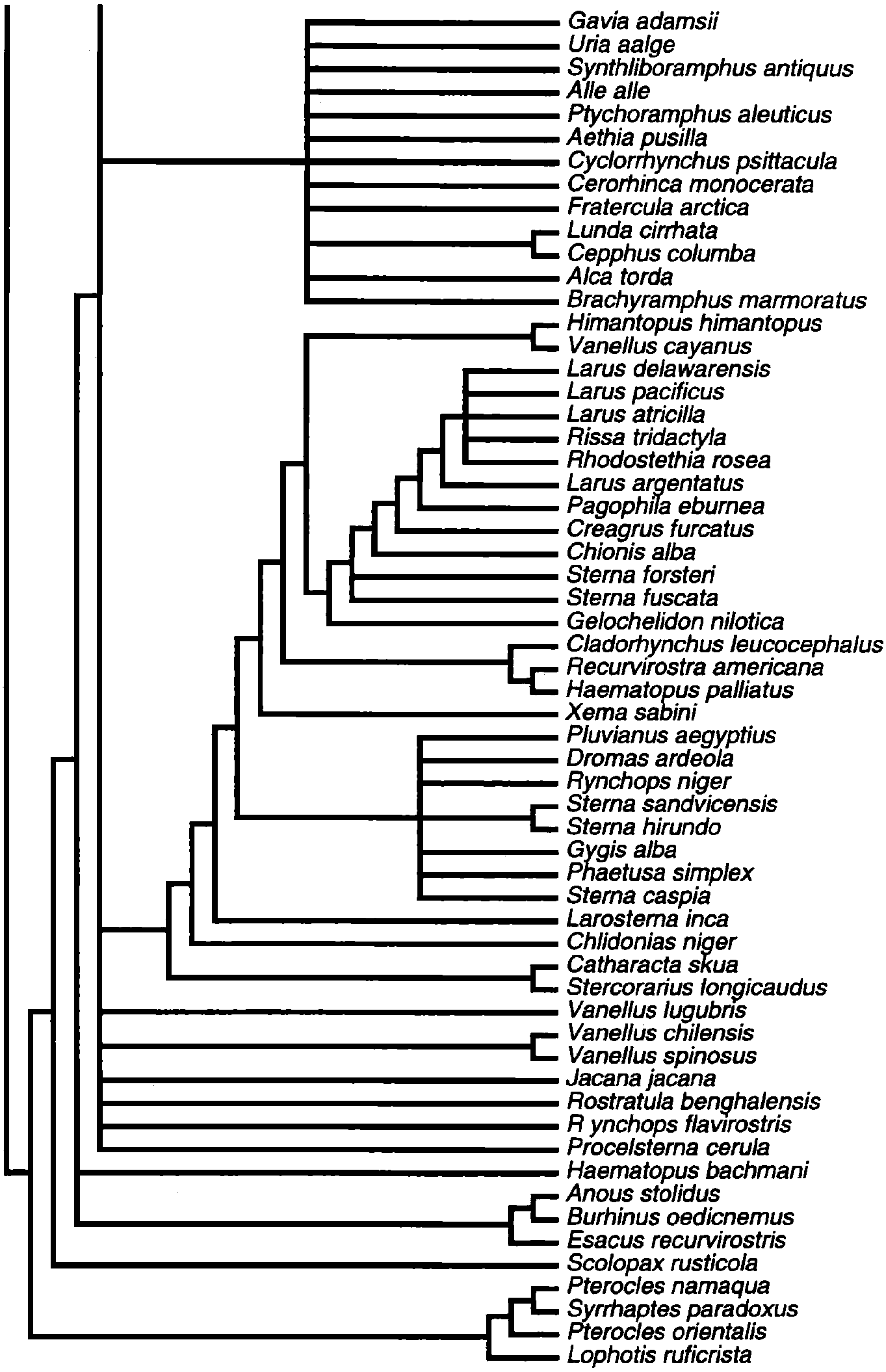


FIG. 145. Continued.

Lophotis ruficrista (a bustard) in the secondmost basal clade. The coot grouped in a small clade with *Scolopax minor* and *Vanellus indicus*.

Although this first analysis gave unsatisfactory resolution at deeper nodes of the tree and never found a single shortest tree, it provided some positive initial insights on the usefulness of feather characters in phylogeny reconstruction. Because some of the traditionally recognized clades were recovered, the parsimony analysis was continued in an attempt to find fewer most-parsimonious trees.

The second set of analyses involved matching the taxa of the initial data set to those used by Strauch (1978). This reduced the number of taxa to 90 and allowed use of 68 skeletal characters from Strauch's osteological study. Analyses were conducted on feather and osteological characters alone, and on all characters combined.

When feather characters (38 total) were analyzed alone with this taxa list, 3,750 trees with 15 apparent islands of 250 trees were hit one time each. The osteological analysis (68 characters) of this taxa list resulted in 7,000 shortest trees with 28 apparent islands hit one time each.

In the analysis using all 106 characters (feather and osteological), 22 apparently separate islands of 12–250 trees each were hit one to three times. The number of equally shortest trees was 4,770. Shortest trees were obtained in 29 replications.

Consensus trees for the second set of analyses using Strauch's taxa list are not presented here because this set of runs did not produce significantly better-resolved or fewer numbers of minimum-length trees than the initial data set. However, the total-evidence tree using Strauch's data supported three main clades (plovers and stilts; terns, gulls, noddies, and skuas; sandpipers, seedsnipes, and *Jacana jacana*), with relationships among those clades unresolved. This analysis, with added skeletal characters, did not reconstruct the same unexpected group of taxa that were noted in the first analysis using only the feather characters (e.g., a clade of *Fulica, Scolopax minor,* and *Vanellus indicus*). This analysis also provided insight to the utility of combining osteological and feather characters. The main difference in the combined-character analysis and the trees in the initial data set is that the initial analysis using feather characters alone resulted in the placement of the sandpipers on the same clade with the plovers (except *Vanellus*). This is not congruent with the skeletal tree in the second set of analyses, which places plovers with the Ibisbill and stilts, not with sandpipers. Because the second set of analyses also produced high numbers of equally parsimonious trees, the list of taxa was further reduced in hopes of obtaining fewer trees.

The third set of analyses contained a subset of the taxa used by Chu (1995) in his reduced-matrix analysis of Strauch's osteological characters. Taking into account Chu's revised characters, this resulted in 53 taxa and 106 characters (feather and osteological). Again, analysis was conducted on independent and combined data sets. Because this set of analyses resulted in finite numbers of shortest trees, the final results of character analysis are based on these runs.

Osteological Results

This analysis employed the same constraints as the initial data set, except this time MAXTREES was set to 500. The strict consensus of the 284 most-parsimonious trees is shown in Figure 146. Five islands of 3–203 trees were found. Trees of minimal length (303) were found in each of 100 replications. Tree indices

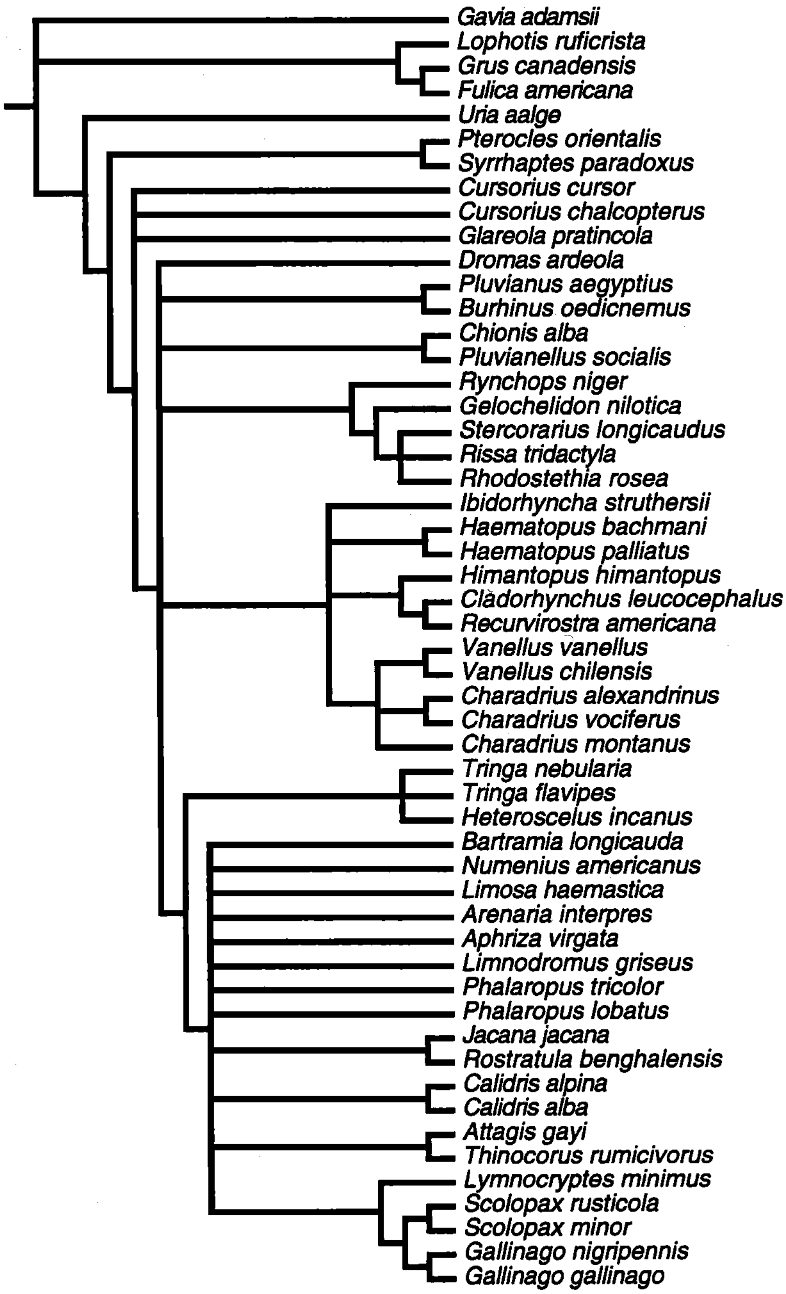


FIG. 146. Strict consensus of 284 trees using 53 taxa and 68 osteological characters.

are provided in Table 2. Outgroups consist of *Lophotis, Grus,* and *Fulica* (Gruiformes), all forming one clade with an unresolved relationship to *Gavia* (loon). *Uria aalge* (Alcidae) is next on the ladder and is sister to a sandgrouse clade, which is sister to the rest of the charadriiform clade. The rest of the taxa are in clades whose relationships to one another are unresolved. The three main ingroup

TABLE 2. Tree indices for skeletal, feather, and total-evidence (combined) trees.

Index*	Skeleton	Feather	Combined
CI	0.275	0.231	0.292
RI	0.576	0.467	0.610
RC	0.158	0.108	0.178

* CI = consistency index; RI = retention index; RC = rescaled consistency index.

clades are part of a polytomy with *Dromas,* a *Pluvianus/Burhinus* clade, and a *Chionis/Pluvianellus* clade. The first major clade consists of *Rynchops* (a skimmer), *Gelochelidon* (a tern), *Stercorarius* (a jaeger), *Rissa* (a kittiwake), and *Rhodostethia* (a gull), with the skimmer as the most basal member. The second major clade is composed of a loosely resolved group of Recurvirostridae (stilts), Charadriidae (plovers), Haematopodidae (oystercatchers), and Ibidorhynchidae (Ibisbill); and the third and most structured clade is a grouping of sandpipers mixed among Thinocoridae (seedsnipes), and a jacana plus *Rostratula* (a painted-snipe). The best-resolved group in this clade is that of *Lymnocryptes minimus* (Jack Snipe), snipes, and woodcocks.

The results of this analysis are not consistent with those reported by Chu (1995) even though the same characters (minus character 11) and many of the same taxa are used here. His analysis yielded much better resolution at deeper nodes (Fig. 2) and consisted of three clades: alcids (sister to the rest of the order); skuas, gulls, plovers, and pratincoles on one clade; and thick-knees, sandpipers, and seedsnipes on the other. An additional difference in this analysis from Chu's is that he used a hypothetical ancestor rather than actual outgroups.

DOWNY FEATHER RESULTS

Downy feather characters were subjected to the same constraints as the osteological characters. In this analysis, 16 apparently separate islands with 72–500 trees each were found between 1 and 12 times each. Shortest trees (length = 265) were obtained in 67 of 100 runs. In this analysis, 6,646 shortest trees were found. A strict consensus is shown in Figure 147 and tree indices are reported in Table 2.

A basal polytomy of various taxa including outgroup species, *Haematopus bachmani* (Black Oystercatcher), *Vanellus chilensis* (Southern Lapwing), *Jacana jacana* (Wattled Jacana), *Rostratula* (painted-snipe), *Bartramia, Numenius, Limosa, Scolopax* (sandpipers), *Stercorarius* (jaeger), *Burhinus oedicnemus* (Eurasian Thick-knee), and five other clades, each with two or more taxa, was recovered in this analysis. The best-resolved and most-derived clade consists mainly of sandpipers, plovers, seedsnipes, and pratincoles. In this clade, the best-resolved group is the relationship of *Attagis/Thinocorus/Glareola* clade as the sister to the coursers. Another major clade that is less resolved consists of stilts and avocet/*Haematopus palliatus* (oystercatcher)/*Pluvianus* (Egyptian Plover)/*Dromas* (Crab Plover)/skimmer, gulls, a tern, and *Chionis* (sheathbill). A smaller clade shows *Lophotis* (a bustard) as sister to the sandgrouse. Feather characters consistently group *Gavia* (loon) with *Uria aalge* (Common Murre), and *Fulica* (coot) with *Scolopax minor.*

The feather tree is mainly consistent (except *Numenius, Limosa, Scolopax*) with

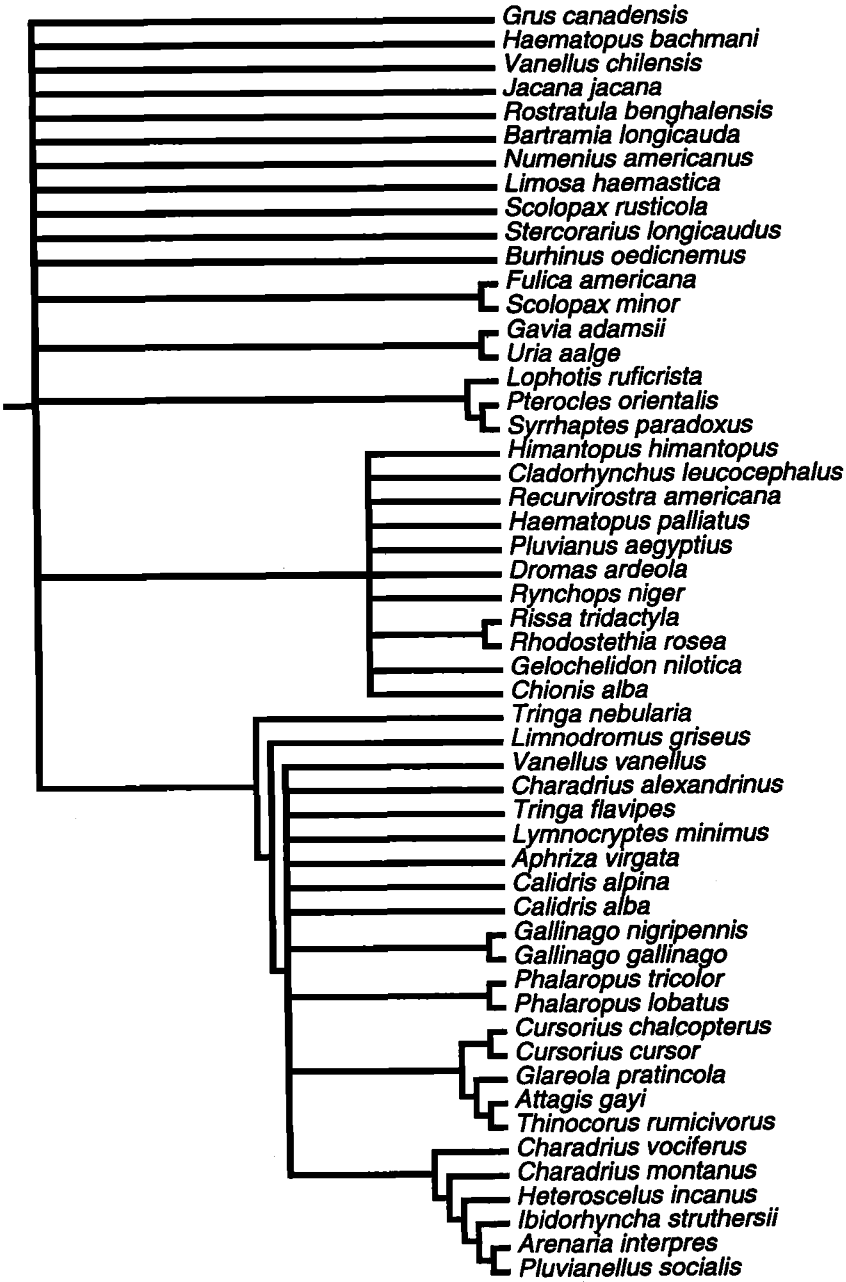


FIG. 147. Strict consensus of 6,646 trees using 53 taxa and 38 microscopic downy feather characters.

the skeletal tree in placing stilts, avocet, an oystercatcher, gulls, a tern, and a skimmer in a clade separate from the sandpiper clade. The feather tree is incongruent with the skeletal tree in placing the sandpipers and the plovers in the same clade. Osteological characters place plovers with avocet and oystercatchers.

