THE FUNCTIONAL ANATOMY OF THE SKIN MUSCLES IN PHASIANINAE

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This is to certify that the

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of the Skin Muscles
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presented by

David R. Osborne

has been accepted towards fulfillment
of the requirements for

PhD degree in Zoology

George J. Wallace
George J. Wallace
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Date September 20, 1968

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ABSTRACT

THE FUNCTIONAL ANATOMY OF THE SKIN MUSCLES IN PHASIANINAE

By

David R. Osborne

Although a great deal of information is available concerning the descriptions, functions, causations and the origin and evolution of feather displays, little is known about the mechanisms responsible for positioning the feather in display. Two categories of skin muscles associated with the feathers may be involved: (1) the striated dermal muscles and (2) the smooth feather muscles.

This study was undertaken to describe the gross morphology of the skin muscles and attempt to determine their relationship to feather display.

Feather displays and the gross anatomy of the smooth and striated muscles of the skin are described and compared among several representatives of 4 genera of the Subfamily Phasianinae. The Ring-necked Pheasant is used as a type for comparison with other forms.

Deductions of muscle action are based upon morphological evidence, from observations of feather movement

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during display and preening, and from experiments involving muscle stimulation and muscle extirpation in live birds.

Examination of pterylosis showed few differences in the arrangement of the feathers among taxa. Differences in the relative thickness of the skin in different regions of the plumage among birds corresponded to the localization of specialized display feathers, to the enlargement of follicles and to the relative development of the feather muscles.

Pavo is distinctive from the other forms in having intercalary downs present among contour feathers of the crown and pelvic tract.

Three functional types of smooth muscles associated with the feathers are described: (1) musculoelastic tissue, (2) tensor muscles and (3) feather muscles. Musculoelastic tissue shows little variability among taxa.

Smooth tensor muscles of the skin are of limited distribution in the birds I examined. They showed great variability among taxa. All are attached to follicles of specialized display feathers.

The relative development, pattern and arrangement of the feather muscles differ appreciably among pterylae in individual males of the same species. This appears related to the fact that feathers in different regions of the plumage on the same individual may assume different feather postures during display.

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David R. Osborne

Feather musculature and feather displays were most similar in homologous regions among different breeds of chickens and among congeneric species.

The gross pattern of the feather muscles is similar in both sexes of the same species, but feather musculature is less well developed in the hens. This appears to be because hens sometimes perform feather displays that are similar to but weaker than those of males.

Greatest differences in the size, arrangement and pattern of the feather and tensor muscles are found in homologous dorsally located tracts among males of different genera. This appears to be because most conspicuous feather displays in homologous regions in males entail strikingly different movements of the feathers.

Results from preliminary experiments involving direct stimulation of the dermal and feather muscles demonstrated that the dermal muscles move the skin while the feather muscles move the feathers.

The distribution and arrangement of the dermal muscles differ little in homologous regions among taxa.

Histological examination of teased dermal muscles at the insertions revealed that they did not attach to the follicles; only smooth muscles do.

Dermal muscles show little, if any, relationship to feather displays. Apparently they act to tighten the skin in particular regions of the body which in turn appears to be coordinated with other body functions.

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Finally, results of this study strongly suggest that modifications of the feather muscles appear to be adaptations for feather displays in order to make movement of the feathers possible. This in turn makes particular regions of the plumage more conspicuous.

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THE FUNCTIONAL ANATOMY OF THE SKIN MUSCLES IN PHASIANINAE

By

David R.oy Osborne

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
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DOCTOR OF PHILOSOPHY

Department of Zoology

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ACKNOWLEDGMENTS

I wish to express my sincere appreciation to Dr. Peter Stettenheim for his interest, advice and aid throughout the course of this study and for perusing the several drafts of the manuscript. Appreciation is also expressed to Dr. George J. Wallace and Dr. Alfred M. Lucas for their critical review of the final draft and to Dr. Rollin H. Baker, Dr. James C. Higgins and Dr. Robert K. Ringer for their helpful suggestions.

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Gratitude is expressed to Dr. Alfred M. Lucas and to Dr. Peter Stettenheim of the Avian Anatomy Project, U. S. Department of Agriculture, Department of Poultry Science, Michigan State University for making available portions of their unpublished manuscript on Avian Integument.

Special thanks are extended to my wife, Alice, for her patience, help and encouragement during the past four years.

I am also indebted to many members of the Michigan Game Breeders Association who donated birds for this work.

I am grateful to the faculty, staff and Mrs. Dale Henderson of the Department of Zoology of Michigan State University for their help.

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INTRODUCTION

The positioning of body feathers during display has been the subject of numerous investigations in avian behavior. Descriptions of feather displays occurring during courtship or agonistic behavior have been reported for many birds (Hingston, 1933; Stoner, 1940; Andrew, 1961; Armstrong, 1965). Feather displays may be non-specialized in which there is a generalized raising of all body feathers, occurring for example in the Zebra Finch, *Poephila guttata* (Morris, 1954) or in the Chaffinch, *Fringilla coelebs* (Hinde, 1953). According to Morris (1956), feather displays may also be specialized where exaggerated movements of body feathers are restricted to certain areas of the plumage (e.g., the ruff of the Great Crested Grebe (*Podiceps cristatus*), the crest of the Sulphur-crested Cockatoo (*Kakatoe galerita*), the "beard" of the Capercaillie (*Tetrao urogallus*), and the "eye" tufts of the Superb Bird-of-paradise (*Lophorina superba*).

The origin and evolution of display functions from non-display functions were first termed by Huxley (1923) as "ritualization". The origin and evolution of feather displays from non-signal functions have recently received considerable attention (Daanje, 1950; Morris, 1956; Tinbergen,

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1952, 1954; Andrew, 1961). It is generally assumed that feather displays are derived from feather movements which occur during thermo-regulation (Morris, 1956); but feather movements which occur during preening and shaking of the feathers, shaping the nest cup and during defecation are also considered as possible sources (Andrew, 1961: 338).

Although a great deal of information is available concerning the descriptions, functions, causations and origin and evolution of feather display, little is known about the motor mechanism responsible for positioning the feathers.

Two categories of skin muscles are associated with the feathers and appear to be involved in feather movement. First are the dermal components of body muscles, apparently first described by Jacquemin (1836). These striated muscles are innervated by spinal nerves, originate from the skeleton or a part of a body muscle, and insert onto the under surface of the skin. The second category includes the smooth feather muscles and a deeper network of musculoelastic tissue. The feather muscles, apparently first described by Nitzsch (1840), link adjacent feathers and are innervated by the sympathetic (Langley, 1904; Ostman et al., 1963a) and possibly the parasympathetic nervous systems (Ostman et al., 1963a). Feather muscles are located within the dermis.

Very little is known about the arrangement and distribution of feather muscles in birds. Brief descriptions were given by Seuffert (1862) for several birds of prey and

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waterfowl. He found feather muscles associated with contour body feathers, rectrices, remiges and down. Lowe (1933) described and figured the gross arrangement of the feather muscles in the Magellanic Penguin, *Sphenicus magellanicus*, and the Crested Screamer, *Chauna torquata* (*Chauna salvadorii*).

Published information concerning the action of the dermal and feather muscles in feather movement is contradictory and confusing. Owen (1842, 1866) related the distinct and extensive dermal muscles in the South Island Kiwi (*Apteryx australis*) to the burrowing habits of the species which shakes off loose earth from its plumage while excavating its chamber. Helm (1884, 1886) examined both the dermal and the feather muscles in numerous birds, but his account of the feather muscles is brief. He concluded that the size of the feather muscles varied over the body with the size and frequency of feather movement and that the action of these muscles was to assist in the ruffling and laying down of contour feathers. He also concluded that a ruffling of the plumage was possible with the dermal muscles.