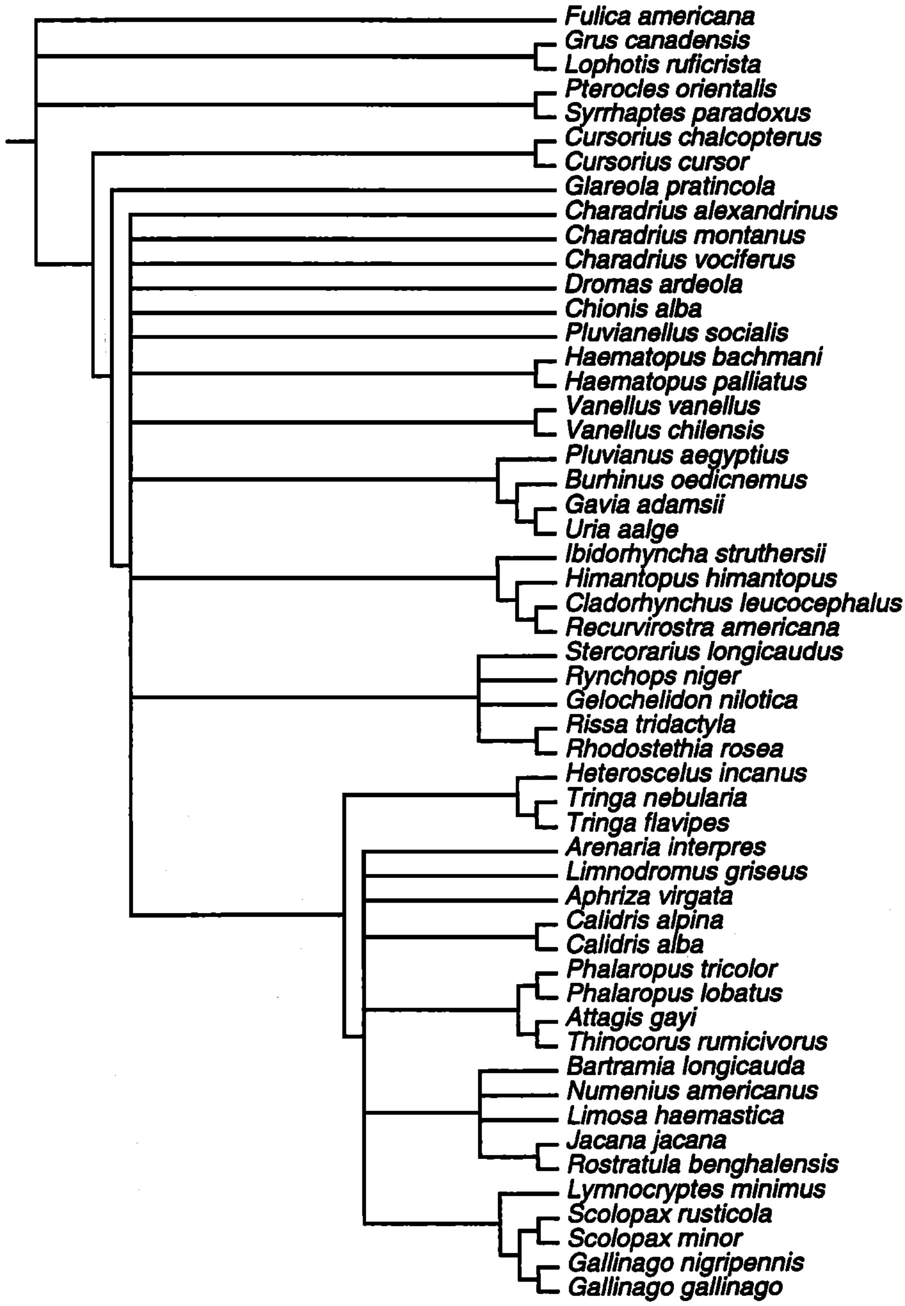


FIG. 148. Strict consensus of 154 trees using 53 taxa and 106 characters (38 feather; 68 osteological).

TOTAL-EVIDENCE RESULTS

When all characters were combined, 154 trees with four islands from 24 to 56 trees each were found. Shortest trees (length = 641) were obtained in 54 of 100 replications. The strict consensus tree is shown in Figure 148. Tree consistencies are reported in Table 2. The total-evidence tree was consistent with ingroup monophyly except that *Gavia* (loon) grouped with *Uria* (murre). Two of the three coursers (*Cursorius chalcopterus, C. cursor*) in this study are sisters to the rest of the order; sandgrouse are placed among the outgroups. Most ingroup members are part of a large polytomy. Within this polytomy, a small clade consisting of *Uria, Gavia, Burhinus*, and *Pluvianellus* is well resolved, as is another small clade of stilts/avocet. Another clade is composed of gulls and a tern, a skua, and a skimmer. The largest clade in the polytomy consists of sandpipers, seedsnipes, and a jacana with the tribe Tringini as the sister to that clade. *Lymnocryptes minimus* is resolved as the sister to the snipes and woodcocks.

The combined analysis is consistent with the skeletal tree in holding together the sandpipers and seedsnipes. However, the sandpiper/seedsnipe clade is better resolved than that portrayed in the skeletal tree alone and supports the idea that the added feather characters help resolve these relationships. On the other hand, the relationships of the plovers, "gull group," alcids, and thick-knee break down in the combined analysis when compared to the skeletal tree, suggesting that feather characters are conflicting with osteological characters here. Indices reported in Table 2 show that the total-evidence tree has higher CI, RI, and RC values than either of the other two separate analyses.

CHARACTER ANALYSIS

The RI was compared for all characters on the skeletal, feather, and total-evidence trees (Table 3). Skeletal characters were compared on feather trees and feather characters were compared on the skeletal trees. All characters were compared on the total-evidence tree.

Table 4 reports character scores for character performance on each tree. On the skeletal tree, 78.4% of the characters have a best score of 0.500 or better and 38.4% of the characters have 0.800 or better. Three of the skeletal characters (character numbers 64, 66, 92) are not included in the RI output because they are uninformative. When feather characters are fit onto the skeleton tree, 8 of the 36 informative feather characters (22.2%) have a score of 0.500 or better. These feather characters include no. 2, subpennaceous region pigmentation; no. 8, barb pigmentation; no. 10, barbule length; no. 12, node location; no. 19, nodal points; no. 22, distal pigment distribution; no. 26, morphology of first node; and no. 27, internode pigmentation. However, none of the feather characters has a score higher than 0.615 (no. 12) on the skeletal tree.

Approximately 83% of the feather characters have a score of 0.500 or better on the feather trees. However, only 13.8% (5 of 36) of these characters are 0.800 or better. Two feather characters are autapomorphic (barbule symmetry, distal cell morphology) and one shows no change (distal cell length). Of the 65 informative skeletal characters, 18 scored 0.500 or better on the feather tree (27.6%) and 1 character scored better than 0.800.

The combined-character tree had feather character indices of 0.500 or better

TABLE 3. Retention indices for best scores of each character on each tree. Characters 1–38 are feather characters; characters 39–106 are skeletal characters.

	Tree				Tree		
Character	Skeleton	Feather	Combined	Character	Skeleton	Feather	Combined
1	0.313	0.500	0.500	54	0.800	0.400	0.800
2	0.591	0.818	0.682	55	0.833	0.167	0.667
3	0.333	0.417	0.333	56	0.792	0.708	0.792
4	0.417	0.833	0.500	57	1.000	0.500	1.000
5	0.375	0.625	0.500	58	0.667	0.667	0.667
6	0.316	0.421	0.421	59	0.842	0.316	0.737
7	0.300	0.450	0.350	60	1.000	0.333	1.000
8	0.500	0.688	0.625	61	0.870	0.478	0.826
9	0/0	0/0	0/0	62	0.333	0.000	0.000
10	0.500	0.500	0.500	63	0.667	0.250	0.583
11	0.333	0.333	0.667	64	—	—	—
12	0.615	0.615	0.692	65	0.500	0.000	0.500
13	0.471	0.706	0.588	66	—	—	—
14	0.250	0.750	0.500	67	0.667	0.250	0.583
15	0.167	0.667	0.500	68	0.538	0.385	0.308
16	0.300	0.500	0.500	69	0.571	0.476	0.429
17	0.407	0.593	0.519	70	0.400	0.100	0.300
18	0.000	0.667	0.333	71	0.500	0.000	0.500
19	0.500	0.750	0.667	72	1.000	0.300	0.900
20	0.412	1.000	0.647	73	0.417	0.417	0.333
21	0.478	0.783	0.609	74	0.615	0.538	0.462
22	0.522	0.696	0.696	75	1.000	0.400	0.800
23	0.222	0.889	0.556	76	0.750	0.375	0.875
24	0.231	0.538	0.231	77	0.880	0.640	0.880
25	0.143	0.714	0.429	78	0.333	0.333	0.667
26	0.567	0.700	0.600	79	0.667	0.222	0.556
27	0.526	0.632	0.474	80	1.000	0.571	1.000
28	—	—	—	81	0.957	0.652	0.913
29	—	—	—	82	0.545	0.364	0.545
30	0.167	0.500	0.167	83	0.750	0.625	0.750
31	0.400	0.600	0.400	84	0.500	0.000	0.000
32	0.304	0.783	0.478	85	0.000	0.000	0.000
33	0.417	0.667	0.500	86	0/0	0/0	0/0
34	0.250	0.500	0.250	87	1.000	0.500	1.000
35	0.400	0.700	0.500	88	0.467	0.467	0.600
36	0.429	0.571	0.429	89	0.333	0.333	0.333
37	0.200	0.400	0.200	90	0.000	0.000	0.000
38	0.000	1.000	1.000	91	0.667	0.444	0.778
39	0.750	0.375	0.750	92	—	—	—
40	0.500	0.000	0.333	93	0.250	0.250	0.500
41	0.846	0.615	0.846	94	0.600	0.300	0.550
42	0.857	0.429	0.762	95	0.286	0.286	0.286
43	0.944	0.556	0.944	96	0.300	0.200	0.300
44	0.889	0.333	0.667	97	0.846	0.583	0.692
45	0.500	0.000	0.250	98	0.688	0.312	0.688
46	0.636	0.364	0.636	99	0.600	0.280	0.600
47	0/0	0/0	0/0	100	0.800	0.560	0.800
48	0.833	0.667	0.833	101	0.778	0.444	0.741
49	0.857	0.571	0.857	102	1.000	1.000	1.000
50	0.882	0.412	0.882	103	0.000	0.000	0.000
51	0.500	0.000	0.000	104	0.667	0.333	0.667
52	1.000	0.571	1.000	105	1.000	0.500	1.000
53	0.900	0.450	0.900	106	0.667	0.333	0.667

TABLE 4. Performance of characters (retention indices) on each separate tree and on total-evidence tree. Parentheses indicate total number of characters. Thirty-eight feather characters and 68 osteological characters were used.

Tree	Best score (RI)*	
	0.500	0.800
Skeleton		
Skeleton characters	78.4% (51)	38.4% (25)
Feather characters	22.2% (8)	0
Feather		
Skeleton characters	27.6% (18)	1.5% (1)
Feather characters	83.3% (30)	13.8% (5)
Total-evidence		
Skeleton characters	72.3% (47)	32.3% (21)
Feather characters	61.1% (22)	2.7% (1)

* RI = retention index.

for 61.1% of the feather characters and 72.3% of the skeletal characters. However, skeletal characters fare much better with 32.3% of these characters having RIs of 0.800 or better, whereas only 2.7% (1 of 36) of the feather characters score this high on the combined tree.

The highest tree indices are reported on the total-evidence tree (Table 2). Although skeletal tree scores are only slightly higher than the feather tree scores, resolution in the deep parts of the total-evidence tree resembles resolution in the deep parts of the skeletal tree, and differs from the lack of resolution at the base of the feather tree. Therefore, in the total-evidence analysis, the skeletal characters seem to be playing an important role in resolving deep parts of the tree.

The main differences in the skeletal and feather trees is in the placement of the plovers. The skeletal characters place the plovers in the same clade as the oystercatchers and stilts, whereas the feather characters place most of the plovers within the sandpiper/seedsnipe clade. The suggestion that plovers are more closely related to sandpipers than gulls is consistent with traditional taxonomy (e.g., Lowe 1931; Wetmore 1960), but differs from the recent analyses of Chu (1995) and Sibley and Ahlquist (1990). Björklund (1994) reanalyzed some of the same taxa and characters that Strauch (1978) used and found the sandpipers and plovers to form a clade, each being monophyletic in respect to the other. Feather characters show strongest resolution for Thinocoridae (seedsnipes) and Glareolidae (coursers), and for placing the *Lophotis* (a bustard) in the same clade with Pteroclidae (sandgrouse), but feather characters also fully resolve a *Arenaria/Pluvianellus/Ibidorhyncha/Heteroscelus/Charadrius montanus/C. vociferus* clade. Skeletal and feather trees are congruent in placing the stilts and oystercatchers in the same clade, and in grouping the two snipes and the two sandgrouse.

DISCUSSION

Previous studies on the variation of plumulaceous feather characters, such as those by Chandler (1916) and Brom (1991), are broad-based surveys that effectively describe the variation between major groups of birds. However, these studies lack the in-depth, detailed descriptions of intrafamilial variation within orders that are necessary to fully assess the true variation of feather characters. Part 1 of this study involved examination of downy feather characters of many or in some cases, all species within each of the families of Charadriiformes. The importance of such a baseline study is revealed in the results of that study: the discovery of different microstructures and pigmentation patterns in different down types, the description and discovery of villi on certain species of shorebirds, the wide range of variation that is evident in some groups (scolopacids), and the consistency of feather microstructures in others (alcids, gulls).

Character selection and coding was the most difficult aspect of this phylogenetic analysis. The characters used here possibly could be coded in a more liberal fashion, or some multistate characters possibly could be separated and made binary. Characters used in this study may or may not be applicable to other groups of birds and additional characters may be discovered in other groups. Conducting searches for characters is best done using the methods employed in this study, that is, a thorough analysis of as many species as possible. For feathers, the search for characters is best done using LM.

The relationships of scolopacids and charadriids using the feather character data are in contrast to osteological results of Chu (1995) and DNA analysis of Sibley and Ahlquist (1990). However, analysis of osteological characters in this study did not yield the same results as those of Chu (1995), even though most of the same taxa and most of the same characters were used in the same type of analysis. This could be due to the use of real outgroups in this study as opposed to a hypothetical ancestor, or to the use of a slightly different taxa list. Chu's study used more than 73 taxa; this study used 53 of those same taxa for osteological tree analysis.

CONVERGENCE

Although the results of this study support the idea that microscopic feather characters are helpful in tracking phylogenetic relationships, some inconsistencies are noted between the results of the feather analyses and traditional classification of Charadriiformes. At least one of these inconsistencies (loon and alcids) that is based on feather analysis is most probably due to convergence. Although Storer (1960) suggested that loons were derived from the common ancestor of the charadriiform lineage, the similarities observed in feather characters are most likely due to similar environmental effects on feather structure. Loons and alcids, together with penguins, grebes, and some other diving birds all have very similar plumulaceous microstructures. The feather characters that link these seemingly unrelated taxa are simplified or nonexpanded nodal structures on barbules with long, fringelike prongs that are located at nodes on the distal end of the barbule (Figs. 105, 110). These features are also noticed in varying degrees in other water-dwelling species (e.g., boobies, pelicans, cormorants, and anhingas). Diving ducks generally do not have the same microscopic structures observed here (with the exception of *Biziura lobata* [Musk Duck], which does not exhibit typical nodal morphology of other Anseriformes). This provides microscopic evidence of convergence in feather structures of plumulaceous barbules and strongly implies a functional adaptation for nodal structures. In order to perform deep dives, birds have anatomical adaptations that prevent buoyancy of their normally light and airy bodies. An example of this is noted in loons, auklets, and penguins, which have more dense, solid bones that allow them to dive deeper than if they had the pneumatized skeleton of most other birds (Ehrlich et al. 1988). The simplification in plumulaceous feather structures observed in these diving birds could be another adaptation that prevents buoyancy. Penguins have the ability to flatten and compress the external plumage (pennaceous feathers) to form a water-tight barrier to the skin when diving (Williams 1995). Additionally, diving penguins can squeeze air out of their feathers as they enter the water, leaving a fine stream of air bubbles in their wake. The microscopic feather structures described here might greatly facilitate air flow out of the downy insulatory layer of feathers. This microstructure is in contrast to an extremely enlarged node in other species, which probably acts to trap air between nodes making loss of air more difficult.

The true function of the various nodal structures of plumulaceous barbules is unknown. However, if the expanded nodal structures act to trap air and provide insulation, and simplified nodal structures allow quick dispersion of air that otherwise would remain trapped behind the nodes, then this speculation of functional adaptations in nodal morphology requires further study in other groups of birds. If this is a case of homoplasy due to convergence, the use of feather characters in phylogenetic analyses is not nullified because all types of morphological data exhibit some degree of homoplasy.

CONCLUSIONS

The phylogenetic significance of microscopic feather characters has been suggested since Chandler's (1916) time. However, without rigid empirical methods of testing multiple characters simultaneously, researchers could only speculate about the adaptive or evolutionary meaning of those characters. Additionally, examinations of pterylosis by Nitzsch (1840) and of pennaceous feather structure by Mascha (1904) concluded that the taxonomic distribution of the feather characters used in their studies did not lead to natural classifications of birds. Even after Chandler (1916) presented his preliminary phylogenetic hypothesis of bird relationships based on feather characters, the field of epiphyology remained silent for many years. It was as though systematists had written off the possible importance of feather characters to the study of avian systematics and evolution. A recent quote by Sibley and Ahlquist (1990:434) reveals the attitude that still prevails among some scientists concerning feather characters: "It seems clear that feather structure is a flimsy basis for speculations about phylogeny." Unqualified statements such as this, in addition to few descriptive studies on the variation of the plumulaceous microscopic structures within and among groups of birds, have led researchers to look elsewhere for phylogenetically informative characters (osteology, myology, vocalizations, molecules). However, the preliminary work of Reaney et al. (1978), Brom (1991), and Dove (1994, 1997, 1998b) on plumulaceous feather structure and Chu (1998) on integumentary characters continues to show that definite synapomorphies exist among closely related groups of birds using these characters. Until now, the possibility that microscopic feather characters are tied to genealogic relationships has never been thoroughly investigated using empirical methods such as parsimony analysis.

This study has shown that feather characters may be used to infer phylogenetic relationships. The results of this study suggest that these microscopic feather characters are best utilized in combination with other morphological data (e.g., skeletal data). In the character analysis part of this study, feather character RIs were similar to those of skeletal characters. Additionally, feather tree indices and character scores were lower but comparable with those obtained from skeletal trees. These results are consistent with Chu's (1998) study comparing osteological and integumentary (plumage and molt patterns, soft-part colors) characters to show that the latter perform comparatively well relative to the former. Microscopic feather characters are good at resolving relationships of some groups (sandpipers) and therefore complement osteological characters well in a combined analysis. In this study, the interpretation of better performance of skeletal characters may be complicated by the fact that the feather characters contain a higher proportion of multistate characters, and that fewer feather characters were available for analysis.

It is time for avian systematists to stop the casual dismissal of using nontraditional characters for phylogenetic analysis and recognize that unexplored data sets such as these, previously assumed to be a "flimsy basis for speculations about phylogeny," are worthy of re-examination. Until the characters are tested in a phylogenetic format, using empirical methods, the value of these characters cannot be determined. This study supports the use of microscopic plumulaceous feather characters in phylogeny reconstruction and shows that these characters are not dramatically more homoplasious than osteological characters.

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APPENDIX 1

FEATHER TERMINOLOGY

Because general feather terms are not uniform among sources, the definitions used in this monograph are provided below. Terms and definitions have been compiled from Chandler (1916), Lucas and Stettenheim (1972), and those most commonly used by Laybourne and Dove (pers. comm.).

Afterfeather. Secondary structure of contour feathers that originates on the ventral side of body feathers at the superior umbilicus. Present on feathers of most birds but sometimes absent or vestigial. Resembles main feather in having shaft with vanes on each side but is always downy in appearance and texture. Seven different types of afterfeathers are described in Lucas and Stettenheim (1972:253–255). Proposed function is to provide additional insulation.

Afterfeather down. The downy barbs of the afterfeather. Microscopic characters of afterfeather down are usually more similar to true down than to contour feather down.

Aftershaft. Main stem or rachis of afterfeather. Also called hyporachis. Chandler (1916) used the term aftershaft to refer to the complete afterfeather (shaft plus vanes); here it is used to designate only the rachis of the afterfeather.

Apteria. Featherless or bare spaces between or among the feather tracts of birds.

Barb. Primary branch of rachis. Barbs are further divided into barbules. Pennaceous barbs are stiff and collectively form the feather vane. Plumulaceous (downy) barbs are soft and fluffy and are located at the bases of most contour feathers.

Barbule. Smallest division of a feather. Branches off the rachilla and collectively forms a vanule. Divided into a base and a pennulum. Downy barbules have diagnostic microcharacters that aid in the identification of some groups of birds.

Basal cell. The first cell of the base of the plumulaceous barbule (see base).

Basal plumulaceous region. The plumulaceous region of the contour feather that is just above the umbilical region. This region and the umbilical region usually contain barbs that have the most diagnostic barbule characters.

Base. The most proximal portion of the barbule that attaches to the rachilla. Usually delineated by a distinct cell division just before the pennulum. The barbule base is composed of a basal cell or fused cells that are usually flattened and straplike in appearance. This region has also been referred to as the base region, basal cell, base of pennulum, ventral lamella, and ventral flange.

Calamus. Very basal end of quill. Mostly implanted in the feather follicle; divided from rachis at the superior umbilicus.

Contour feather down. The plumulaceous region or the downy area located at the base of most contour feathers. The barbs that make up the downy area of the contour feather have variations in the barbule microstructures that aid in the identification of some groups of birds. For microscopic studies, the contour feather plumulaceous regions are divided into the umbilical, basal, intermediate, and distal sections (Fig. 5).

Distal. Orientation term, refers to area farthest away from rachis, rachilla, or dermis.

Distal plumulaceous region. The plumulaceous region of the contour feather that is most distal to the dermis (Fig. 5).

Dorsal. Outer side of the feather that is exposed, regardless of body position.

Downy barb. See definition for plumulaceous barb. Found at the base of the feather, on afterfeather or on true down. The rachilla of downy barbs is not very stiff and the barbules are soft and filamentous.

Downy barbule. See definition for plumulaceous barbule. Consists of segments of single long cells attached to the straplike base cells. Segments are either uniformly thick or swollen (nodes) at their distal end. The downy barbule as a whole appears tapered because each segment is slightly narrower than the cell proximal to it. Synonymous with pennulum.

Epiphyology. As defined by Chandler (1916), "... the study of the development, morphology, and phytogenesis of vertebrate scales, hair, and feathers, and any other homologous or analogous structures."

Furrowed. Refers to the texture and wrinkled or groovelike appearance of the barbule surface, particularly the internode, when viewed with high-powered scanning electron microscopy.

Internode. The area of the pennulum (barbule) that is between two nodes.

Intermediate plumulaceous region. The plumulaceous region of the contour feather that is in between the basal and distal plumulaceous sections (Fig. 5).

Natal down. Downy covering of newly hatched birds.

Node. Occurs at the junction of cells on plumulaceous barbules. This term specifically applies to the distal portion of the cells along the telescoping pennulum that are expanded or swollen. The main portion of the cell is usually the internode; the node usually refers to the section where two cells join. The node often contains pigment and has spines or prongs at the junction with the next distal cell. Morphology of node structures and pigmentation patterns aid in the identification of groups of birds.

Node shape. Refers to the shape of the nodal structure (e.g., triangular, straight, expanded) at cell junctions along the pennulum.

Pennaceous barb. Primary branch of rachis that further subdivides into somewhat flattened barbules that have interlocking hooklets on distal barbules. Texture is stiff. These barbs make up the feather surface.

Pennaceous region. Region of the feather that has pennaceous barbs with interlocking hooklets. Makes up the vanes of a feather and forms the surface of contour feathers.

Pennulum. Synonymous with downy barbule. The pennulum of the pennaceous feather bears hooklets.

Pigmentation. In downy barbs, this refers to the melanin granules that are located at nodes and internodes of the barbules. Patterns of pigmentation are used to aid in identification of groups of birds.

Pigment shape. Refers to the shape (e.g., teardrop, diamond, round) of the pigment at the node.

Plumulaceous barb (downy barb). In the downy feather, the primary branch of rachis that subdivides into filamentous barbules. Texture is soft and fluffy. Located at the base of most contour feathers. Downy barbs have no interlocking hooklets. True down and afterfeather down are made up entirely of downy barbs, whereas most contour feathers have downy barbs only at the base of the feather.

Plumulaceous barbule (downy barbule). Branches from downy barbs. Composed of a compressed, straplike base and a filiform pennulum with no hooklets. Found at the base of most contour feathers, in true and afterfeather down.

Plumulaceous region (downy region). Region of contour feather that has downy barbs. Plumulaceous areas of contour feathers are usually divided into four regions, umbilical, basal, intermediate, and distal (Fig. 5).

Plumule. Down feather of adult birds, synonymous with true down.

Prong. Very long thickened projection of varying lengths at the nodes of plumulaceous barbules.

Proximal. Orientation term, used in reference to the structure to which it applies. Proximal refers to the area nearest the rachilla, rachis, or part of the feather nearest the dermis.

Pterylum. A feather tract or area of skin on a bird where feathers grow.

Quill. Longitudinal axis of a feather. Includes both the rachis and the calamus.

Rachilla. Little rachis, or midrib of plumulaceous barb that branches into barbules. Synonymous with Chandler's (1916) ramus.

Rachis. Main shaft of feather; distal to calamus on feather. The rachis and calamus together make up the quill.

Spine. Short thin projection of varying lengths with needlelike tip at the nodes of plumulaceous barbules. Spines are shorter than prongs.

Subpennaceous region. Located at the base of the plumulaceous barb in many species of birds. Has structural similarities to pennaceous barbs. Barbule microstructure of this region can be used for barb orientation; distal vanule has hooklets similar to those of the pennaceous feather. Region varies in length and pigmentation, often pigmented more heavily on the distal vanule. The subpennaceous region is composed of barbules that are not similar to regular downy barbules because they do not have expanded or pigmented, distinct nodes on the pennulum. The term subpennaceous is defined by Dove (1997) because of the morphological similarities to pennaceous barbules and because this region subtends the more distal pennaceous vanes (see Fig. 6).

Superior umbilicus. Pore at the distal end of the calamus at the junction of the rachis and the aftershaft.

Teleoptile. A mature feather.

Trailing pigment. Refers to pigmentation pattern at the internodes of plumulaceous barbules. Occurs when pigmentation that is usually concentrated at the node extends posteriorly to the node into the internode. The majority of the pigmentation is in the node but varying degrees of pigment that are continuous with the node follow along posteriorly to the node.

Transparent process. Part of the nodal structure that surrounds the pigment and flares out from the pennulum at the node to form a rounded or somewhat pointed projection. Because plumulaceous barbules are transparent, the outlines of these nodal processes are easily observed with light microscopy.

True down. Synonym of "plumules" of Lucas and Stettenheim (1972). A down feather that grows in either the apteria or pterylae, or both. True down grows directly from the skin and is composed of a very fine rachis of varying lengths with filamentous barbs. Provides insulation.

Umbilical plumulaceous region. Region of the plumulaceous contour feather located just below the basal plumulaceous region. The umbilical region is at the very base of the contour feather. Barbs are usually shorter in this region than in the basal region (Fig. 5).

Vane. Part of the feather on each side of the rachis that is composed of barbs and barbules. Inner vane is overlapped by outer vane of adjacent feather.

Vanule. Part of the feather on each side of the rachilla that is composed of barbules. Same relation as vane to rachis but smaller divisions.

Ventral. The underside of the feather that is not exposed and is nearest the body of the bird. The same side as the superior umbilicus.

Villus (plural, villi). Small, transparent projection that is located only on the base cell(s) of plumulaceous barbules. Found in such groups as hummingbirds, passerines, woodpeckers, and some shorebirds. Morphologies may differ among groups in which they are found.

APPENDIX 2
SPECIMENS EXAMINED

Specimens used in phylogenetic study of microscopic variation in downy feathers are listed. Additional species from a reference collection were also examined for general descriptions. Species codes follow Edwards (1982).