It was Langley's (1904) detailed analysis on the structure, innervation, and action of the feather muscles in the chicken and pigeon which focused attention upon the feather muscles as functioning to position the feathers. After observation and stimulation of the sympathetic nervous system and spinal nerves, he concluded that the feather muscles act to erect, depress and retract the feathers,

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A search of the literature reveals very little information on the relationship of the dermal and feather muscles to feather display. Hemming (1844: 212), in his analysis of the display of the Indian Peafowl (*Pavo cristatus*), reported that the small muscles between the quills of the train were inadequate alone to raise and spread the train and that elevation of the tail played the major role in elevating the train. Viallane (1878) stated that two dermal muscles, M. temporo-alaire (= M. cucullaris pars propatagialis) and M. fronto-iliac (= M. latissimus dorsi dorsocutaneus), were responsible for the display in the Superb Bird-of-paradise (*Lophorina superba*). Similarly, Pycraft (1905) concluded that the dermal slips of M. pectoralis controlled the elevation of pectoral feathers in the display of the Lesser Bird-of-paradise (*Paradisea minor*). He also noted strands of "minute" muscle passing from feather to feather but did not comment on their role in display. Stettenheim *et al*. (1963: 920), in a comprehensive study of the arrangement and action of the feather muscles in Single Comb White Leghorn chickens (*Gallus gallus*), found that feather musculature was heaviest and most complex on the dorsal region of the neck. They related this to the fact that the most conspicuous displays of these birds entail pronounced raising of the hackles.

Several factors may account for the lack of knowledge concerning the action of the skin muscles in positioning the

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feathers. First, in many studies on the descriptive and functional anatomy of the appendicular muscles the common procedure is to remove the skin and discard it. In this way both the feather muscles and some of the insertion ends of the dermal muscles are lost. Second, if the dermal muscles are studied without examining the skin, erroneous conclusions can be formulated on muscle course, action and function. This may have contributed to the confusing descriptions which I found in the literature on the dermal muscles. I know of no thorough morphological investigations on both the dermal and the smooth muscles in a closely related group of birds having different habits. Also, subsequent to Langley, I know of no studies involving observation and experimentation on muscle action and feather movements in live birds.

This study was undertaken in an attempt to determine the relationship of the striated and smooth muscles of the skin to feather display in certain representatives of the Subfamily Phasianinae. Birds of this group were selected because they represent a relatively closely-knit group taxonomically, are of large size, are easy to maintain in captivity, and because they possess modified feathers such as crests, hackles, capes and trains which are displayed during courtship or reproductive fighting. My hypothesis is that differences in feather display are related to morphological variations in one or both categories of skin muscles.

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The generalized and specialized feather displays of single comb White Leghorn, bantam Rhode Island Red and Araucana chickens (*Gallus gallus*), Golden and Lady Amherst Pheasants (*Chrysolophus pictus* and *C. amherstiae*), the Indian Peafowl (*Pavo cristatus*), and the Ring-necked Pheasant (*Phasianus colchicus*) will be described. An attempt will be made to standardize the terminology of the dermal muscles. Similarities and differences in the gross morphology of the dermal and feather musculature will be compared and related to feather display.

The action of the feather and dermal muscles in moving the feathers will be deduced from morphological evidence, from observations of feather movement during display and preening, and from experiments involving nerve and muscle stimulation and muscle extirpations in live birds.

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METHODS

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Birds used in this study were captive adult Ring-necked Pheasants (*Phasianus colchicus*), Single Comb White Leghorn, Araucana and bantam Rhode Island Red chickens (*Gallus gallus*), Golden and Lady Amherst Pheasants (*Chrysolophus pictus* and *C. amherstiae*), and Indian Peafowls (*Pavo cristatus*). For the sake of brevity, generic names used in the text refer to the above representatives of the genus and not to the entire genus. *Chrysolophus*, when used, refers to both *Chrysolophus pictus* and *C. amherstiae*. Nomenclature for the pheasants is from Delacour (1951). Descriptions for *Phasianus* are presented first, then comparisons are made with the other representatives.

Single Comb White Leghorn chickens were obtained from the Department of Poultry Science at Michigan State University, East Lansing, Michigan; the bantam Rhode Island Red and Araucana chickens, peafowl, Ring-necked and ornamental pheasants, from local game breeders. All birds were of known age and many were utilized for several different aspects of this study.

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The study was conducted at the W. K. Kellogg Bird Sanctuary, Kalamazoo County, Michigan. Breeding pairs were housed separately in an outdoor aviary, but several male Lady Amherst Pheasants and a trio of peafowl roamed freely on the grounds. Food, a sanctuary preparation of commercial mixtures, and water were readily available.

DETERMINING FEATHER MOVEMENTS AND POSTURES

During Reproductive Displays

Frontal or lateral displays are given by males toward females during courtship and toward other males of the same species during agonistic behavior. In the display the male gives either a side or frontal orientation of the body toward the subject. Both frontal and lateral displays include movements of head, wing, tail and feathers. Although these displays have been described previously for numerous members of the Subfamily Phasianinae (Seth-Smith, 1925; Beebe, 1931; Huxley and Bond, 1941; Delacour, 1951; and Shenkel, 1956, 1958), little is known about the localization of specialized display feathers, the form and extent of feather movement, and the movement and postures of non-display feathers.

I often initiated displays by introducing new birds to males already acclimated to females in the cage. Since the sanctuary is frequented by many people, most birds became readily adjusted to the presence of humans. For this reason a blind was not required for observing the displays.

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Observations were made in the early morning and late evening during the spring of 1965, 66, and 67. Feather movements and postures were photographed on 8 mm movie film at 18 frames per second and examined later at full, stop and reverse speeds. Frames which showed the various feather postures that certain regions of the plumage assumed during display were selected to make the drawings.

Since this is not strictly an ethological study, the entire sequence of reproductive behavior patterns is not analyzed for its functional implications. Rather, emphasis is placed upon describing the extent and form of movement of the body feathers as a basis for explaining muscle action. Movements of the wings, body and tail were noted but were considered of secondary importance to movements of body feathers.

In descriptions of feather postures I followed the terminology of Morris (1956: 80). In some instances new postures, not mentioned by Morris, had to be named and described. Other behavioral terminologies are from numerous sources (Andrew, 1961; Dilger, 1962; Etkin, 1964: 206-227; and McKinney, 1965: 123-130).

During Preening

I made observations on feather movements and postures during preening of aviary birds and compared them with my observations of feather movements of homologous regions during display. These observations were made at a distance of 10 feet or mor

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Observations of feather movements during preening were also made in the laboratory on partially defeathered Single-Comb White Leghorn chickens. I found that I could stimulate birds to preen by wetting the plumage and then providing heat. After being held under tap water for about one minute each bird was placed in a 15" x 24" x 15" wire cage. Three birds were observed individually for 20 minutes twice a day for a period of 5 days. A 100-watt goose-neck lamp provided the heat. Groups of feathers were clipped or plucked from areas of the dorsal cervical, interscapular, dorsopelvic and femoral tract, thus forming gaps in the plumage so that the stubs of individual feathers and the skin could be observed. Observations were made at a distance of 3 feet.

DETERMINING PTERYLOSIS

Pterylosis is defined as the distribution of feathers on the skin (Harrison, 1964: 670). Contour feathers may be uniformly distributed on the skin as in the penguins (Spheniscidae). However, in most birds feathers grow from definite tracts (pterylae) on the skin with intervening bare areas (apteria). Pterylosis of many birds was described by Nitzsch and Burmeister (1867). In this study I have followed the terminology of Lucas and Stettenheim (1965: 3).

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In this study contour feathers were plucked from feather tracts in birds anesthetized with Equi-Thesin® (2.5 to 4.7 ml/Kg body weight) injected intravenously into the basilical vein. A light plane of anesthesia as defined by Fedde, *et al*. (1963) was used. At this plane of anesthesia a chicken responds to pinching of the comb, but shows no response to pinching of the skin or toes. After administration of Equi-Thesin® the feathers in the follicle are loose and easily plucked. The action of Equi-Thesin® appears to be similar to that of tranquilizing drugs (Sturkie *et al*., 1958) and other anesthetics (Ostman *et al*., 1963b) in affecting feather release.

As the contour feathers were removed, each follicle was marked with India ink. Follicles of downs located in apteria were not marked due to the small size of the follicle. Photographs were taken of the marked bird and the negatives were used to produce the drawings.

One disadvantage of this method of determining pterylosis is that it is very tedious and time consuming. Another is that it was difficult to mark the small, numerous follicles located on the skin covering the head.