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
465194	N4a4	*Grus canadensis*	Sandhill Crane	Breast, down, afterfeather	3	
271001	B1a3	*Gavia adamsii*	Yellow-billed Loon	Breast	1	
237242	B1a3	*Gavia adamsii*	Yellow-billed Loon	Breast	1	
325306	B1a3	*Gavia adamsii*	Yellow-billed Loon	Breast	1	
332238	B1a3	*Gavia adamsii*	Yellow-billed Loon	Breast, down, afterfeather	3	
559809	B1a3	*Gavia adamsii*	Yellow-billed Loon	Breast	1	Right vane
239376	N11c3	*Fulica americana*	American Coot	Breast	1	Right vane
242441	N11c3	*Fulica americana*	American Coot	Breast	1	
285403	N11c3	*Fulica americana*	American Coot	Breast, down, afterfeather	3	
352248	N11c3	*Fulica americana*	American Coot	Breast	1	
414640	N11c3	*Fulica americana*	American Coot	Breast	1	Right vane
217502	N3a12	*Lophotis ruficrista*	Red-crested Bustard	Breast	1	Right vane
243329	N3a12	*Lophotis ruficrista*	Red-crested Bustard	Breast, down, afterfeather	3	
243333	N3a12	*Lophotis ruficrista*	Red-crested Bustard	Breast	1	
520017	N3a12	*Lophotis ruficrista*	Red-crested Bustard	Breast	1	
222020	P10a6	*Haematopus palliatus*	American Oystercatcher	Breast	1	Right vane
368599	P10a6	*Haematopus palliatus*	American Oystercatcher	Breast, down, afterfeather	3	
400191	P10a6	*Haematopus palliatus*	American Oystercatcher	Breast	1	Right vane
471185	P10a6	*Haematopus palliatus*	American Oystercatcher	Breast	1	
471186	P10a6	*Haematopus palliatus*	American Oystercatcher	Breast	1	
131849	P10a7	*Haematopus bachmani*	Black Oystercatcher	Breast, down, afterfeather	3	
170298	P10a7	*Haematopus bachmani*	Black Oystercatcher	Breast	1	
258027	P10a7	*Haematopus bachmani*	Black Oystercatcher	Breast	1	
588899	P10a7	*Haematopus bachmani*	Black Oystercatcher	Breast	1	
588901	P10a7	*Haematopus bachmani*	Black Oystercatcher	Breast	1	
152876	P11a1	*Himantopus himantopus*	Pied Stilt	Breast	1	Right vane
261157	P11a1	*Himantopus himantopus*	Pied Stilt	Breast	1	
367021	P11a1	*Himantopus himantopus*	Pied Stilt	Breast, down, afterfeather	3	
401258	P11a1	*Himantopus himantopus*	Pied Stilt	Breast	1	
409309	P11a1	*Himantopus himantopus*	Pied Stilt	Breast	1	Right vane

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
59919	P11a4	*Cladorhynchus leucocephalus*	Banded Stilt	Breast, down, afterfeather	2	Right vane
582470	P11a4	*Cladorhynchus leucocephalus*	Banded Stilt	Breast	1	Juvenile
59920	P11a4	*Cladorhynchus leucocephalus*	Banded Stilt	Breast, afterfeather	2	Female
141486	P11a6	*Recurvirostra americana*	American Avocet	Breast	1	Right vane
204387	P11a6	*Recurvirostra americana*	American Avocet	Breast	1	
204414	P11a6	*Recurvirostra americana*	American Avocet	Breast, down, afterfeather	3	
208031	P11a6	*Recurvirostra americana*	American Avocet	Breast	1	
242968	P11a6	*Recurvirostra americana*	American Avocet	Breast	1	Right vane
159720	P12a1	*Ibidorhyncha struthersii*	Ibisbill	Breast	1	Female
192464	P12a1	*Ibidorhyncha struthersii*	Ibisbill	Breast	1	Female
237646	P12a1	*Ibidorhyncha struthersii*	Ibisbill	Breast	1	Female
296151	P12a1	*Ibidorhyncha struthersii*	Ibisbill	Breast, down, afterfeather	3	
522822	P12a1	*Ibidorhyncha struthersii*	Ibisbill	Breast	1	Right vane, female
216169	P13a1	*Pluvianus aegyptius*	Egyptian Plover/Courser	Breast	1	
458211	P13a1	*Pluvianus aegyptius*	Egyptian Plover/Courser	Breast, down, afterfeather	3	
468429	P13a1	*Pluvianus aegyptius*	Egyptian Plover/Courser	Breast	1	
569342	P13a1	*Pluvianus aegyptius*	Egyptian Plover/Courser	Breast	1	Right vane
117798	P13a4	*Cursorius chalcopterus*	Bronze-winged Courser	Breast	1	Right vane, female
216168	P13a4	*Cursorius chalcopterus*	Bronze-winged Courser	Breast	1	Right vane, female
437251	P13a4	*Cursorius chalcopterus*	Bronze-winged Courser	Breast, down, afterfeather	3	
460101	P13a4	*Cursorius chalcopterus*	Bronze-winged Courser	Breast	1	
517947	P13a6	*Cursorius cursor*	Cream-colored Courser	Breast	1	
517948	P13a6	*Cursorius cursor*	Cream-colored Courser	Breast, down, afterfeather	3	
517952	P13a6	*Cursorius cursor*	Cream-colored Courser	Breast	1	Right vane
517953	P13a6	*Cursorius cursor*	Cream-colored Courser	Breast	1	Right vane
551077	P13a6	*Cursorius cursor*	Cream-colored Courser	Breast	1	
37709	P13b1	*Glareola pratincola*	Collared Pratincole	Breast	1	Right vane
527266	P13b1	*Glareola pratincola*	Collared Pratincole	Breast	1	
527267	P13b1	*Glareola pratincola*	Collared Pratincole	Breast, down, afterfeather	3	
527268	P13b1	*Glareola pratincola*	Collared Pratincole	Breast	1	Right vane, female
550489	P13b1	*Glareola pratincola*	Collared Pratincole	Breast	1	Female
279023	P13c1	*Stiltia isabella*	Australian Pratincole	Breast	1	Right vane
405698	P13c1	*Stiltia isabella*	Australian Pratincole	Breast, down, afterfeather	3	
405699	P13c1	*Stiltia isabella*	Australian Pratincole	Breast	1	Female

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
405700	P13c1	*Stiltia isabella*	Australian Pratincole	Breast	1	Right vane, female
405701	P13c1	*Stiltia isabella*	Australian Pratincole	Breast	1	
98038	P14a1	*Vanellus vanellus*	Northern Lapwing	Breast	1	
98039	P14a1	*Vanellus vanellus*	Northern Lapwing	Breast	1	Right vane
116740	P14a1	*Vanellus vanellus*	Northern Lapwing	Breast	1	Right vane, female
236884	P14a1	*Vanellus vanellus*	Northern Lapwing	Breast	1	
325641	P14a1	*Vanellus vanellus*	Northern Lapwing	Breast, down, afterfeather	3	
180309	P14a13	*Vanellus indicus*	Red-wattled Lapwing	Breast	1	Right vane
278226	P14a13	*Vanellus indicus*	Red-wattled Lapwing	Breast	1	Right vane
358634	P14a13	*Vanellus indicus*	Red-wattled Lapwing	Breast, afterfeather	2	
360601	P14a13	*Vanellus indicus*	Red-wattled Lapwing	Breast, down	2	
399897	P14a13	*Vanellus indicus*	Red-wattled Lapwing	Breast	1	
217422	P14a16	*Vanellus lugubris*	Senegal Plover	Breast	1	
424712	P14a16	*Vanellus lugubris*	Senegal Plover	Breast	1	Right vane, female
435644	P14a16	*Vanellus lugubris*	Senegal Plover	Breast, down, afterfeather	3	
455163	P14a16	*Vanellus lugubris*	Senegal Plover	Breast	1	
545847	P14a16	*Vanellus lugubris*	Senegal Plover	Breast	1	Right vane, female
316376	P14a22	*Vanellus cayanus*	Pied Lapwing/Plover	Breast	1	Right vane, female
326614	P14a22	*Vanellus cayanus*	Pied Lapwing/Plover	Breast, down, afterfeather	4	
351814	P14a22	*Vanellus cayanus*	Pied Lapwing/Plover	Breast	1	
383222	P14a22	*Vanellus cayanus*	Pied Lapwing/Plover	Breast	1	Right vane, female
515372	P14a22	*Vanellus cayanus*	Pied Lapwing/Plover	Breast	1	
368590	P14a23	*Vanellus chilensis*	Southern Lapwing	Breast, down, afterfeather	4	
372482	P14a23	*Vanellus chilensis*	Southern Lapwing	Breast	1	Right vane
383411	P14a23	*Vanellus chilensis*	Southern Lapwing	Breast	1	
444335	P14a23	*Vanellus chilensis*	Southern Lapwing	Breast	1	
444340	P14a23	*Vanellus chilensis*	Southern Lapwing	Breast	1	Right vane
243089	P14a7	*Vanellus spinosus*	Spur-winged Plover	Breast	1	Right vane
551016	P14a7	*Vanellus spinosus*	Spur-winged Plover	Breast, down, afterfeather	3	
551018	P14a7	*Vanellus spinosus*	Spur-winged Plover	Breast	1	
551019	P14a7	*Vanellus spinosus*	Spur-winged Plover	Breast	1	
552147	P14a7	*Vanellus spinosus*	Spur-winged Plover	Breast	1	Right vane
213999	P14b11	*Charadrius tricollaris*	Three-banded Plover	Breast	1	Right vane
487730	P14b11	*Charadrius tricollaris*	Three-banded Plover	Breast, down, afterfeather	3	
518825	P14b11	*Charadrius tricollaris*	Three-banded Plover	Breast	1	

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
527253	P14b11	*Charadrius tricollaris*	Three-banded Plover	Breast	1	Female
569312	P14b11	*Charadrius tricollaris*	Three-banded Plover	Breast	1	Sex unknown
342130	P14b14	*Charadrius alexandrinus*	Kentish Plover	Breast	1	
517922	P14b14	*Charadrius alexandrinus*	Kentish Plover	Breast	1	
517926	P14b14	*Charadrius alexandrinus*	Kentish Plover	Breast, down, afterfeather	3	
548380	P14b14	*Charadrius alexandrinus*	Kentish Plover	Breast	1	Right vane
548384	P14b14	*Charadrius alexandrinus*	Kentish Plover	Breast	1	Right vane
337041	P14b23	*Charadrius mongolus*	Mongolian Plover	Breast	1	
405648	P14b23	*Charadrius mongolus*	Mongolian Plover	Breast	1	
496830	P14b23	*Charadrius mongolus*	Mongolian Plover	Breast	1	Right vane
526403	P14b23	*Charadrius mongolus*	Mongolian Plover	Breast, down, afterfeather	3	
608896	P14b23	*Charadrius mongolus*	Mongolian Plover	Breast	1	Right vane
257223	P14b27	*Charadrius mongolus*	Mongolian Plover	Breast	1	
480302	P14b27	*Charadrius montanus*	Mountain Plover	Breast	1	Right vane
564315	P14b27	*Charadrius montanus*	Mountain Plover	Breast	1	
564316	P14b27	*Charadrius montanus*	Mountain Plover	Breast, down, afterfeather	3	
564317	P14b27	*Charadrius montanus*	Mountain Plover	Breast	1	Right vane
66273	P14b33	*Anarhynchus frontalis*	Wrybill	Breast	1	Sex unknown
109171	P14b33	*Anarhynchus frontalis*	Wrybill	Breast	1	
109173	P14b33	*Anarhynchus frontalis*	Wrybill	Breast, down, afterfeather	3	
109174	P14b33	*Anarhynchus frontalis*	Wrybill	Breast	1	Right vane
261253	P14b38	*Pluvialis squatarola*	Black-bellied/Gray Plover	Breast	1	
261258	P14b38	*Pluvialis squatarola*	Black-bellied/Gray Plover	Breast	1	
285664	P14b38	*Pluvialis squatarola*	Black-bellied/Gray Plover	Breast, down, afterfeather	3	
419088	P14b38	*Pluvialis squatarola*	Black-bellied/Gray Plover	Breast	1	Right vane
437744	P14b38	*Pluvialis squatarola*	Black-bellied/Gray Plover	Breast	1	Right vane
102031	P14b40	*Eudromias morinellus*	Eurasian Dotterel	Breast	1	
113320	P14b40	*Eudromias morinellus*	Eurasian Dotterel	Breast, down, afterfeather	3	
113325	P14b40	*Eudromias morinellus*	Eurasian Dotterel	Breast	1	Female
234557	P14b40	*Eudromias morinellus*	Eurasian Dotterel	Breast	1	Female
331526	P14b40	*Eudromias morinellus*	Eurasian Dotterel	Breast	1	Sex unknown
420701	P14b6	*Charadrius vociferus*	Killdeer	Breast, down, afterfeather	3	
463213	P14b6	*Charadrius vociferus*	Killdeer	Breast	1	
463694	P14b6	*Charadrius vociferus*	Killdeer	Breast	1	Right vane

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
464127	P14b6	*Charadrius vociferus*	Killdeer	Breast	1	
597672	P14b6	*Charadrius vociferus*	Killdeer	Breast	1	Right vane
36784	P15a8	*Jacana jacana*	Wattled Jacana	Breast	1	Right vane
284654	P15a8	*Jacana jacana*	Wattled Jacana	Breast	1	
368580	P15a8	*Jacana jacana*	Wattled Jacana	Breast	1	
513842	P15a8	*Jacana jacana*	Wattled Jacana	Breast	1	Right vane
516168	P15a8	*Jacana jacana*	Wattled Jacana	Breast, down, afterfeather	3	
384986	P16a1	*Rostratula benghalensis*	Greater Painted-snipe	Breast, down, afterfeather	3	
385754	P16a1	*Rostratula benghalensis*	Greater Painted-snipe	Breast	1	Right vane
433108	P16a1	*Rostratula benghalensis*	Greater Painted-snipe	Breast	1	
458213	P16a1	*Rostratula benghalensis*	Greater Painted-snipe	Breast	1	Right vane
474929	P16a1	*Rostratula benghalensis*	Greater Painted-snipe	Breast	1	
141476	P17a12	*Numenius americanus*	Long-billed Curlew	Breast	1	
208033	P17a12	*Numenius americanus*	Long-billed Curlew	Breast, down, afterfeather	3	
241909	P17a12	*Numenius americanus*	Long-billed Curlew	Breast	1	
260656	P17a12	*Numenius americanus*	Long-billed Curlew	Breast	1	Right vane
396840	P17a12	*Numenius americanus*	Long-billed Curlew	Breast	1	Right vane
239368	P17a13	*Bartramia longicauda*	Upland Sandpiper	Breast	1	Right vane
260654	P17a13	*Bartramia longicauda*	Upland Sandpiper	Breast	1	Right vane
418702	P17a13	*Bartramia longicauda*	Upland Sandpiper	Breast	1	
464984	P17a13	*Bartramia longicauda*	Upland Sandpiper	Breast, down, afterfeather	3	
529794	P17a13	*Bartramia longicauda*	Upland Sandpiper	Breast	1	
154444	P17a17	*Tringa nebularia*	Common Greenshank	Breast	1	
273730	P17a17	*Tringa nebularia*	Common Greenshank	Breast	1	Right vane
253524	P17a17	*Tringa nebularia*	Common Greenshank	Breast	1	Right vane
479562	P17a17	*Tringa nebularia*	Common Greenshank	Breast, down, afterfeather	3	
551047	P17a17	*Tringa nebularia*	Common Greenshank	Breast	1	
464676	P17a2	*Limosa haemastica*	Hudsonian Godwit	Breast	1	
589317	P17a2	*Limosa haemastica*	Hudsonian Godwit	Breast	1	
589318	P17a2	*Limosa haemastica*	Hudsonian Godwit	Breast	1	Right vane
589319	P17a2	*Limosa haemastica*	Hudsonian Godwit	Breast	1	Right vane
589320	P17a2	*Limosa haemastica*	Hudsonian Godwit	Breast, down, afterfeather	3	
435040	P17a20	*Tringa flavipes*	Lesser Yellowlegs	Breast	1	
435041	P17a20	*Tringa flavipes*	Lesser Yellowlegs	Breast	1	Right vane