An advantage of this method is that the marking of follicles and then photographing the bird provides a visible

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record of the gross pattern of pterylosis which can be compared tract by tract to the distribution of the follicles and skin muscles of other representatives. This method also shows the relative size of the feather follicles in different regions of the body. It was especially useful for designating particular rows of follicles and individual follicles for subsequent determinations of their feather lengths, weights and muscle mass.

The gross pattern of the body tracts is first described for Phasianus and then compared with the other forms. Details of the capital, alar, subhumeral, and caudal tracts are omitted from this study.

PREPARATION OF SKINS

Skins were prepared from fresh, frozen and alcoholic specimens. In all instances fresh material produced a better preparation. In alcoholic specimens, feather and dermal muscles were often too brittle to dissect and often were distorted and appeared to be in various states of contraction. Musculature was often deteriorated in specimens frozen for more than 2 years.

All live birds were killed by over-anesthetizing with Equi-Thesin® rather than by cervical dislocation, bleeding, or by the "stick" method of King (1921). Feather tightening results after death by cervical dislocation (Peterson and Ringer, 1963) and bleeding (Klose et al., 1961; 1962).

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My efforts to "stick" birds were not successful. Over-anesthetizing results in a loosening of the feathers after death (Peterson and Ringer, 1963). The same mechanism that affects feather tightening may affect the contraction of the feather muscles. Hence over-anesthetizing was used to kill birds in an attempt to have the feather muscles in as relaxed a state as possible. All contour feathers were then plucked from the body.

Skins were prepared for examination according to the technique developed by Dr. A. M. Lucas and his associates of the U. S. Department of Agriculture Avian Anatomy Investigations at Michigan State University.[1]

Skin containing the feather muscles and the insertion ends of the dermal muscles was removed in sections, mounted on wire cloth and fixed in Bouins fixative (75 parts saturated picric acid, 25 parts formalin--full strength, and 5 parts glacial acetic acid). Time of fixation ranged from 5 to 12 hours depending upon the thickness of the skin. During fixation picric acid stains the muscle tissue a light yellow. Skins were then removed from the wire cloth and stored in 70 per cent ethyl alcohol until dissections could be made.

Carcasses were placed in crocks containing 5 per cent formalin. Two changes of fluid were made after several weeks.

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[1] The citation refers to the manuscript of "Avian Anatomy. Integument," currently in the process of final editing; the manuscript will be published for the U. S. Department of Agriculture by the Government Printing Office.

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Carcasses were then stored in embalming fluid (78 parts 70 per cent ethyl alcohol, 20 parts glycerin, and 2 parts of full strength formalin). The embalming mixture eliminated the unpleasant volatile odor of formalin and made the tissues pliable and easy to work with when the dermal muscles were reexamined. No mold or bacteria formed in the crocks and the birds were preserved satisfactorily for 3 years.

I determined the insertion, course, distribution, attachment to the skin, and the relationship of the dermal muscles to the feather follicles by examining the under surface of fixed skins.

I found it easiest to examine and dissect the feather muscles from the internal surface. This required removing the dermal muscles, connective tissue, excess fat and the larger peripheral nerves and blood vessels from the undersurface of the skin. The gross arrangement, distribution and pattern of the feather musculature, as viewed with the unaided eye, was described first. Finer details of the arrangement and the pattern were then determined by dissection at the subgross level with the aid of a 0.7 to 30 power Bausch and Lomb stereomicroscope. Muscle type (striated or smooth) of teased muscles attached to the feather follicle was determined with the light microscope. Teased muscles were stained with hematoxylin according to standard histologic procedure.

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I attempted to determine whether a relationship existed between the degree of muscle development and feather size in certain regions. The degree of muscle development was estimated by determining muscle volume or muscle weight.

I determined the volume of the muscles of a particular follicle by measuring the length, width and thickness of each dissected muscle with a micrometer, multiplying these dimensions together and summing the values of all rows. The lengths of muscles, including the tendons of attachment, were measured from follicle wall to follicle wall. The width and thickness of the muscles were measured at the belly.

Prior to determination of muscle mass the skins were washed in 70 per cent ethyl alcohol for 25 minutes to remove the picric acid. For skins which were excessively fatty the alcohol treatment was preceded by a 15 minute wash in chloroform. Individual muscles were dissected free, removed, grouped as to muscle type (erector, depressor or retractor), air dried for 24 hours and weighed to the nearest 0.1 mg with a Mettler H16 balance.

Feathers were weighed to the nearest 0.1 mg and feather length was measured from the inferior umbilicus to the longest barb to the nearest millimeter.

Feather muscles were examined in day old Ring-necked Pheasants in order to ascertain the degree of development of this system in newly hatched birds.

Nomenclature for the dermal muscles is reviewed in a later section. I have followed the terminology of George and

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Berger (1966) for the tongue and jaw musculature; Langley (1904) and Stettenheim *et al*. (1963) for the feather muscles.

DETERMINING MUSCLE ACTION AND FUNCTION

Analysis of the functional significance of the dermal and smooth muscle components is, by necessity, based on deductive reasoning. Conclusions on muscle action are only hypotheses and must be treated as such. Only after the hypotheses have been tested by extensive experiments can they be relied upon, and even then there is a chance that some important factor has been overlooked. The deductive method of functional anatomy is based partly on a consideration of the laws of mechanics and partly on a consideration of the relative development of the muscles in forms having different habits. For example, if the distribution, course, mode of attachment, shape and mass of certain feather or dermal muscles differ among representatives which have different feather displays, then the basic assumption is that these differences are somehow associated with feather display.

Deductions of muscle action and function in this study are based primarily upon morphological evidence. Evidence is also obtained from preliminary experiments involving muscle and nerve stimulation and extirpations of certain dermal and feather muscles in live birds.

In the experiments on muscle stimulation, birds were lightly anesthetized with Equi-Thesin® (2.5 to 4.7 ml/kg body weight). If respiration ceased, birds were given unidirectional a

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unidirectional artificial respiration according to the technique of Burger and Lorenz (1960). The experiments were designed to provide information concerning the action of the dermal and feather muscles in positioning the skin and feathers in different regions of the body.

The method of Langley (1904) was used to stimulate cervical spinal roots, peripheral nerves and dermal muscles in chickens. A Harvard model 935B stimulator was used to supply the stimulus. Details on the strength, frequency and duration of the stimulus and the selection of dermal muscles for stimulation in this experiment are presented later in the text.

The technique used and difficulties encountered in attempting to stimulate the feather muscles in chickens are presented in the section on smooth muscles.

To determine the function of the dermal and feather muscles in display, unilateral and bilateral extirpations of certain dermal or feather muscles associated with specialized display areas of the plumage were performed in anesthetized chickens and Golden Pheasants. After the operations birds were allowed to recover overnight. They were then resubmitted to agonistic and courtship situations. Similarities and differences in feather movement during display between controls, experimental and sham operated birds were noted and compared.

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RESULTS AND DISCUSSION

DESCRIPTION OF FEATHER DISPLAYS

Prior to describing feather displays it may be helpful to present a brief review on the terminology of feather postures. Morris (1956) describes 4 basic postures which the body feathers can take during display. Starting from a _relaxed_ (=_normal_) posture, feathers can be depressed tightly against the body to give a _sleeked_ posture, or elevated slightly to produce a _fluffed_ posture. When feathers are fully erected and the tips of the feathers are spaced wide apart so as to give a jagged appearance to the plumage, they are then in a _ruffled_ posture. It is important to realize that these feather postures differ primarily on the degree of their elevation from the surface of the body.

Ring-necked Pheasant

A _lateral_ courtship display is given by males toward females during the breeding season (Figure 1). Prior to the display (Figure 1-1), the male is usually in an _upright_ posture. This posture is also assumed between consecutive _lateral_ displays. In the _upright_ posture both wings are slightly lowered and the rump feathers are exposed.

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Body feathers are in a normal position, the tail is compressed and the "ear" tufts are elevated and inclined outward.

"Ear" tufts are feathers which arise from two accessory integumentary structures ("ears") located dorsal to the external ear opening on the dorsal lateral surface of the head (Figures 1, 7, 23A). They serve no auditory function. They are not present in hens.

"Ear" tufts are often maintained in an elevated and inclined position throughout the breeding season. When males become frightened, they are lowered with the rest of the body plumage. "Ear" tufts appear to move as a unit, as if the integumentary "ears" were involved. Tips of the feathers do not appear separated from one another as do feathers which are fluffed or ruffled.

During the lateral display (Figures 1-2 and 1-3) the male is crouched, feet together, with neck bent and head low, as close to the hen as possible. Wattles of the face are flushed deep red. The tail, tilted toward the hen, is spread. The inner wing (i.e., that closer to the female) is lowered somewhat further than the outer wing. Body feathers are fluffed.

There also appears to be a general swelling of the body. This may be caused by inflation of the air sacs and may result in some movement of the feathers.

The dorsolateral orientation of the body appears to be accompanied not only by a general fluffing of the body

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feathers, but also a shifting of the plumage to the side closest to the hen. This is most noticeable in the rump region. Shifting of the plumage to one side appears to result in a slight separation of the feathers between the rump and thigh on the opposite side.

Since the lateral display is brief, lasting from 5 to 15 seconds, the sequence of feather movements is difficult to determine even from movies. My observations suggest that fluffing of the feathers occurs just prior to swelling of the body. Then as swelling increases, the dorsolateral aspect of the body is tilted toward the female, the plumage of the rump shifts and separation of the feathers occurs on the opposite side.

Throughout the lateral display the hen is usually relaxed. Her feathers are normal and she stands in a somewhat low position. I did not observe any attempts at copulation after the display.

Other feather movements, apparently not associated with the display, appeared to be related to the extension and retraction of the head and neck, and involved feathers covering the neck. For example, as the head was extended, feathers of the neck moved apart but did not alter their vertical position relative to the surface of the body.

Golden Pheasant and Lady Amherst Pheasant

The lateral courtship displays of male Golden Pheasants and Lady Amherst Pheasants are very similar. No differences

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were apparent between the two species either in the form or the extent of the display. Both species are known to interbreed in captivity and the hybrids are fertile. Several postures in the courtship display of the Lady Amherst male are shown in Figure 2.

When there are no females present the male assumes a general upright posture (Figure 2-1) with his wings folded over the back concealing the bright yellow feathers of the rump. Crest, cape and body feathers are in a relaxed posture and the tail is compressed. Between lateral displays, and in the presence of hens, both wings are lowered slightly, exposing the yellow feathers of the rump.

During pursuit of the hen (Figure 2-2), feathers of the cape are extended slightly forward and upward, equally, on both sides to the level of the mandible. Body feathers are in a relaxed posture. The male pursues the hen with his head and tail extended.

At the height of the lateral display, when the head of the male is as close to the face of the hen as possible, his body is arched and tilted toward her. His head and neck are slightly extended with the bill pointing upward but completely hidden from her view by full extension of the cape feathers on the side closest to her (Figures 2-3, 2-4 and 2-5). Positioning of the cape feathers is the most conspicuous aspect of the feather display. Cape feathers are not erected perpendicularly from the surface of the body

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as in feathers which have a ruffled posture. Movement of the tips of the cape feathers is downward from the neck, along the lateral surface of the head, and then anteriorly and upward toward the eye. It results in a conspicuous and uniformly spread fan (Figure 2-5). The movement of the cape is parallel to the long axis of the body.

As in the Ring-necked Pheasant, the display is accompanied by swelling of the body and shifting of rump plumage. However, shifting of the plumage is more noticeable in Golden Pheasants than in Ring-necks.

The tail is slanted and spread only on the side facing the hen. The wing on this side is lower than the wing on the opposite side. Feet are always placed one in front of the other, depending upon the side displayed. When displaying to the left, the left foot of the male is placed forward.

The display is fully lateral. When the hen is in front of the male the male arches his body and curves his tail around her (Figure 2-4). Either side of the cape can be extended. At no time did I observe both sides of the cape fully extended together, nor did the crest feathers elevate. The lateral display is held as long as the head of the hen is near the face of the male. Only after the hen moves away does the cape partially retract and the body plumage return to normal position. Hissing occurs during swelling of the body. The lateral display lasts for several seconds, the time depending upon the position of the hen. Once I

Figure 1.--Courtship display of the male Ring-necked Pheasant. (1) Upright posture, (2 and 3) lateral display postures. Drawn from motion pictures.

Figure 2.--Courtship display of the male Lady Amherst Pheasant. (1) pre-display posture, (2) pursuit posture, (3, 4, and 5) lateral display postures. C--cape, D--feathers of the rump. Drawn from motion pictures. The number in parentheses refers to the number of frames subsequent to the preceding posture.

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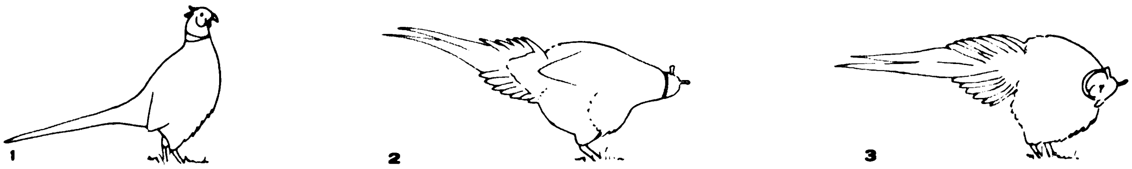

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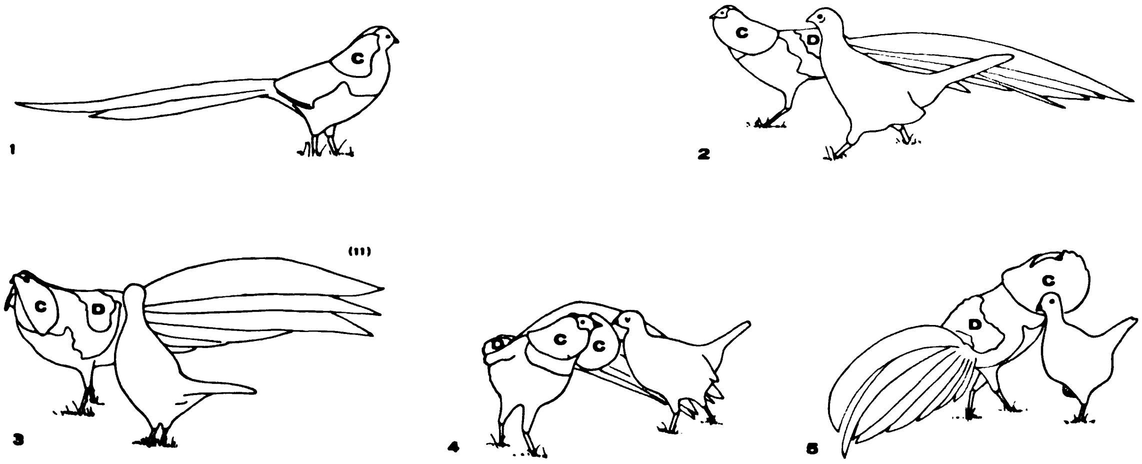

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<u>Domestic Chicken</u>

<u>Frontal</u>, <u>lateral</u> and numerous other displays are given by male chickens during agonistic behavior. In determining feather displays during agonistic behavior, observations were made using 6 male and 3 female Single-Comb White Leghorn chickens, 8 male and 5 female bantam Rhode Island Reds, and 1 pair of Araucanas.

No differences were observed in feather displays among the different breeds. When a rival male is introduced into the territory of another, the dominant male frequently assumes an <u>upright</u> posture (Figure 3-1). In this pose the body feathers are <u>relaxed</u>. Often the dominant male will crow (Figure 3-2). During crowing there is a moderate <u>fluffing</u> of the breast feathers. Plumage falls back to a <u>normal</u> posture after crowing.

Initial challenge to a rival begins with a <u>lateral</u> display (Figure 4-1). During the <u>lateral</u> display the dominant male <u>shuffles</u>("<u>waltzing</u>" of Wood-Gush, 1954) toward the rival and presents the dorsolateral aspect of his body to him. Body feathers are <u>fluffed</u> and the outer wing is dropped close to the ground. Primaries are slightly separated. No <u>swelling</u> of the body was observed, nor did I hear

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any sounds produced. The rival either counters with a *lateral* display of his own, submits by avoidance, "ignores" the challenge by redirection activities (e.g., pecking or scratching at the ground; "*tidbitting*" of Domm and Davis, 1948) or assumes a *frontal* display.