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
529805	P17a20	*Tringa flavipes*	Lesser Yellowlegs	Breast	1	
529806	P17a20	*Tringa flavipes*	Lesser Yellowlegs	Breast, down, afterfeather	3	
529808	P17a20	*Tringa flavipes*	Lesser Yellowlegs	Breast	1	Right vane
141026	P17a24	*Catoptrophorus semipalmatus*	Willet	Breast, down, afterfeather	3	
239364	P17a24	*Catoptrophorus semipalmatus*	Willet	Breast	1	
242103	P17a24	*Catoptrophorus semipalmatus*	Willet	Breast	1	Right vane
396841	P17a24	*Catoptrophorus semipalmatus*	Willet	Breast	1	
479321	P17a24	*Catoptrophorus semipalmatus*	Willet	Breast	1	Right vane
111505	P17a25	*Xenus cinereus*	Terek Sandpiper	Breast	1	Right vane
120619	P17a25	*Xenus cinereus*	Terek Sandpiper	Breast	1	Right vane
210926	P17a25	*Xenus cinereus*	Terek Sandpiper	Breast	1	
276411	P17a25	*Xenus cinereus*	Terek Sandpiper	Breast, down, afterfeather	3	
313045	P17a25	*Xenus cinereus*	Terek Sandpiper	Breast	1	
342157	P17a27	*Actitis macularia*	Spotted Sandpiper	Breast	1	Right vane
422270	P17a27	*Actitis macularia*	Spotted Sandpiper	Breast	1	
470415	P17a27	*Actitis macularia*	Spotted Sandpiper	Breast	1	Right vane
479325	P17a27	*Actitis macularia*	Spotted Sandpiper	Breast, down, afterfeather	1	
530950	P17a27	*Actitis macularia*	Spotted Sandpiper	Breast	1	
157602	P17a29	*Heteroscelus incanus*	Wandering Tattler	Breast	1	Right vane
301018	P17a29	*Heteroscelus incanus*	Wandering Tattler	Breast	1	Right vane
435021	P17a29	*Heteroscelus incanus*	Wandering Tattler	Breast, down, afterfeather	3	
435903	P17a29	*Heteroscelus incanus*	Wandering Tattler	Breast	1	
544562	P17a29	*Heteroscelus incanus*	Wandering Tattler	Breast	1	
212181	P17a30	*Prosobonia cancellata*	Sharp-billed Sandpiper	Breast	1	Right vane, female
329899	P17a30	*Prosobonia cancellata*	Sharp-billed Sandpiper	Breast, down, afterfeather	3	
212870	P17b1	*Arenaria interpres*	Ruddy Turnstone	Breast	1	Right vane
221891	P17b1	*Arenaria interpres*	Ruddy Turnstone	Breast	1	
239910	P17b1	*Arenaria interpres*	Ruddy Turnstone	Breast	1	
262278	P17b1	*Arenaria interpres*	Ruddy Turnstone	Breast	1	Right vane
342152	P17b1	*Arenaria interpres*	Ruddy Turnstone	Breast, down, afterfeather	3	
150163	P17c1	*Scolopax rusticola*	Eurasian Woodcock	Breast	1	
314016	P17c1	*Scolopax rusticola*	Eurasian Woodcock	Breast, down, afterfeather	3	
414855	P17c1	*Scolopax rusticola*	Eurasian Woodcock	Breast	1	Right vane
424547	P17c1	*Scolopax rusticola*	Eurasian Woodcock	Breast	1	Right vane

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
552733	P17c1	*Scolopax rusticola*	Eurasian Woodcock	Breast	1	
421483	P17c6	*Scolopax minor*	American Woodcock	Breast	1	
421494	P17c6	*Scolopax minor*	American Woodcock	Breast	1	Right vane
421503	P17c6	*Scolopax minor*	American Woodcock	Breast, down, afterfeather	3	
564420	P17c6	*Scolopax minor*	American Woodcock	Breast	1	Right vane
565942	P17c6	*Scolopax minor*	American Woodcock	Breast	1	
109583	P17d16	*Lymnocryptes minimus*	Jack Snipe	Breast	1	
113213	P17d16	*Lymnocryptes minimus*	Jack Snipe	Breast	1	Right vane
424542	P17d16	*Lymnocryptes minimus*	Jack Snipe	Breast, down, afterfeather	3	
424545	P17d16	*Lymnocryptes minimus*	Jack Snipe	Breast	1	
424546	P17d16	*Lymnocryptes minimus*	Jack Snipe	Breast	1	Right vane
272378	P17d18	*Limnodromus griseus*	Short-billed Dowitcher	Breast, down, afterfeather	3	
272379	P17d18	*Limnodromus griseus*	Short-billed Dowitcher	Breast	1	Right vane
589234	P17d18	*Limnodromus griseus*	Short-billed Dowitcher	Breast	1	
589236	P17d18	*Limnodromus griseus*	Short-billed Dowitcher	Breast	1	Right vane
589251	P17d18	*Limnodromus griseus*	Short-billed Dowitcher	Breast	1	
214697	P17d6	*Gallinago nigripennis*	Ethiopian Snipe	Breast	1	Right vane
519162	P17d6	*Gallinago nigripennis*	Ethiopian Snipe	Breast	1	Right vane
527257	P17d6	*Gallinago nigripennis*	Ethiopian Snipe	Breast	1	
527258	P17d6	*Gallinago nigripennis*	Ethiopian Snipe	Breast	1	
527259	P17d6	*Gallinago nigripennis*	Ethiopian Snipe	Breast, down, afterfeather	3	
394247	P17d9	*Gallinago gallinago*	Common Snipe	Breast, down, afterfeather	3	
463019	P17d9	*Gallinago gallinago*	Common Snipe	Breast	1	Right vane
464124	P17d9	*Gallinago gallinago*	Common Snipe	Breast	1	Right vane
468069	P17d9	*Gallinago gallinago*	Common Snipe	Breast	1	
533594	P17d9	*Gallinago gallinago*	Common Snipe	Breast	1	
300352	P17e1	*Aphriza virgata*	Surfbird	Breast	1	Right vane
363617	P17e1	*Aphriza virgata*	Surfbird	Breast	1	
414812	P17e1	*Aphriza virgata*	Surfbird	Breast, down, afterfeather	3	
588963	P17e1	*Aphriza virgata*	Surfbird	Breast	1	
588964	P17e1	*Aphriza virgata*	Surfbird	Breast	1	Right vane
422429	P17e13	*Calidris bairdii*	Baird's Sandpiper	Breast	1	Right vane
422458	P17e13	*Calidris bairdii*	Baird's Sandpiper	Breast	1	Right vane
464264	P17e13	*Calidris bairdii*	Baird's Sandpiper	Breast, down, afterfeather	3	

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
465278	P17e13	*Calidris bairdii*	Baird's Sandpiper	Breast	1	
495929	P17e13	*Calidris bairdii*	Baird's Sandpiper	Breast	1	
262273	P17e18	*Calidris alpina*	Dunlin	Breast	1	
463003	P17e18	*Calidris alpina*	Dunlin	Breast, down, afterfeather	3	
479595	P17e18	*Calidris alpina*	Dunlin	Breast	1	Right vane
589223	P17e18	*Calidris alpina*	Dunlin	Breast	1	Right vane
589231	P17e18	*Calidris alpina*	Dunlin	Breast	1	
102068	P17e20	*Eurynorhynchus pygmeus*	Spoon-billed Sandpiper	Breast, down, afterfeather	3	
114780	P17e20	*Eurynorhynchus pygmeus*	Spoon-billed Sandpiper	Breast	1	
120589	P17e20	*Eurynorhynchus pygmeus*	Spoon-billed Sandpiper	Breast	1	
120590	P17e20	*Eurynorhynchus pygmeus*	Spoon-billed Sandpiper	Breast	1	Right vane
120591	P17e20	*Eurynorhynchus pygmeus*	Spoon-billed Sandpiper	Breast	1	Right vane
56927	P17e21	*Limicola falcinellus*	Broad-billed Sandpiper	Breast	1	Right vane
102110	P17e21	*Limicola falcinellus*	Broad-billed Sandpiper	Breast	1	Right vane
415287	P17e21	*Limicola falcinellus*	Broad-billed Sandpiper	Breast, down, afterfeather	3	
415288	P17e21	*Limicola falcinellus*	Broad-billed Sandpiper	Breast	1	
415289	P17e21	*Limicola falcinellus*	Broad-billed Sandpiper	Breast	1	
340328	P17e22	*Micropalama himantopus*	Stilt Sandpiper	Breast	1	Right vane
435174	P17e22	*Micropalama himantopus*	Stilt Sandpiper	Breast	1	
435176	P17e22	*Micropalama himantopus*	Stilt Sandpiper	Breast	1	Right vane
435177	P17e22	*Micropalama himantopus*	Stilt Sandpiper	Breast	1	
533604	P17e22	*Micropalama himantopus*	Stilt Sandpiper	Breast, down, afterfeather	3	
76759	P17e23	*Tryngites subruficollis*	Buff-breasted Sandpiper	Breast	1	Right vane
93232	P17e23	*Tryngites subruficollis*	Buff-breasted Sandpiper	Breast	1	
283700	P17e23	*Tryngites subruficollis*	Buff-breasted Sandpiper	Breast, down, afterfeather	3	
284982	P17e23	*Tryngites subruficollis*	Buff-breasted Sandpiper	Breast	1	
285060	P17e23	*Tryngites subruficollis*	Buff-breasted Sandpiper	Breast	1	Right vane
103025	P17e24	*Philomachus pugnax*	Ruff	Breast	1	Right vane
191361	P17e24	*Philomachus pugnax*	Ruff	Breast	1	
191365	P17e24	*Philomachus pugnax*	Ruff	Breast	1	
191369	P17e24	*Philomachus pugnax*	Ruff	Breast	1	Right vane
234550	P17e24	*Philomachus pugnax*	Ruff	Breast, down, afterfeather	3	
212831	P17e3	*Calidris canutus*	Red Knot	Breast, down, afterfeather	3	
240279	P17e3	*Calidris canutus*	Red Knot	Breast	1	

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
283343	P17e3	*Calidris canutus*	Red Knot	Breast	1	Right vane
298649	P17e3	*Calidris canutus*	Red Knot	Breast	1	
524202	P17e3	*Calidris canutus*	Red Knot	Breast	1	Right vane
341122	P17e4	*Calidris alba*	Sanderling	Breast	1	
342212	P17e4	*Calidris alba*	Sanderling	Breast	1	Right vane
422317	P17e4	*Calidris alba*	Sanderling	Breast	1	Right vane
423002	P17e4	*Calidris alba*	Sanderling	Breast	1	
529826	P17e4	*Calidris alba*	Sanderling	Breast, down, afterfeather	3	
212696	P17e5	*Calidris pusilla*	Semipalmated Sandpiper	Breast	1	
212699	P17e5	*Calidris pusilla*	Semipalmated Sandpiper	Breast	1	Right vane
212860	P17e5	*Calidris pusilla*	Semipalmated Sandpiper	Breast	1	
357394	P17e5	*Calidris pusilla*	Semipalmated Sandpiper	Breast	1	Right vane
421770	P17e5	*Calidris pusilla*	Semipalmated Sandpiper	Breast, down, afterfeather	3	
381266	P17e11	*Calidris minutilla*	Least Sandpiper	Breast, down, afterfeather	3	
381267	P17e11	*Calidris minutilla*	Least Sandpiper	Breast	1	Right vane
419775	P17e11	*Calidris minutilla*	Least Sandpiper	Breast	1	
421765	P17e11	*Calidris minutilla*	Least Sandpiper	Breast	1	Right vane
448047	P17e11	*Calidris minutilla*	Least Sandpiper	Breast	1	
241328	P18a1	*Phalaropus tricolor*	Wilson's Phalarope	Breast	1	Female
464287	P18a1	*Phalaropus tricolor*	Wilson's Phalarope	Breast	1	Female
464289	P18a1	*Phalaropus tricolor*	Wilson's Phalarope	Breast	1	Right vane, female
465738	P18a1	*Phalaropus tricolor*	Wilson's Phalarope	Breast, down, afterfeather	3	Female
564087	P18a1	*Phalaropus tricolor*	Wilson's Phalarope	Breast	1	Right vane, female
261092	P18a2	*Phalaropus lobatus*	Northern Phalarope	Breast	1	Female
272706	P18a2	*Phalaropus lobatus*	Northern Phalarope	Breast	1	Right vane, female
468072	P18a2	*Phalaropus lobatus*	Northern Phalarope	Breast	1	Female
533605	P18a2	*Phalaropus lobatus*	Northern Phalarope	Breast	1	Right vane, female
533606	P18a2	*Phalaropus lobatus*	Northern Phalarope	Breast, down, afterfeather	3	Female
287859	P1a1	*Uria aalge*	Common Murre	Breast	1	Right vane
287897	P1a1	*Uria aalge*	Common Murre	Breast	1	Right vane
363611	P1a1	*Uria aalge*	Common Murre	Breast	1	
366461	P1a1	*Uria aalge*	Common Murre	Breast, down, afterfeather	3	
464446	P1a1	*Uria aalge*	Common Murre	Breast	1	
89142	P1a12	*Synthliboramphus antiquus*	Ancient Murrelet	Breast	1	

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
92986	P1a12	*Synthliboramphus antiquus*	Ancient Murrelet	Breast	1	Right vane
365363	P1a12	*Synthliboramphus antiquus*	Ancient Murrelet	Breast	1	
366528	P1a12	*Synthliboramphus antiquus*	Ancient Murrelet	Breast, down, afterfeather	3	
415739	P1a12	*Synthliboramphus antiquus*	Ancient Murrelet	Breast	1	Right vane
381208	P1a14	*Alle alle*	Dovekie	Breast	1	
393537	P1a14	*Alle alle*	Dovekie	Breast	1	Right vane
394490	P1a14	*Alle alle*	Dovekie	Breast	1	Right vane
399652	P1a14	*Alle alle*	Dovekie	Breast	1	
531516	P1a14	*Alle alle*	Dovekie	Breast, down, afterfeather	3	
543949	P1a15	*Ptychoramphus aleuticus*	Cassin's Auklet	Breast	1	Right vane
543974	P1a15	*Ptychoramphus aleuticus*	Cassin's Auklet	Breast	1	Right vane
543976	P1a15	*Ptychoramphus aleuticus*	Cassin's Auklet	Breast	1	
543980	P1a15	*Ptychoramphus aleuticus*	Cassin's Auklet	Breast	1	
543986	P1a15	*Ptychoramphus aleuticus*	Cassin's Auklet	Breast, down, afterfeather	3	
151459	P1a18	*Aethia pusilla*	Least Auklet	Breast	1	Right vane
200968	P1a18	*Aethia pusilla*	Least Auklet	Breast	1	Right vane
575152	P1a18	*Aethia pusilla*	Least Auklet	Breast, down, afterfeather	3	
589697	P1a18	*Aethia pusilla*	Least Auklet	Breast	1	
589701	P1a18	*Aethia pusilla*	Least Auklet	Breast	1	
92947	P1a19	*Cyclorrhynchus psittacula*	Parakeet Auklet	Breast	1	
242727	P1a19	*Cyclorrhynchus psittacula*	Parakeet Auklet	Breast	1	Right vane
493708	P1a19	*Cyclorrhynchus psittacula*	Parakeet Auklet	Breast, down, afterfeather	3	
589630	P1a19	*Cyclorrhynchus psittacula*	Parakeet Auklet	Breast	1	Right vane
589635	P1a19	*Cyclorrhynchus psittacula*	Parakeet Auklet	Breast	1	
258004	P1a20	*Cerorhinca monocerata*	Rhinoceros Auklet	Breast	1	Right vane
258005	P1a20	*Cerorhinca monocerata*	Rhinoceros Auklet	Breast, down, afterfeather	3	
406340	P1a20	*Cerorhinca monocerata*	Rhinoceros Auklet	Breast	1	
415748	P1a20	*Cerorhinca monocerata*	Rhinoceros Auklet	Breast	1	
532836	P1a20	*Cerorhinca monocerata*	Rhinoceros Auklet	Breast	1	Right vane
381216	P1a21	*Fratercula arctica*	Common Puffin	Breast	1	Right vane
381217	P1a21	*Fratercula arctica*	Common Puffin	Breast	1	
381223	P1a21	*Fratercula arctica*	Common Puffin	Breast	1	
381224	P1a21	*Fratercula arctica*	Common Puffin	Breast, down, afterfeather	3	
399645	P1a21	*Fratercula arctica*	Common Puffin	Breast	1	Right vane

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
158055	P1a23	*Lunda cirrhata*	Tufted Puffin	Breast	1	Right vane
166798	P1a23	*Lunda cirrhata*	Tufted Puffin	Breast	1	
242725	P1a23	*Lunda cirrhata*	Tufted Puffin	Breast	1	
467422	P1a23	*Lunda cirrhata*	Tufted Puffin	Breast	1	Right vane
589737	P1a23	*Lunda cirrhata*	Tufted Puffin	Breast, down, afterfeather	3	
84795	P1a3	*Alca torda*	Razorbill	Breast	1	Right vane
111726	P1a3	*Alca torda*	Razorbill	Breast	1	Right vane
395938	P1a3	*Alca torda*	Razorbill	Breast	1	
395939	P1a3	*Alca torda*	Razorbill	Breast	1	
589584	P1a3	*Alca torda*	Razorbill	Breast, down, afterfeather	3	
115842	P1a6	*Cepphus columba*	Pigeon Guillemot	Breast	1	Right vane
151577	P1a6	*Cepphus columba*	Pigeon Guillemot	Breast	1	Right vane
258009	P1a6	*Cepphus columba*	Pigeon Guillemot	Breast	1	
270561	P1a6	*Cepphus columba*	Pigeon Guillemot	Breast	1	Nonbreeding male
270987	P1a6	*Cepphus columba*	Pigeon Guillemot	Breast	1	
271039	P1a6	*Cepphus columba*	Pigeon Guillemot	Breast, down, afterfeather	3	
270833	P1a8	*Brachyramphus marmoratus*	Marbled Murrelet	Breast	1	
286900	P1a8	*Brachyramphus marmoratus*	Marbled Murrelet	Breast	1	
287708	P1a8	*Brachyramphus marmoratus*	Marbled Murrelet	Breast	1	Right vane
589644	P1a8	*Brachyramphus marmoratus*	Marbled Murrelet	Breast, down, afterfeather	3	
589647	P1a8	*Brachyramphus marmoratus*	Marbled Murrelet	Breast	1	Right vane
589669	P1a8	*Brachyramphus marmoratus*	Marbled Murrelet	Breast	1	Nonbreeding male
128810	P2a1	*Dromas ardeola*	Crab Plover	Breast	1	
519155	P2a1	*Dromas ardeola*	Crab Plover	Breast	1	Right vane
519156	P2a1	*Dromas ardeola*	Crab Plover	Breast, down, afterfeather	3	
519157	P2a1	*Dromas ardeola*	Crab Plover	Breast	1	
519159	P2a1	*Dromas ardeola*	Crab Plover	Breast	1	Right vane, female
22267	P3a1	*Catharacta skua*	Great Skua	Breast	1	Right vane, sex?
57121	P3a1	*Catharacta skua*	Great Skua	Breast	1	
105946	P3a1	*Catharacta skua*	Great Skua	Breast	1	
576076	P3a1	*Catharacta skua*	Great Skua	Breast, down, afterfeather	3	
608904	P3a1	*Catharacta skua*	Great Skua	Breast	1	Right vane, sex?
401022	P3a7	*Stercorarius longicaudus*	Long-tailed Skua	Breast	1	Right vane
401023	P3a7	*Stercorarius longicaudus*	Long-tailed Skua	Breast	1	

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
422932	P3a7	*Stercorarius longicaudus*	Long-tailed Skua	Breast	1	
422933	P3a7	*Stercorarius longicaudus*	Long-tailed Skua	Breast, down, afterfeather	3	
495273	P3a7	*Stercorarius longicaudus*	Long-tailed Skua	Breast	1	Right vane
240227	P4a1	*Rynchops niger*	Black Skimmer	Breast	1	
271460	P4a1	*Rynchops niger*	Black Skimmer	Breast	1	Right vane
415715	P4a1	*Rynchops niger*	Black Skimmer	Breast	1	Right vane
415717	P4a1	*Rynchops niger*	Black Skimmer	Breast, down, afterfeather	3	
415718	P4a1	*Rynchops niger*	Black Skimmer	Breast	1	
264970	P4a2	*Rynchops flavirostris*	African Skimmer	Breast, down, afterfeather	4	Right vane, female
380336	P5a14	*Larus delawarensis*	Ring-billed Gull	Breast	1	
464999	P5a14	*Larus delawarensis*	Ring-billed Gull	Breast	1	Right vane
565129	P5a14	*Larus delawarensis*	Ring-billed Gull	Breast, down, afterfeather	3	
575660	P5a14	*Larus delawarensis*	Ring-billed Gull	Breast	1	Right vane
589443	P5a14	*Larus delawarensis*	Ring-billed Gull	Breast	1	
103386	P5a2	*Larus pacificus*	Pacific Gull	Breast	2	Immature, one right vane
211894	P5a2	*Larus pacificus*	Pacific Gull	Breast, down, afterfeather	3	
277276	P5a2	*Larus pacificus*	Pacific Gull	Breast	1	
271271	P5a24	*Larus argentatus*	Herring Gull	Breast	1	Right vane
487511	P5a24	*Larus argentatus*	Herring Gull	Breast	1	
536490	P5a24	*Larus argentatus*	Herring Gull	Breast	1	Right vane
589430	P5a24	*Larus argentatus*	Herring Gull	Breast, down, afterfeather	3	
589431	P5a24	*Larus argentatus*	Herring Gull	Breast	1	
177071	P5a43	*Rissa tridactyla*	Black-legged Kittiwake	Breast	1	Right vane
394570	P5a43	*Rissa tridactyla*	Black-legged Kittiwake	Breast, down, afterfeather	3	
394571	P5a43	*Rissa tridactyla*	Black-legged Kittiwake	Breast	1	Right vane
394573	P5a43	*Rissa tridactyla*	Black-legged Kittiwake	Breast	1	
394577	P5a43	*Rissa tridactyla*	Black-legged Kittiwake	Breast	1	
464757	P5a45	*Xema sabini*	Sabine's Gull	Breast	1	Right vane
495942	P5a45	*Xema sabini*	Sabine's Gull	Breast, down, afterfeather	3	
497525	P5a45	*Xema sabini*	Sabine's Gull	Breast	1	Right vane
572638	P5a45	*Xema sabini*	Sabine's Gull	Breast	1	
589515	P5a45	*Xema sabini*	Sabine's Gull	Breast	1	
401031	P5a46	*Rhodostethia rosea*	Ross's Gull	Breast	1	Right vane

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
495943	P5a46	*Rhodostethia rosea*	Ross's Gull	Breast, down, afterfeather	3	
536455	P5a46	*Rhodostethia rosea*	Ross's Gull	Breast	1	
536457	P5a46	*Rhodostethia rosea*	Ross's Gull	Breast	1	Right vane
536459	P5a46	*Rhodostethia rosea*	Ross's Gull	Breast	1	
479605	P5a47	*Pagophila eburnea*	Ivory Gull	Breast, down, afterfeather	3	
399572	P5a47	*Pagophila eburnea*	Ivory Gull	Breast	1	Sex?
399578	P5a47	*Pagophila eburnea*	Ivory Gull	Breast	2	One right vane
399579	P5a47	*Pagophila eburnea*	Ivory Gull	Breast	1	Sex?
469300	P5a47	*Pagophila eburnea*	Ivory Gull	Breast	1	Sex?
131674	P5a48	*Creagrus furcatus*	Swallow-tailed Gull	Breast	1	Right vane
316899	P5a48	*Creagrus furcatus*	Swallow-tailed Gull	Breast	1	Right vane
434875	P5a48	*Creagrus furcatus*	Swallow-tailed Gull	Breast, down, afterfeather	3	
543878	P5a48	*Creagrus furcatus*	Swallow-tailed Gull	Breast	1	
543879	P5a48	*Creagrus furcatus*	Swallow-tailed Gull	Breast	1	
135284	P5a7	*Larus atricilla*	Laughing Gull	Breast	1	
140191	P5a7	*Larus atricilla*	Laughing Gull	Breast	1	
160898	P5a7	*Larus atricilla*	Laughing Gull	Breast	1	Right vane
589456	P5a7	*Larus atricilla*	Laughing Gull	Breast	1	Right vane
597457	P5a7	*Larus atricilla*	Laughing Gull	Breast, down, afterfeather	3	
240206	P5b12	*Sterna sandvicensis*	Sandwich Tern	Breast	1	Right vane
258850	P5b12	*Sterna sandvicensis*	Sandwich Tern	Breast	1	
258851	P5b12	*Sterna sandvicensis*	Sandwich Tern	Breast	1	Right vane
323183	P5b12	*Sterna sandvicensis*	Sandwich Tern	Breast	1	
363763	P5b12	*Sterna sandvicensis*	Sandwich Tern	Breast, down, afterfeather	3	
135285	P5b19	*Sterna hirundo*	Common Tern	Breast	1	
162581	P5b19	*Sterna hirundo*	Common Tern	Breast	1	Right vane
220315	P5b19	*Sterna hirundo*	Common Tern	Breast	1	
421942	P5b19	*Sterna hirundo*	Common Tern	Breast, down, afterfeather	3	
589533	P5b19	*Sterna hirundo*	Common Tern	Breast	1	Right vane
220298	P5b23	*Sterna forsteri*	Forster's Tern	Breast	1	Right vane
415558	P5b23	*Sterna forsteri*	Forster's Tern	Breast	1	Right vane
470422	P5b23	*Sterna forsteri*	Forster's Tern	Breast	1	
532289	P5b23	*Sterna forsteri*	Forster's Tern	Breast, down, afterfeather	3	
589531	P5b23	*Sterna forsteri*	Forster's Tern	Breast	1	

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
166694	P5b30	*Sterna fuscata*	Sooty Tern	Breast	1	
354099	P5b30	*Sterna fuscata*	Sooty Tern	Breast	1	Right vane
485447	P5b30	*Sterna fuscata*	Sooty Tern	Breast	1	
534285	P5b30	*Sterna fuscata*	Sooty Tern	Breast	1	Right vane
534287	P5b30	*Sterna fuscata*	Sooty Tern	Breast, down, afterfeather	3	
15516	P5b38	*Larosterna inca*	Inca Tern	Breast	1	Right vane
212051	P5b38	*Larosterna inca*	Inca Tern	Breast, down, afterfeather	3	
371302	P5b38	*Larosterna inca*	Inca Tern	Breast	1	
371303	P5b38	*Larosterna inca*	Inca Tern	Breast	1	
529087	P5b38	*Larosterna inca*	Inca Tern	Breast	1	Right vane, female
300366	P5b39	*Procelsterna cerulea*	Blue Noddy	Breast	1	
300437	P5b39	*Procelsterna cerulea*	Blue Noddy	Breast, down, afterfeather	3	
300441	P5b39	*Procelsterna cerulea*	Blue Noddy	Breast	1	Right vane
300445	P5b39	*Procelsterna cerulea*	Blue Noddy	Breast	1	Right vane
300450	P5b39	*Procelsterna cerulea*	Blue Noddy	Breast	1	
364561	P5b4	*Chlidonias niger*	Black Tern	Breast	1	
395473	P5b4	*Chlidonias niger*	Black Tern	Breast	2	One right vane
448667	P5b4	*Chlidonias niger*	Black Tern	Breast, down, afterfeather	2	
479314	P5b4	*Chlidonias niger*	Black Tern	Breast, down, afterfeather	3	
497774	P5b4	*Chlidonias niger*	Black Tern	Breast	1	
576194	P5b4	*Chlidonias niger*	Black Tern	Breast	1	
493763	P5b41	*Anous stolidus*	Brown Noddy	Breast	1	Right vane
495042	P5b41	*Anous stolidus*	Brown Noddy	Breast, down, afterfeather	3	
497244	P5b41	*Anous stolidus*	Brown Noddy	Breast	1	
497246	P5b41	*Anous stolidus*	Brown Noddy	Breast	1	
497674	P5b41	*Anous stolidus*	Brown Noddy	Breast	1	Right vane
497586	P5b44	*Gygis alba*	Fairy Tern	Breast	1	
497587	P5b44	*Gygis alba*	Fairy Tern	Breast	1	Right vane
497592	P5b44	*Gygis alba*	Fairy Tern	Breast	1	
497593	P5b44	*Gygis alba*	Fairy Tern	Breast	1	
497595	P5b44	*Gygis alba*	Fairy Tern	Breast, down, afterfeather	3	
128201	P5b5	*Phaetusa simplex*	Large-billed Tern	Breast	1	Right vane
276897	P5b5	*Phaetusa simplex*	Large-billed Tern	Breast	1	Right vane
391951	P5b5	*Phaetusa simplex*	Large-billed Tern	Breast	1	

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
401264	P5b5	*Phaetusa simplex*	Large-billed Tern	Breast	1	
512940	P5b5	*Phaetusa simplex*	Large-billed Tern	Breast, down, afterfeather	3	
252849	P5b6	*Gelochelidon nilotica*	Gull-billed Tern	Breast	1	
276337	P5b6	*Gelochelidon nilotica*	Gull-billed Tern	Breast, down, afterfeather	3	
324845	P5b6	*Gelochelidon nilotica*	Gull-billed Tern	Breast	1	Right vane
324847	P5b6	*Gelochelidon nilotica*	Gull-billed Tern	Breast	1	
589526	P5b6	*Gelochelidon nilotica*	Gull-billed Tern	Breast	1	Right vane
221986	P5b7	*Sterna caspia*	Caspian Tern	Breast	1	
262261	P5b7	*Sterna caspia*	Caspian Tern	Breast, down, afterfeather	3	
299061	P5b7	*Sterna caspia*	Caspian Tern	Breast	1	Right vane
589568	P5b7	*Sterna caspia*	Caspian Tern	Breast	1	Right vane
599867	P5b7	*Sterna caspia*	Caspian Tern	Breast	1	
150455	P6a1	*Chionis alba*	Snowy Sheathbill	Breast	1	Right vane
534269	P6a1	*Chionis alba*	Snowy Sheathbill	Breast, down, afterfeather	3	
548050	P6a1	*Chionis alba*	Snowy Sheathbill	Breast	1	Right vane, female
548072	P6a1	*Chionis alba*	Snowy Sheathbill	Breast	1	Female
548112	P6a1	*Chionis alba*	Snowy Sheathbill	Breast	1	
298361	P6b1	*Pluvianellus socialis*	Magellanic Plover	Breast	1	Right vane, female
485582	P6b1	*Pluvianellus socialis*	Magellanic Plover	Breast, down, afterfeather	3	
485583	P6b1	*Pluvianellus socialis*	Magellanic Plover	Breast	1	Juvenile
317481	P7a1	*Pedionomus torquatus*	Plains-Wanderer	Breast, down, afterfeather	3	Female
317482	P7a1	*Pedionomus torquatus*	Plains-Wanderer	Breast	2	Immature, one right vane
49009	P8a1	*Attagis gayi*	Rufous-bellied Seedsnipe	Breast	1	
49010	P8a1	*Attagis gayi*	Rufous-bellied Seedsnipe	Breast	1	Right vane
237132	P8a1	*Attagis gayi*	Rufous-bellied Seedsnipe	Breast, down, afterfeather	3	
563159	P8a1	*Attagis gayi*	Rufous-bellied Seedsnipe	Breast	1	Right vane
563160	P8a1	*Attagis gayi*	Rufous-bellied Seedsnipe	Breast	1	
15164	P8a3	*Thinocorus orbignyianus*	Gray-breasted Seedsnipe	Breast	1	
15166	P8a3	*Thinocorus orbignyianus*	Gray-breasted Seedsnipe	Breast	1	Right vane
49013	P8a3	*Thinocorus orbignyianus*	Gray-breasted Seedsnipe	Breast	1	
563161	P8a3	*Thinocorus orbignyianus*	Gray-breasted Seedsnipe	Breast, down, afterfeather	3	
159882	P8a4	*Thinocorus rumicivorus*	Least Seedsnipe	Breast	1	
159884	P8a4	*Thinocorus rumicivorus*	Least Seedsnipe	Breast, down, afterfeather	3	
283684	P8a4	*Thinocorus rumicivorus*	Least Seedsnipe	Breast	1	Right vane

APPENDIX 2 Continued.