In the *frontal* display (Figures 4-2, 4-3, 4-4, 4-7, 4-8) both birds spar bill to bill with heads extended and tails somewhat depressed. Hackles of the upper neck are fully *ruffled* while the rest of the body feathers are *sleeked*. Wings are folded and slightly lowered, but are held tightly against the body. In general, except for erection of the hackles, both birds appear streamlined for flight. *Frontal* displays are brief, lasting for several seconds.

In addition to *ruffling* of the neck feathers during the *frontal* display, *ruffled* feathers of the neck were observed to move closer together when the head was retracted and further apart when the head was extended.

Frontal displays are almost always followed by the attack display (Figures 4-5, 4-6), which is usually initiated by the dominant bird. This display is essentially *frontal* and involves flight and body contact. Hackles remain *ruffled* and the rest of the body plumage is *sleeked* even during flight. Attacks are frequent and last until one of the birds submits; normally it is the introduced male. The *lateral* display is dispensed with when attacks are consecutive. I observed *frontal* displays and *attack* occurring

Figure 3.--Postures of a dominant male chicken assumed between attacks during agonistic behavior. (1) upright posture, (2) crowing, (3-7) body and head-shake, (8-11) crowing. Drawn from motion pictures. The upper number in parenthesis refers to the number of frames subsequent to the preceding posture; the lower number in parenthesis refers to the number of frames between 2 consecutive head-shakes.

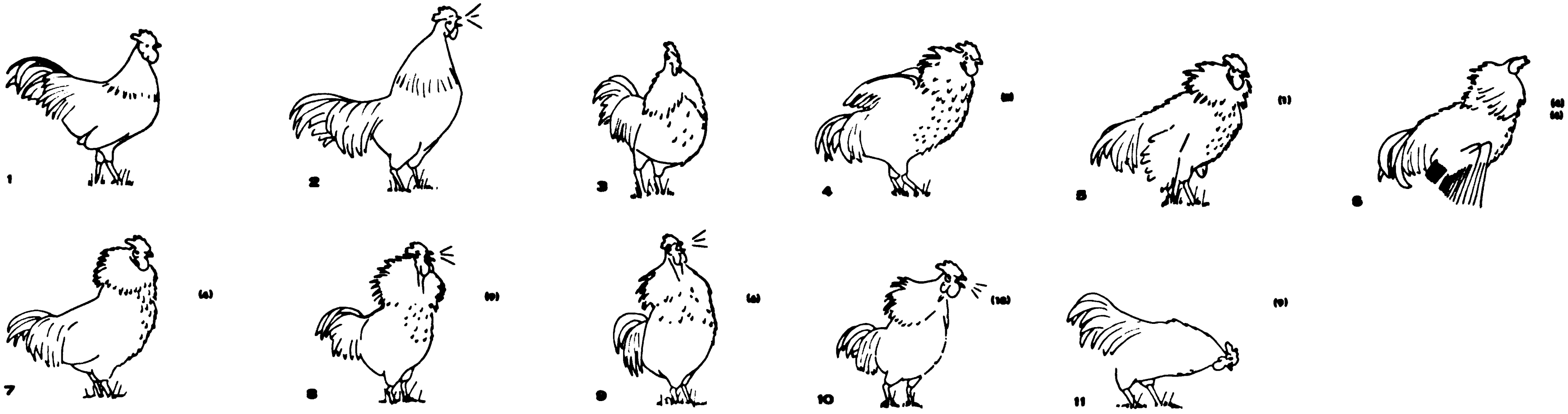
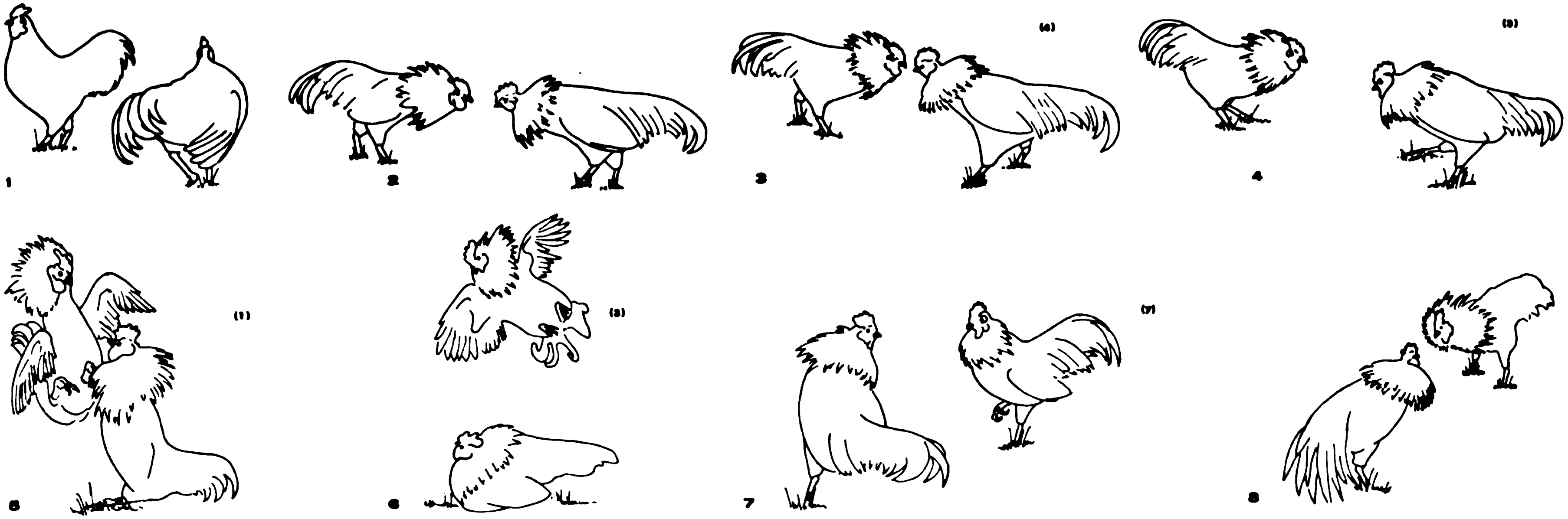


Figure 3

Figure 4.--*Lateral*, *frontal* and *attack* displays of male chickens during agonistic behavior. (1) *lateral* display, (2-4 and 7-8) *frontal* display, (5-6) *attack*. Drawn from motion pictures. The number in parenthesis refers to the number of frames subsequent to the preceding posture.



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Between attacks and frequently in the presence of other males, the dominant male sometimes ruffles his feathers, flaps his wings and shakes his body (Figures 3-3 through 3-7). Feather ruffling occurs over most of the body. Hackle and breast feathers are the first to ruffle. During the body-shake the tail is depressed and the head is slightly retracted. Usually three rapid wing-flaps and two head-shakes to the side are given (Figures 3-4 through 3-6). Body-shaking begins with the head and ends with the tail.

Often the body-shake is immediately followed by crowing (Figures 3-7 through 3-11). Hackles and breast feathers are the only feathers I observed to ruffle during crowing.

In two instances I observed frontal displays between cocks and hens. Both cocks and hens raised the feathers of the upper neck; however, the extent of elevation was much less in hens.

Indian Peafowl

The elaborate courtship display of male peafowls is chiefly frontal. Feathers most conspicuously displayed are those of the lower back. Collectively referred to here as the train, these feathers are long and conceal those of the tail when the bird is not displaying (Figure 5-2). The term tail as used here includes both the pygostyle and the tail feathers (rectrices) and their coverts.

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The male prepares for display by retracting the head and bracing the feet. The bird then leans forward until the breast is almost touching the ground. The tail, with the rectrices spread, is swiftly raised to about 45 degrees and the train moves upward and forward (Figure 5-3). Two to three short flaps of the tail are given as the train is elevated to its maximum angle (about 87 degrees). Fan-like spreading of the feathers of the train occurs as it is being elevated. Anterolateral-most feathers extend forward and downward to the ground. Feathers of the train can be maintained in the *elevated* and *fanned* posture for as long as 40 minutes. If the train drops much less than 87 degrees it is reelevated.

Wing-fluttering occurs after the train is *elevated* and and *fanned*. During *wing-fluttering* both wings appear relaxed and the primaries are separated. Both wings flutter in unison.

Both peacocks and peahens appear to have permanently erected crests, at least I never witnessed one with the crest depressed.

Courtship displays are given during the breeding season, whether or not females are present. I saw peacocks displaying to captive Great Horned Owls (*Bubo virginianus*), hen Ring-necked Pheasants, and hen Golden Pheasants. Peacocks displayed primarily in the early morning and late evening. However, I frequently saw them displaying during mid-day when the sky was overcast.

Figure 5.--Feather movements and postures of the male Indian Peafowl. (1) preening of the back, (2) non-display posture, (3-7) courtship display, involving elevating and spreading of the train to an <u>elevated</u> and <u>fanned</u> posture. Drawn from motion pictures. The number in parenthesis refers to the number of frames subsequent to the preceding posture.

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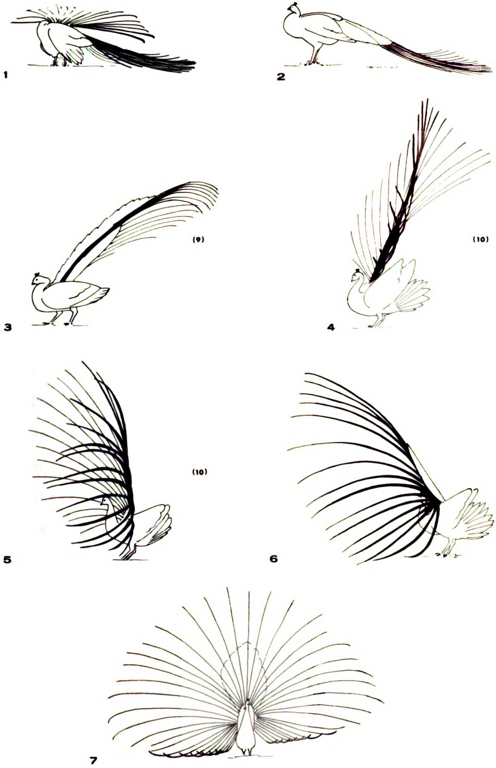

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I observed 3 attempts at copulation. On each occasion the displaying male approached the hen by backing toward her. He then turned, faced her, crouched low and positioned the train well forward over his head. In this pose (Figure 5-6) the tail was vibrated and the train rustled. Rustling of the train lasted from 2 to 5 minutes and was performed only as the male leaned forward toward the hen. At the height of the display the male shrieked, lowered the train and pursued the hen. The 3 attempts at copulation were unsuccessful.

It appeared that elevation of the train was related to the elevation of the tail and the shaking of the posterior body. The short rapid flaps of the partially spread rectrices against the undersurface of the train feathers might explain the method by which the train is elevated from a horizontal resting position to a vertical position. If this were true, removal of the rectrices should alter the capacity of the train to elevate.

I tested this theory in one male. When the rectrices were clipped close to the skin, the bird could still elevate, spread and rustle his train. I could not detect any noticeable differences between the experimental bird and a normal bird in the elevation and spreading of the train except that shaking of the posterior body appeared to be slightly more intense in the bird with the clipped rectrices. However, the shape of the fan, as viewed from the side, was quite irregular in

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quite irregular in the clipped bird. This could be due to the irregularity of the stubs of the rectrices which were braced against the shafts of the train. I also noted that rustling was less intense than in an unclipped bird.

These observations suggest that elevation of the train is not dependent upon the flat surface of the rectrices. The spread rectrices may aid in maintaining the train in a uniformly shaped fan and apparently are involved in rustling of the feathers. But the actual spreading of the train cannot be explained by movements of the tail. It appears that some other mechanism associated with the feathers of the train is responsible for their display.

Summary and Discussion

No significant differences in feather displays were noted among male Single Comb White Leghorn, bantam Rhode Island Red and Araucana chickens or among male *Chrysolophus pictus* and *C. amherstiae*. Great differences in feather displays were found among males of different genera.

In general, most conspicuous feather displays are localized in different regions of the plumage, and homologous regions among birds may be characterized by different feather postures. Also, in a bird which is displaying, feathers in different regions of the plumage may assume different postures. The following is a brief summary of the most significant points I found from my observations on feather display.

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1. "Ear" tufts in cock *Phasianus* appear to be maintained in the *elevated* and *inclined* posture throughout the breeding season; they are capable of being raised and lowered and appear to move as a unit. The integumentary "ears" may be responsible for positioning the "ear" tufts.

2. The crest of *Chrysolophus* males appears permanently depressed and the crest of peacocks and peahens permanently erected.

3. The courtship display of *Phasianus* is characterized by a general *fluffing* of all body feathers.

4. The frontal display of *Gallus* is characterized by strong raising of the hackles and strong depression of the rest of the body feathers. *Ruffling* of the hackles and of other feathers of the body occurs during the *head*- and *body-shake*.

5. In *Chrysolophus*, *extension* of the cape feathers is the most striking feature of the feather displays. Either side of the cape may be extended.

6. Raising and spreading of the train to an *elevated* and *fanned* posture is the most conspicuous feather display of peacocks. Positioning of the train apparently is not dependent upon the rectrices of the tail.

7. *Plumage-shift* occurs in the *lateral* display of *Phasianus* and *Chrysolophus*, but it is most noticeable in *Chrysolophus* where the yellow feathers of the rump appear to shift toward one side of the body.

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8. Feathers of the neck in all birds, regardless of their position in display, appear to move closer together when the head is retracted and further apart when the head is extended.

It is possible that the body feathers are positioned by three different, independent but interacting methods.

First, body feathers may be oriented according to the orientation and position of the body. For example, the *lateral* display itself orients certain regions of the plumage to the subject. The crown feathers of peafowl, if they do serve a display function, are apparently dependent upon the orientation of the head. The positioning of the head in cock Ring-necks close to the face of the hen may serve to draw attention to the "ear" tufts or to the flushed facial wattles.

Second, once the body is oriented further exaggeration of the feather display appears to be accomplished by the movement of individual feathers. Feathers may be elevated at various degrees from the body surface to produce the *sleeked*, *relaxed*, *fluffed* and *ruffled* postures, or they may move forward along the longitudinal plane of the body as in the *extended* feather posture of the cape feathers in *Chrysolophus*. Tips of feathers may also move apart from one another in one plane to give a fan shape to the group of feathers being displayed. These movements and postures appear to have two things in common; that is they do not

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appear to be dependent upon the orientation of the body or the movement of the skin.

A third method by which display feathers may be positioned appears to involve the movement or shifting of the skin which appears to explain the shifting of the rump plumage in *Chrysolophus*.

Whether the skin is involved in the movements of the feathers associated with extension and retraction of the head in non-display and display behavior, and whether the feather postures are dependent or are independent of the movement of the skin is examined further in preening birds.

MOVEMENT OF THE FEATHERS AND THE SKIN DURING PREENING

Birds frequently raise their feathers during preening. The different actions of the bill and postures of the body during preening of particular areas of the plumage have been described for numerous birds (Simmons 1964: 280). McFarland and Baher (1968) recently attempted to determine the effects of (1) ambient temperature, (2) hunger and thirst and (3) agonistic behavior on feather posturing in the Barbary Dove, *Streptopelia decaocto*, (*S. risoria*). They combined the *fluffed* and *ruffled* feather postures under one general category of "*feathers raised*". Their results indicate that Barbary Doves raise their feathers when cold and depress them when hot. No differences between body regions were observed in response to temperature, but in defensive and aggressive

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birds there were marked and characteristic differences. They also noted that feather raising increased during preening.

I attempted to determine the feather postures and the occurrence and extent of feather and skin movement during preening in partially defeathered Single Comb White Leghorn chickens. Birds were clipped and stimulated to preen according to the method previously described. Each bird was observed individually for 20 minutes twice a day for a period of 5 days. Direct observations with the unaided eye were made from a distance of 2 to 3 feet on the movements of the skin and feathers during feather posturing.

During the first several minutes prior to preening shaking of the head and body is frequent and probably serves to remove excess water from the feathers. Ruffling of the feathers occurs during the body and head shake. Most birds begin preening within 2-5 minutes after the water treatment. The most conspicuous form of feather movement during preening is strong erection which positions the feathers in a ruffled posture. Usually feathers are erected before actual manipulation with the bill.