USNM no.*	Species code	Taxon	Common name	Feather type	Number of slides	Comments
284656	P8a4	*Thinocorus rumicivorus*	Least Seedsnipe	Breast	1	Right vane
284845	P8a4	*Thinocorus rumicivorus*	Least Seedsnipe	Breast	1	
115535	P9a1	*Burhinus oedicnemus*	Eurasian Stone-Curlew	Breast	1	Right vane, female
116403	P9a1	*Burhinus oedicnemus*	Eurasian Stone-Curlew	Breast	1	
377232	P9a1	*Burhinus oedicnemus*	Eurasian Stone-Curlew	Breast, down, afterfeather	3	
385741	P9a1	*Burhinus oedicnemus*	Eurasian Stone-Curlew	Breast	1	Right vane
552149	P9a1	*Burhinus oedicnemus*	Eurasian Stone-Curlew	Breast	1	
263617	P9a8	*Esacus recurvirostris*	Great Stone-Curlew	Breast	1	
336972	P9a8	*Esacus recurvirostris*	Great Stone-Curlew	Breast	1	Right vane, female
336973	P9a8	*Esacus recurvirostris*	Great Stone-Curlew	Breast	1	
377528	P9a8	*Esacus recurvirostris*	Great Stone-Curlew	Breast, down, afterfeather	3	
533461	P9a8	*Esacus recurvirostris*	Great Stone-Curlew	Breast	1	Right vane
150189	Q1a2	*Syrrhaptes paradoxus*	Pallas's Sandgrouse	Breast	1	
150190	Q1a2	*Syrrhaptes paradoxus*	Pallas's Sandgrouse	Breast	1	
150191	Q1a2	*Syrrhaptes paradoxus*	Pallas's Sandgrouse	Breast	2	Belly, right vane
304463	Q1a2	*Syrrhaptes paradoxus*	Pallas's Sandgrouse	Breast, down	2	
368032	Q1a2	*Syrrhaptes paradoxus*	Pallas's Sandgrouse	Breast	1	Right vane
545874	Q1a4	*Pterocles namaqua*	Namaqua Sandgrouse	Breast, down, afterfeather	4	Belly
163816	Q1a4	*Pterocles namaqua*	Namaqua Sandgrouse	Breast	1	
263788	Q1a4	*Pterocles namaqua*	Namaqua Sandgrouse	Breast	1	Right vane
433509	Q1a4	*Pterocles namaqua*	Namaqua Sandgrouse	Breast	1	Right vane
545873	Q1a4	*Pterocles namaqua*	Namaqua Sandgrouse	Breast	1	
148261	Q1a7	*Pterocles orientalis*	Black-bellied Sandgrouse	Breast	1	Right vane
333431	Q1a7	*Pterocles orientalis*	Black-bellied Sandgrouse	Breast	1	Right vane
433097	Q1a7	*Pterocles orientalis*	Black-bellied Sandgrouse	Breast	1	
433098	Q1a7	*Pterocles orientalis*	Black-bellied Sandgrouse	Breast	1	
479508	Q1a7	*Pterocles orientalis*	Black-bellied Sandgrouse	Breast	1	Right vane
479508	Q1a7	*Pterocles orientalis*	Black-bellied Sandgrouse	Breast, down, afterfeather	3	

* USNM = United States National Museum (Smithsonian Institution), Washington, DC.

APPENDIX 3 FEATHER CHARACTER MATRIX FOR CHARADRIIFORMES AND OUTGROUPS

Characters (for full description see text). 1. Subpennaceous region. 2. Subpennaceous region pigmentation. 3. Subpennaceous length. 4. Barbule base pigmentation. 5. Barbule base length. 6. Barbule base composition. 7. Barb length. 8. Barb pigmentation. 9. Barbule symmetry. 10. Barbule length. 11. Barbule pigmentation. 12. Node location. 13. Density of nodes per barbule. 14. Proximal node shape. 15. Midsection node shape. 16. Distal node shape. 17. Nodal spines. 18. Nodal prongs. 19. Nodal points. 20. Proximal node pigment shape. 21. Mid-

	Character number													
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Grus canadensis	b	c	a	1	a	c	b	b	1	a	c	b	0	a
Fulica americana	a	?	?	1	b	a	c	b	0	a	c	b	0	a&b
Pterocles namaqua	a	?	?	1	a	b	a	b	1	c	c	b	0	a
Pterocles orientalis	a	?	?	1	a	b	c	b	1	c	c	b	0	a
Syrrhaptes paradoxus	a	?	?	1	a	c	a	b	1	c	c	b	0	a
Lophotis ruficrista	a	?	?	1	a	b	b	b	1	b	c	b	0	a
Gavia adamsii	b	c	a	0	c	c	b	a	1	a	?	c	0	d
*Himantopus himantopus**†	b	c	b	0	b	b	a	a	1	a	?	a	0	a
*Cladorhynchus leucocephalus**†	b	c	b	0	b	b	a	a	1	a	?	a	0	a
*Recurvirostra americana**†	b	c	a	0	b	c	a	a	1	a	?	a	0	a
*Ibidorhyncha struthersii**†	b	a	a	1	a	b	c	d	1	a	b	a	0	a
*Haematopus bachmani**†	b	b	a	1	b	b	b	c	1	a	b	a	0	a
*Haematopus palliatus**†	b	c	a	0	b	b	b	a	1	a	?	a	0	a
*Pluvianus aegyptius**†	c	c	a	0	b	a	a	a	1	a	?	a	0	a
*Cursorius chalcopterus**†	a	?	?	1	b	a	c	b	1	a	c	a	0	a
*Cursorius cursor**†	a	?	?	1	b	a	c	b	1	a	c	b	1	a
*Glareola pratincola**†	b	b	a	1	b	b	a	b	1	a	c	b	0	b
*Stiltia isabella**	a	?	?	1	b	b	a	b	1	a	c	b	0	b
*Vanellus vanellus**†	b	b	b	1	b	a	a	b	1	a	c	a	1	a
*Vanellus indicus**	b	b	a	1	b	a	c	e	1	a	c	a	0	a
*Vanellus lugubris**	b	b	b	1	b	a	a	b	1	a	c	a	0	a
Vanellus cayanus†	b	c	b	0	b	a	a	a	1	a	a	b	0	a
*Vanellus chilensis**†	b	a	b	1	b	a	a	b	1	a	c	a	0	a
*Vanellus spinosus**	b	a	b	1	b	a	a	b	1	a	b	a	0	a
*Charadrius tricollaris**†	a	?	?	1	b	b	a	e	1	a	c	a	1	a
*Charadrius alexandrius**†	a	?	?	1	b	b	a	c	1	a	c	a	1	a
*Charadrius mongolus**	c	a	a	1	b	b	a	c	1	a	c	a	0	a
*Charadrius montanus**†	c	a	a	1	b	a	a	b	1	a	c	a	0	a
*Charadrius vociferus**†	b	a	a	1	b	b	a	b	1	a	c	a	1	a
*Anarhynchus frontalis**	b	a	a	1	b	c	a	e	1	a	b	a	1	a
*Pluvialis squatarola**	b	a	b	1	b	c	a	b	1	a	c	a	0	a
*Eudromias morinellus**	a	?	?	1	b	b	a	b	1	a	c	a	0	a
*Jacana jacana**†	b	b	a	1	b	a	a	b	1	a	c	c	0	a
*Rostratula benghalensis**†	b	b	a	1	b	c	a	b	1	a	c	a	0	a
*Bartramia longicauda**†	b	b	b	1	b	a	a	b	1	a	c	a	0	a
*Numenius americanus**†	b	b	b	1	b	a	a	b	1	a	c	a	0	a
*Tringa nebularia**†	b	a	b	1	b	b	a	b	1	a	c	a	0	a
*Tringa flavipes**†	b	a	a	1	b	b	a	b	1	a	c	a	1	a
*Limosa haemastica**†	b	b	b	1	b	b	a	b	1	a	c	a	0	a
*Catoptrophorus semipalmatus**	b	a	a	1	b	b	c	b	1	a	c	a	0	a
*Xenus cinereus**	b	a	a	1	b	b	a	b	1	a	c	a	0	a
*Actitis macularia**	c	b	a	1	b	c	a	e	1	a	c	a	0	a
*Heteroscelus incanus**†	b	a	b	1	b	b	c	b	1	a	c	a	1	a
*Prosobonia cancellata**	a	?	?	1	b	c	c	b	1	a	c	a	1	a
*Arenaria interpres**†	c	a	a	0	b	b	c	b	1	a	c	a	1	a
*Scolopax rusticola**†	b	b	a	1	a	b	b	b	1	b	c	b	0	b

APPENDIX 3 Extended.

node pigment shape. 22. Distal pigment distribution. 23. Nodal pigment intensity at basal nodes. 24. Nodal pigment intensity at distal nodes. 25. Pigment color. 26. Morphology of first node. 27. Internode pigmentation. 28. Distal cell length. 29. Distal cell morphology. 30. True down pigmentation. 31. True down nodes. 32. True down pigment shape. 33. True down pigmented like contour down. 34. True down pigmented like afterfeather down. 35. Afterfeather pigmentation. 36. Afterfeather down pigmented like contour feather down. 37. Villi. 38. Distal prong morphology.

Character number																							
15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
c	a	c	0	a	g	g	e	1	b	a	b	b	1	0	a	c	?	0	1	c	0	0	?
d	b	a	1	a	b	b	b	2	c	b	c	c	1	0	c	a	a	1	0	c	1	0	1
b	b	b	0	a	f	f	b	1	b	c	b	d	1	0	c	c	e	1	1	c	1	0	?
b	b	c	0	a	f	f	b	1	b	c	b	d	1	0	c	c	e	1	1	c	1	0	?
b	b	b	0	a	f	f	b	1	b	c	b	d	1	0	c	c	e	1	?	?	?	0	?
b	a	c	0	a	g	g	e	2	c	c	b	d	1	0	c	c	f	1	1	c	1	0	?
e	a	a	1	a	?	?	?	?	?	?	b	?	1	0	c	a	b	0	1	b	0	0	2
b	b	c	0	a	?	?	?	?	?	?	a	?	1	0	c	c	a	0	1	b	0	0	?
b	b	b	0	a	?	?	?	?	?	?	c	?	1	0	b	c	b	0	1	b	0	0	?
b	b	b	0	a	?	?	?	?	?	?	c	a	1	0	b	c	b	0	1	b	0	1	?
b	b	b	0	a	d	b	a	?	?	?	a	a	1	0	c	c	c	0	1	c	0	1	?
b	a	c	0	a	c	c	a	1	a	b	c	b	1	0	c	c	b	1	1	c	1	1	?
b	b	c	0	a	?	?	?	?	?	?	c	?	1	0	b	c	b	0	1	b	0	0	?
b	b	b	0	a	?	?	?	?	?	?	a	?	1	0	a	c	?	1	1	a	1	0	?
b	c	c	0	a	d	d	d	2	c	b	a	b	1	0	c	d	c	1	1	c	1	0	?
b	c	c	0	a	d	d	b	2	c	b	a	b	1	0	c	b	c	1	1	c	1	1	?
b	b	a	0	b	d	d	d	2	c	b	a	b	1	0	c	b	c	1	1	c	1	0	?
b	b	a	0	b	d	d	d	2	c	b	a	b	1	0	c	b	c	1	1	c	1	1	?
b	b	c	0	d	d	d	d	2	c	b	a	b	1	0	c	c	c	1	1	c	1	0	?
b	b	b	0	a	b	b	d	2	c	b	c	b	1	0	c	c	a	1	1	c	1	1	?
b	b	b	0	a	c	c	d	1	a	b	c	b	1	0	c	c	a	1	1	c	1	1	?
b	a	c	0	a	?	?	?	?	?	?	a	?	1	0	c	c	a	0	1	b	0	0	?
b	b	c	0	a	c	c	d	1	b	b	a	c	1	0	c	c	a	0	1	c	1	0	?
b	b	c	0	a	c	c	d	1	b	b	a	c	1	0	c	c	a	1	1	c	1	0	?
b	b	b	0	a	d	d	c	2	a	b	a	b	1	0	c	c	c	1	1	c	1	1	?
b	b	b	0	a	d	d	a	2	a	b	a	b	1	0	c	c	c	1	1	c	1	0	?
b	b	b	0	a	d	d	c	2	c	b	a	b	1	0	c	c	c	1	1	c	1	1	?
b	b	b	0	a	d	d	c	2	c	b	a	b	1	0	c	c	d	1	1	c	1	1	?
b	b	b	0	d	d	d	c	2	c	b	a	b	1	0	c	c	c	1	1	c	1	1	?
b	b	b	0	a	d	d	a	2	a	b	a	b	1	0	c	c	c	1	1	c	1	1	?
b	b	b	0	a	b	b	c	2	b	b	a	b	1	0	c	c	a	1	1	c	1	1	?
b	b	c	0	d	d	d	c	2	c	b	c	b	1	0	c	d	d	1	1	c	1	1	?
b	b	b	0	a	c	c	d	2	c	a	b	c	1	0	c	a	b	1	1	c	1	0	?
b	b	b	0	a	b	c	d	2	b	b	b	c	1	0	c	a	a	1	1	c	1	0	?
b	b	b	0	a	b	b	b	2	c	b	a	c	1	0	c	c	a	1	1	c	1	0	?
b	b	b	0	a	b	b	d	2	b	b	c	b	1	0	c	c	a	1	1	c	1	0	?
b	b	c	0	d	b	b	d	2	c	b	c	b	1	0	c	c	c	1	1	c	1	0	?
b	b	c	0	d	d	d	c	2	c	b	a	b	1	0	c	c	c	1	1	c	1	1	?
b	b	b	0	a	b	b	d	2	c	b	c	b	1	0	c	c	a	1	1	c	1	0	?
b	b	b	0	a	b	b	c	2	c	b	a	c	1	0	c	c	a	1	1	c	1	0	?
b	b	b	0	d	d	d	a	2	a	b	a	b	1	0	a	c	?	0	0	c	1	0	?
b	b	b	0	a	d	d	c	2	c	b	a	b	1	0	c	c	c	1	1	c	1	0	?
b	b	b	0	a	d	d	b	2	c	b	a	b	1	0	c	c	c	1	1	c	1	0	?
b	b	b	0	a	d	d	d	2	c	b	a	b	1	1	c	c	c	1	1	c	1	0	?
b	b	b	0	a	d	e	c	2	c	b	c	a	1	0	c	d	d	1	1	c	1	1	?
a	a	c	0	a	c	c	d	1	b	a	b	c	1	0	c	d	b	1	1	c	1	0	?

APPENDIX 3 Continued.

Taxon	Character number													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
*Scolopax minor**†	b	b	a	1	a	b	c	b	1	b	c	b	0	a
*Lymnocryptes minimus**†	a	?	?	1	b	b	a	b	1	a	c	a	1	a
*Limnodromus griseus**†	c	b	a	1	b	b	a	b	1	a	c	a	1	a
*Gallinago nigripennis**†	b	b	a	1	b	b	a	b	1	a	c	a	1	a
*Gallinago gallinago**†	b	b	a	1	b	b	a	b	1	a	c	a	1	a
*Aphriza virgata**†	b	b	a	1	b	b	a	b	1	a	c	a	1	a
*Calidris bairdii**	c	b	a	1	b	b	a	b	1	a	c	a	1	a
*Calidris alpina**†	c	b	a	1	b	b	a	b	1	a	c	a	1	a
*Calidris canutus**	c	b	a	1	b	b	a	b	1	a	c	a	1	a
*Calidris alba**†	b	a	a	1	b	b	a	b	1	a	c	a	1	a
*Calidris pusilla**	a	?	?	1	b	b	a	b	1	a	c	a	1	a
*Calidris minutilla**	a	?	?	1	b	b	a	b	1	a	c	a	1	a
*Limicola falcinellus**	b	c	a	1	b	c	a	b	1	a	c	a	1	a
*Eurynorhynchus pygmeus**	a	?	?	1	b	c	a	e	1	a	c	a	1	a
*Micropalama himantopus**	c	a	a	1	b	a	a	b	1	a	c	a	0	a
*Tryngites subruficollis**	b	c	a	1	b	a	b	e	1	a	c	a	1	a
*Philomachus pugnax**	b	a	a	1	b	c	a	b	1	a	c	a	0	a
*Phalaropus tricolor**†	a	?	?	1	b	b	a	e	1	a	c	a	1	a
*Phalaropus lobatus**†	a	?	?	1	b	b	b	c	1	a	c	a	1	a
*Uria aalge**†	b	b	a	1	c	d	a	c	1	a	c	c	0	d
Synthliboramphus antiquus	b	b	a	1	c	d	a	d	1	a	c	c	0	d
Alle alle	b	b	c	1	c	d	a	b	1	a	c	c	0	d
Ptychoramphus aleuticus	b	b	a	1	c	d	a	b	1	a	b	c	0	d
Aethia pusilla	b	b	b	1	c	d	a	b	1	a	c	a	0	d
Cyclorrhynchus psittacula	b	b	c	1	c	d	a	b	1	a	b	c	0	c
Cerorhinca monocerata	b	b	a	1	c	d	a	b	1	a	c	c	0	d
Fratercula arctica	b	b	b	1	c	d	a	b	1	a	c	c	0	d
Lunda cirrhata	b	b	b	1	c	d	c	b	1	a	c	c	0	d
Alca torda	b	b	c	1	c	d	a	b	1	a	c	c	0	d
Cepphus columba†	b	b	b	1	c	d	c	b	1	a	c	c	0	d
Brachyramphus marmoratus	b	b	b	1	c	d	a	e	1	a	c	c	0	d
*Dromas ardeola**†	b	c	a	0	b	b	b	a	1	a	?	a	0	a
*Catharacta skua**	b	c	a	0	b	a	b	d	1	a	b	a	0	a
*Stercorarius longicaudus**†	b	c	b	1	b	a	c	d	1	a	b	a	0	a
*Rynchops niger**†	b	c	a	0	b	a	a	a	1	a	a	a	0	a
*Rynchops flavirostris**	b	b	a	1	b	a	a	c	1	a	c	a	0	a
*Larus delawarensis**	b	c	a	0	b	b	c	a	1	a	?	b	0	a
Larus pacificus†	b	c	a	0	b	a	c	a	1	a	?	b	0	a
*Larus argentatus**	b	c	a	0	b	c	b	a	1	a	?	b	0	a
Larus atricilla†	b	c	a	0	b	c	c	a	1	a	?	b	0	a
*Rissa tridactyla**†	b	c	a	0	b	a	c	a	1	a	?	b	0	a
*Xema sabini**	b	c	b	0	b	a	a	a	1	a	?	a	1	a
*Rhodostethia rosea**†	b	c	b	0	b	a	c	a	1	a	?	b	0	a
Pagophila eburnea†	b	c	a	0	b	c	b	a	1	a	?	b	0	a
*Creagrus furcatus**	b	c	a	0	b	c	b	a	1	a	?	a	0	a
*Sterna sandvicensis**	b	c	b	0	b	a	a	a	1	a	?	a	0	a
*Sterna hirundo**	b	c	b	0	b	a	a	a	1	a	?	a	0	a
Sterna forsteri	b	c	b	0	b	c	a	a	1	a	?	a	0	a
Sterna fuscata	b	c	b	0	b	c	a	a	1	a	?	a	0	a
*Larosterna inca**	b	c	b	1	b	a	a	d	1	a	b	a	0	a
Procelsterna cerulea	b	b	a	1	b	c	a	b	1	a	b	a	0	a
*Chlidonias niger**	b	c	a	1	b	c	a	d	1	a	?	a	0	a
*Anous stolidus**	b	c	b	1	b	c	c	a	1	a	b	c	0	a
*Gygis alba**	b	c	b	0	b	c	a	a	1	a	?	a	0	a
*Phaetusa simplex**	b	c	b	0	b	c	a	a	1	a	?	a	0	a
*Gelochelidon nilotica**†	b	c	b	0	b	b	a	a	1	a	?	a	0	a

APPENDIX 3 Continued, Extended.

Character number																							
15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
d	a	c	0	a	b	b	d	2	c	b	c	c	1	0	c	d	a	1	1	c	1	0	?
b	b	b	0	a	d	d	d	2	c	b	c	c	1	0	c	c	c	1	1	c	1	1	?
b	b	c	0	d	b&c	c&d	d	2	c	b	c	b	1	0	c	c	c	1	1	c	1	0	?
b	c	b	0	a	d	b	d	2	c	b	b	c	1	0	c	c	c	1	1	c	1	0	?
c	c	b	0	a	d	b	d	2	c	b	b	c	1	0	c	c	c	1	1	c	1	0	?
b	b	c	0	d	d	d	c	2	c	b	a	b	1	0	c	c	c	1	1	c	1	0	?
b	b	b	0	a	d	d	c	2	c	b	a	a	1	0	c	d	d	1	1	c	1	1	?
b	b	c	0	d	d	d	c	2	c	b	a	b	1	0	c	d	c	1	1	c	1	0	?
b	b	c	0	d	d	d	c	2	c	b	a	b	1	0	c	c	c	1	1	c	1	0	?
b	b	c	0	d	d	a	c	2	c	b	a	a	1	0	c	d	c	1	1	c	1	0	?
b	b	c	0	d	d	d	c	2	c	b	a	b	1	0	c	c	c	1	1	c	1	1	?
b	b	c	0	d	d	e	c	2	c	b	a	a	1	0	c	c	d	1	1	c	1	0	?
b	b	b	0	a	d	d	c	2	c	b	a	b	1	0	c	c	c	1	1	c	1	0	?
b	b	b	0	a	d	d	a	2	c	b	c	a	1	0	c	c	c	1	1	c	1	1	?
b	b	b	0	a	d	d	d	2	c	b	c	b	1	0	c	c	c	1	1	c	1	1	?
b	b	c	0	d	d	d	d	2	c	b	c	b	1	0	c	c	c	1	1	c	1	1	?
b	b	b	0	a	b	d	d	2	c	b	c	b	1	0	c	c	c	1	1	c	1	1	?
b	b	a	0	b	d	b	c	2	c	b	b	c	1	0	c	c	c	1	1	c	1	1	?
b	b	a	0	b	d	b	c	2	a	b	b	b	1	0	c	c	c	1	1	c	1	1	?
e	c	a	1	a	c	c	a	1	b	a	b	b	1	0	c	a	b	1	1	c	1	0	2
e	c	a	1	a	b	b	c	2	b	b	b	b	1	0	c	a	b	1	1	b	1	0	2
e	c	a	1	a	b	b	d	2	b	b	b	c	1	0	c	a	b	1	1	c	1	0	2
e	c	a	1	a	c	c	d	1	b	b	b	b	1	0	c	a	b	1	1	c	1	0	2
d	c	a	1	a	b	b	d	2	b	b	b	b	1	0	c	a	b	1	1	b	1	0	2
e	c	a	1	a	c	a	a	1	a	b	b	b	1	0	c	a	b	1	1	b	1	0	1
e	c	a	1	a	c	c	d	1	b	a	b	b	1	0	c	a	b	1	1	c	1	0	1
e	c	a	1	a	c	c	d	1	b	a	b	b	1	0	c	a	b	1	1	c	1	0	1
e	c	a	1	a	c	c	d	2	b	a	b	c	1	0	c	a	b	1	1	c	1	0	1
e	c	a	1	a	c	c	d	1	b	b	b	b	1	0	c	a	b	1	1	b	1	0	1
e	c	a	1	a	c	c	d	1	b	a	b	c	1	0	c	a	b	1	1	c	1	0	1
e	c	a	1	a	c	a	a	2	b	b	b	b	1	0	c	a	a	1	1	b	1	0	2
b	b	b	0	a	c	?	?	?	?	?	b	?	1	0	a	c	?	1	1	a	1	0	?
b	b	c	1	a	?	?	?	?	?	?	b	b	1	0	c	c	b	1	1	d	1	0	2
b	b	c	1	a	c	c	a	1	b	b	b	b	1	0	c	c	b	1	1	b	1	0	1
b	b	b	0	a	?	?	?	?	?	?	b	?	1	0	b	c	b	0	0	a	1	0	?
b	b	b	0	a	c	a	d	1	c	b	b	b	1	0	b	c	b	1	1	b	1	0	?
b	a	a	0	c	?	?	?	?	?	?	b	?	1	0	c	b	a	0	0	b	0	0	?
b	a	a	0	c	?	?	?	?	a	b	b	?	1	0	c	b	c	0	0	b	1	0	?
b	a	a	0	c	?	?	?	?	?	?	b	?	1	0	b	b	a	0	1	b	1	0	?
b	b	a	0	c	?	?	?	?	?	?	b	?	1	0	c	b	c	0	1	b	0	0	?
b	b	a	0	c	?	?	?	?	?	?	b	?	1	0	c	b	c	0	0	a	1	0	?
b	b	b	0	a	?	?	?	?	?	?	b	?	1	0	c	b	c	0	1	b	0	0	?
b	a	b	0	c	?	?	?	?	?	?	b	?	1	0	b	b	c	0	1	c	1	0	?
b	b	a	0	c	?	?	?	?	?	?	b	?	1	0	b	b	a	0	0	a	1	0	?
b	b	d	0	e	?	?	?	?	?	?	b	?	1	0	b	b	a	0	0	a	1	0	?
b	b	d	0	e	?	?	?	?	?	?	b	?	1	0	a	c	?	1	1	a	1	0	?
b	b	d	0	a	?	?	?	?	?	?	b	?	1	0	a	c	?	1	1	a	1	0	?
b	b	d	0	e	?	?	?	?	?	?	b	?	1	0	c	c	a	0	0	a	1	0	?
b	b	d	0	e	?	?	?	?	?	?	b	?	1	0	c	c	a	0	0	a	1	0	?
b	b	b	0	a	c	a&b	a	1	b	b	b	a	1	0	c	c	b	1	1	b	1	0	?
b	b	b	0	a	b	c	a	2	b	b	b	b	1	0	c	c	b	1	1	c	1	0	?
b	b	b	0	a	b&c	a&b	a	?	?	?	b	a	1	0	c	c	a	1	1	c	1	0	?
e	b	b	0	a	g	?	?	1	a	a	b	b	1	0	c	c	b	0	0	d	1	0	?
b	b	b	0	a	?	?	?	?	?	?	b	?	1	0	a	c	?	1	1	a	1	0	?
b	b	c	0	a	?	?	?	?	?	?	b	?	1	0	a	c	?	1	1	a	1	0	?
b	b	b	0	a	?	?	?	?	?	?	b	?	1	0	c	c	a	0	0	a	0	0	?

APPENDIX 3 Continued.

Taxon	Character number													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
*Sterna caspia**	b	c	b	0	b	b	c	a	1	a	?	a	0	a
*Chionis alba**†	b	c	a	0	b	b	b	a	1	a	?	a	0	a
*Pluvianellus socialis**†	c	a	a	1	b	b	c	e	1	a	c	a	1	a
Pedionomus torquatus	a	?	?	1	b	b	c	b	1	a	c	a	0	a
*Attagis gayi**†	a	?	?	1	a	b	a	b	1	b	c	a	0	b
*Thinocorus orbignyianus**	a	?	?	1	a	c	a	b	1	a	c	a	1	b
*Thinocorus rumicivorus**†	a	?	?	1	b	c	a	b	1	a	c	a	1	b
*Burhinus oedicnemus**†	b	b	b	1	b	a	b	b	1	a	b	c	0	a
Esacus recurvirostris†	b	b	b	1	b	c	b	b	1	a	b	a	0	a

* Taxa shared with Strauch's (1978) list.
† Taxa shared with Chu's (1995) list.

APPENDIX 3 Continued, Extended.

Character number																							
15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
b	b	b	0	a	?	?	?	?	?	?	b	?	1	0	a	c	?	1	1	a	1	0	?
b	b	d	0	e	a	a	a	1	a	a	b	a	1	0	c	c	a	0	0	a	1	0	?
b	b	b	0	a	d&e	d	c	2	a	b	c	a	1	0	c	d	c	1	1	c	1	0	?
b	b	c	0	d	d	d	b	2	c	b	c	b	1	0	c	c	c	1	1	c	1	0	?
c	b	a	0	b	e	e	c	2	c	b	c	a	1	0	c	b	d	1	1	c	1	0	?
c	b	a	0	b	e	e	c	2	c	b	c	b	1	0	c	b	d	1	1	c	1	0	?
c	b	a	0	b	e	e	c	2	c	b	c	a	1	0	c	b	d	1	1	c	1	0	?
e	c	c	0	a	c	c	a	1	a	a	b	b	1	0	c	c	b	1	1	c	1	0	?
b	b	c	0	a	c	c	a	?	?	?	b	b	1	0	c	c	b	1	1	c	1	0	?

APPENDIX 4 OSTEOLOGICAL CHARACTER MATRIX FOR OUTGROUP TAXA

Sixty-eight osteological characters coded for six outgroup taxa in this study. Character descriptions follow Strauch (1978). Strauch's character numbers 51 and 59 were rejected by Chu (1995) and not coded here. Character number 11 was coded according to Strauch.

	Taxon					
Character no.	*Grus canadensis*	*Fulica americana*	*Pterocles orientalis*	*Syrrhaptes paradoxus*	*Lophotis ruficrista*	*Gavia adamsii*
1	a	a	b	b	a	b
2	b	b	a	a	b	a
3	a	a	a	a	a	a
4	a	a	a	a	a	a
5	b	b	b	b	b	b
6	a	a	a	a	a	a
7	a	b	a	a	b	b
8	b	b	b	b	b	a
9	a	a	a	a	a	a
10	a	b	b	b	a	a
11	a	a	b	b	a	a
12	a	a	a	a	a	a
13	a	a	a	a	a	b
14	b	b	b	b	b	b
15	b	b	b	b	b	a
16	b	b	b	b	b	b
17	b	b	?	?	b	b
18	b	b	a	a	a	a
19	a	a	a	a	a	a
20	a	a	a	a	a	c
21	b	b	c	c	a	b
22	a	a	?	?	a	a
23	a	a	b	b	a	a
24	?	?	?	?	?	?
25	?	?	?	?	?	?
26	?	?	?	?	?	?
27	?	?	?	?	?	?
28	?	?	?	?	?	?
29	?	?	?	?	?	?
30	?	?	?	?	?	?
31	d	c	e	e	e	d
32	c	a	a	a	b	?
33	a	a	a	a	a	a
34	a	a	a	a	a	a
35	d	a	b	a	b	d
36	a	a	b	b	b	a
37	b	b	c	c	c	c
38	b	b	a	a	b	b
39	a	a	b	b	b	a
40	a	b	b	b	a	a
41	a	a	a	?	b	a

APPENDIX 4 Continued.

	Taxon					
Character no.	*Grus canadensis*	*Fulica americana*	*Pterocles orientalis*	*Syrrhaptes paradoxus*	*Lophotis ruficrista*	*Gavia adamsii*
42	a	a	a	a	a	a
43	a	a	a	a	a	a
44	b	b	b	b	b	b
45	a	a	a	a	a	a
46	a	a	a	a	a	a
47	?	?	?	?	?	?
48	a	a	a	a	a	a
49	?	?	?	?	?	?
50	b	a	c	c	a	c
51						
52	a	a	b	b	a	b
53	?	a	a	a	b	a
54	c	a	a	a	c	a
55	a	a	a	a	a	a
56	a	b	b	b	a	a
57	b	b	a	b	c	a
58	a	a	b	a	b	b
59						
60	a	a	b	b	a	a
61	b	b	b	b	c	b
62	a	a	b	b	a	b
63	a	a	a	a	b	c
64	b	a	a	a	b	b
65	a	a	a	a	a	?
66	a	a	a	a	a	a
67	a	a	a	a	a	a
68	a	a	a	a	a	a
69	a	a	a	a	a	a
70	a	a	a	a	b	b

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