Feathers of one area of the body may raise even when another area is actually being preened. The occurrence of feather ruffling during preening of certain regions of the plumage is shown in Table 1. In general, feathers of target areas (i.e., those areas of the plumage actually being

TABLE 1

Occurrence of feather ruffling during preening of certain regions of the plumage in Single Comb White Leghorn chickens. A = always occurred, F = frequently occurred, I = infrequently occurred, O = did not occur.

	Areas of the Plumage Ruffled								
Areas	d.	inter-	v.	mid-					l.
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TABLE 1

Occurrence of feather ruffling during preening of certain regions of the plumage in Single Comb White Leghorn chickens. A = always occurred, F = frequently occurred, I = infrequently occurred, O = did not occur.

	Areas of the Plumage Ruffled									
Areas preened	d. neck	inter- scap.	v. neck	mid- back	rump	breast	abd.	hum.	th.	l. leg
d. neck[1]	O	O	O	O	O	O	O	O	O	O
inter- scap.	I[2]	A	O	F	I	O	O	F	I	O
v. neck	O	O	A[2]	O	O	I	O	F	O	O
mid-back	O	F	O	A	F	O	O	O	O	O
rump	I[2]	A	O	A	A	O	O	O	O	O
breast	O	O	I[2]	O	O	A	O	F	O	O
adb.	O	O	O	O	O	O	A	O	O	O
hum.	O	F	O	I	O	O	O	A	O	O
th.	O	A	O	A	A	O	O	O	A[3]	O
l. leg	O	O	O	O	O	O	O	O	O	A[3]

[1] See text.

[2] Ruffling occurred near thoracic region of the body.

[3] Feathers fluffed.

Abbreviations: d.=dorsal, interscap.=interscapular, v.=ventral, abd.=abdominal, hum.=humeral, th.=thigh, l=lower.

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manipulated with the bill) ruffle more frequently than feathers in those areas not being preened. Except for the anterior dorsal region of the neck and the region of the lower leg, feathers of the target areas are always ruffled when they are preened.

The fact that ruffling of the hackles does not occur during preening appears to be related to the method of preening these feathers. Preening of the hackles is performed by rubbing the head and dorsal park of the neck on the uropygial gland, whereas feathers in other areas, including the lower leg, are manipulated with the bill. When the lower leg is preened the erection of feathers is slight. It may be that the feathers of the lower leg are not capable of full erection. We know from observations during display that the hackles are capable of full erection.

During feather ruffling, feathers slowly raise upward and anteriorly from a relaxed position. Some rotation of the feathers occurs particularly along the dorsolateral region of the body. Feather erection during preening of the back appears to start at the lower back and progresses, wave-like, anteriorly. However, feather erection involves groups of feathers. Feathers may be capable of moving individually, but I never saw only one feather elevated and the adjacent feathers depressed.

Clipping of certain feathers allows the skin to be exposed for observation. Apparently clipping of the feathers

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does not inhibit feather ruffling, for the stubs of clipped feathers erected in a manner similar to those of adjacent tract feathers. However, the extent of erection was much less noticeable in clipped feathers. I could not detect any movement of the skin as the feathers were being elevated or depressed nor could I detect any movement of follicles from which feathers had been plucked.

Some movements of the skin and feathers were noticeable in the neck region and did not appear to be related to elevation or depression of the feathers. As birds extended the head and neck in order to preen certain inaccessible areas, the skin of the neck appeared to stretch and feather shafts moved apart, anteroposteriorly, without elevating or depressing. In this instance skin and feather movements appeared to be coordinated with movements of the head and neck. However, when the head and neck were retracted, there was a short delay before the skin of the neck was retracted and the feather shafts drawn together. It appears that drawing of the feathers closer together, after the head is retracted originates in the skin itself, and that movement of the skin does not place the feather in an erected or depressed position.

Birds often depress the body feathers when being transferred to and from the observation cage. Transferring and handling of the birds may have frightened them. Evidently strong depression of the body feathers is a typical response

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of most birds when frightened (Andrew, 1956; Marler, 1956; McFarland and Baher, 1968). However, in addition to depression, the feathers of the neck also moved closer together around the neck. In birds in which the feathers had been clipped along one side of the neck I noted that the skin was drawn inward and tightly about the neck.

Summary and Discussion

1. Except for the hackles and feathers of the lower leg, body plumage is ruffled during preening.

2. Feathers in areas other than those preened may also ruffle, but they do so less frequently than feathers in the areas being manipulated by the bill.

3. That hackles, although capable of ruffling, are not ruffled during preening appears to be related to the method of preening these feathers.

4. Feathers of the lower leg elevate slightly when preened.

5. Observations on the movement of feather shafts during erection and depression of clipped feathers, support the hypothesis that feather raising and lowering are not dependent upon the movement of the skin.

6. Movement of the skin of the neck, anteriorly or posteriorly, appears to cause feather shafts to move closer together or further apart depending upon the extension or retraction of the head. The movement of feather shafts closer together or further apart apparently can occur with the neck

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feathers in the relaxed, ruffled, or sleeked posture. This form of feather movement was also observed in the frontal display with the hackles fully erected.

7. Constriction of the skin about the neck, occurring when chickens are frightened, apparently causes the feathers to move closer together transversely without altering the degree of feather erection.

8. Frightened chickens depress the body feathers. No differences between body regions were observed in feather depression. These observations are in general agreement with the observations of Andrew (1956) on buntings, Marler (1956) on chaffinches and McFarland and Baher (1968) on doves.

These limited observations substantiate my original observations of feather movement in display and suggest again that there are two basic methods of positioning the feathers:

(1) Feathers which are positioned in various degrees of elevation from the body appear to be postured independently of the movement of the skin.

(2) Feather movements in which feather shafts move closer together or further apart appear to be dependent upon the movement of the skin.

A shifting of the plumage was not observed as feathers were elevated during preening. Based upon my observations of shifting of the plumage in the lateral display of *Chrysolophus*, where feathers did not appear to alter their

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PTERYLOSIS

General

I have demonstrated that the most conspicuous and specialized displays of body feathers are localized in certain regions of the body of Phasianids (e.g., anterior dorsal neck of Gallus and Chrysolophus, and the rump of Pavo). It may be that differences in the location of display feathers among males of different genera are related to differences in their pattern and distribution on the skin and also related to differences in the pattern and distribution of the musculature associated with display and non-display feathers in homologous regions. In this section I have examined the relationship of display feathers to the pattern of pterylosis.

Birds were anesthetized, the feathers removed and the feather follicles marked according to the methods previously described. I examined 10 specimens of Phasianus, 6 of Gallus, 6 of Chrysolophus and 2 of Pavo.

The gross pattern of feathering is first presented for Phasianus; then comparisons are made with the other forms. Some features of the localized display feathers are also described. Descriptions of the gross feather pattern are based upon the distribution of the follicles and their arrangem

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arrangement into rows. The terminology of Heimerdinger (1964) is used for describing follicle rows. A brief review of her terminology follows:

A row--is a group of feathers arranged either in a straight line or in an inverted V, or chevron shape, with the apex of the chevron pointing anteriorly and two arms extending posterolaterally out from the apical feather (e. g., feathers of the interscapular tract are typically arranged into chevron-shaped rows; see Figures 8 and 29).

A complete row--has a central apical feather and two lateral arms of variable length.

An incomplete row--lacks the central feather and may also lack the first few feathers of the arms.

A gapped row--contains the central feather but lacks one or more feathers in the arms.

A hash-marked row--is a single armed row of feathers.

The terms "anterior", "upper" or "up" are used in my descriptions as synonyms for cephalic or cranial. "Posterior", "lower", and "down" are used for caudal.

Lateral, ventral and dorsal views showing the pterylosis of a Phasianus male are shown in Figures 6, 7 and 8. In these illustrations the pattern of follicle rows may not always be clearly evident to the reader. This may be due to (1) the crowding of the follicles together in particular regions (e.g., head), (2) the curvature of the body, or (3) the presence of intercalary contour feathers found among the "nor

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Description for Phasianus

A brief general description of the pterylae and apteria of Phasianus is presented. Details of the subdivisions of the capital, and the subhumeral, posthumeral, alar and caudal tracts are omitted.

Pterylae

Capital tract.--This tract covers the head and has numerous subdivisions. Since the follicles of the capital tract are small, numerous and close together, only the posterior portions of this tract were marked by the method described previously. A pattern of rows is not evident to the unaided eye. Follicles of the "ears" appeared somewhat larger than adjacent follicles which may be related to the fact that "ear" tufts are slightly longer than those feathers on the rest of the head. Stiff auricular feathers are found around the external ear opening and bristles are present on the facial wattles.

Dorsal cervical tract.--This single median tract covers the anterodorsal 1/3 of the neck. Its anterior boundary is marked by the posterior border of the skull. Anteriorly it is continuous with the capital and ventral cervical tracts. Posteriorly it narrows and is continus with the interscapular tract. Follicles of the dorsal cervical tract are symmetrically arranged in chevron-shaped rows with the apex of the

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of the chevron pointing anteriorly. The apical feathers are the longest in a chevron row (Table 2).

Interscapular tract.--This single median tract is located mid-dorsally over the posterior neck and between the shoulders. It is the posterior continuation of the dorsal cervical tract and is distinguished from it by being uniformly narrow. The junction of the dorsal cervical and the interscapular tract is arbitrarily placed where the lengths of chevron rows change from being irregular to uniform (Figure 8). The posterior boundary of the interscapular tract is marked by the presence of an apterium which may be either devoid of follicles or with 2 to 3 follicles present mid-dorsally.

Dorsal and pelvic tracts.--These single median tracts are located on the dorsal side of the trunk. The anterior boundary of the dorsal tract is marked by the posterior limit of the interscapular apterium (Figure 8). A junction between the dorsal and pelvic tracts could not be distinguished by the pattern of follicle arrangement. The junction is arbitrarily placed with respect to a transverse line connecting the proximal heads of the femurs. Collectively the tracts are referred to as the dorsopelvic tract. It is widest anteriorly and narrowest posteriorly where it terminates at the uropygial pland. Follicles are arranged into chevron-shaped rows and apical feathers within a chevron row are the longest (Table 2). In general the length of feathers increases posteriorly within the tract.

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Ventral cervical tracts.--These are paired tracts covering the ventrolateral surface of the neck. They merge with one another anteriorly to a single tract which is continuous with the capital and dorsal cervical tracts. The posterior boundary is marked by the lateral junction of the marginal coverts of the alar tract. Apical feathers of the symmetrically arranged chevron-shaped rows are the longest.

Pectoral tracts.--These paired tracts cover the ventrolateral surface of the breast. The tract is continuous anteriorly with the ventral cervical tract. The anterior boundary is marked by the lateral junction of the marginal coverts of the alar tract. The posterior limit, about midway down the trunk, is formed by a gradual diminution of row length. Follicles are typically arranged into unsymmetrical chevron-shaped rows (Table 2). The angle of each arm of a chevron row is more acute and the follicles within a row are closer together at the posterior border of the tract.

Sternal tracts.--These narrow paired tracts are located on the ventral surface of the trunk, one on each side of the keel. The anterior boundary begins about half-way down the pectoral tract and appears to be separated from the pectoral tract by a small space. Evidently this is not true for passerine birds where the anterior boundary of the sternal tract originates from the medial arms of the pectoral tract. (Heimerdinger, 1964). The sternal tract is continuous posteriorly with the abdominal tract. I have arbitrarily placed t

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placed the junction between the two at the posterior boundary of the keel (Figure 7). Follicles are usually arranged in single-armed rows.

Abdominal tracts.--These paired tracts are the posterior continuations of the sternal tracts and cover the ventral surface of the abdomen. The tracts merge in a mid-ventral line just anterior to the anal opening where they terminate. Here, follicles are arranged in chevron-shaped rows. Feathers increase in length posteriorly within the tract.

Lateral body tracts.--These are paired tracts covering the lateral surface of the trunk. Follicles are spaced widely apart and I could not detect a pattern of rows (Figure 6). Feathers of this tract are semiplumes.

Femoral tracts.--These paired tracts cover the lateral surface of the thigh. A pattern of chevron-shaped rows is not clear. Follicle rows course anterodorsally and posterodorsally with reference to a mid-dorsal longitudinal line. This pattern is obscured by the presence of intercalary follicles at the posterior border of the tract. Intercalary follicles are defined as follicles which are found between rows of follicles "typical" of the tract. They are associated with the borders of most tracts but are most consistently present and conspicuous in the femoral tract.

Crural tracts.--These are paired tracts covering the external and internal surface of the leg. Follicle rows course anterodorsally and posterodorsally with reference to a mid-dorsal longitudinal line. Posterodorsally directed follicle rows of the external surface are continuous with the anterodorsal feather rows of the internal surface. Feathers are longer and closer together on the anterior and posterior borders of the tract. On the internal surface feathers are shorter and more sparsely distributed.

Humeral tracts.--These paired rectangular tracts cover the dorsal anterior end of the humerus. The anterior rows of humeral feathers merge with the rows of marginal coverts. Follicle rows course dorsally with reference to a mid-dorsal longitudinal line. Feathers are close together within rows and increase in length posteriorly within the tract.

Subhumeral tracts.--These paired tracts, which are not figured, cover the undersurface of the humerus and are concealed from view when the wing is folded.

Posthumeral tracts.--Paired and located on the caudal border of the upper arm between the last secondary and the humeral tract. Not figured.

Alar tracts.--These paired tracts cover the upper and undersurface of the wing and have numerous subdivisions. They are not figured.

Caudal tract.--This tract includes the feathers of the tail (rectrices and their coverts) and also those feathers which are located lateral and posterior to the uropygial gland. It is not figured.

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Apteria

I have previously defined apteria as bare regions on the skin. However, down feathers may be present in some apteria. Included with the description of each of the following apteria is a general statement of the amount of feathering on it.

Lateral cervical apteria.--Paired and covering the side of the neck between the dorsal cervical and ventral cervical tracts. Down feathers are usually absent except anteriorly.

Ventral cervical apterium.--Single and median covering the ventral surface of the neck between the right and left ventral cervical tracts. This apterium is sparsely feathered.

Scapular apteria.--Paired and located between the interscapular and humeral tracts. One or 2 longitudinal rows of down are present.

Lateral pelvic apteria.--Paired and located between the pelvic and femoral tracts. Down feathers are frequent and appear randomly distributed.

Lateral body apteria.--Paired. The space surrounding the lateral body tract. These apteria are sparsely feathered.

Pectoral apteria.--Paired. The space between the pectoral and sternal tracts. These apteria are sparsely feathered.

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Sternal apterium.--Single and median. The space between right and left sternal tracts. Feathers are absent in this apterium.

Crural apteria.--Paired. The space between the crural and femoral tracts. Crural apteria are sparsely feathered.

Median abdominal apterium.--Single. The space between right and left abdominal tracts. Feathers are absent in this apterium.

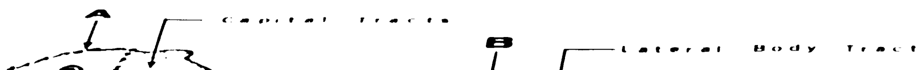
Lateral abdominal apteria.--Paired. The space lateral to the abdominal tracts. These apteria are sparsely feathered.

Interscapular apterium.--Single and median. One or 2 down feathers may be present mid-dorsally. The space is located mid-dorsally at the posterior border of the interscapular tract. It is similar to the spinal space of *Bonasa* (Nitzsch and Burmeister, 1867; Trainer, 1947), *Perdix*, *Meleagris* and *Lophophorus* (Nitzsch and Burmeister, 1867) and *Lophortyx* (Clark, 1898), and the dorsal apterium of *Colinus* and *Coturnix* (Brewer, 1961).

Comparison

The gross pattern of pterylosis is similar in all forms studied and in general agrees with the descriptions of Nitzsch and Burmeister (1867) and Clark (1898). I did not detect any obvious differences among *Phasianus*, *Gallus* and *Chrysolophus* in the gross pattern of the ventral, humeral, crural, femoral and lateral body tracts. I did find differences within the dorsal pterylae. These differences occurred in areas which are involved in display.

Figure 6.--Lateral view of a male Phasianus colchicus showing pterylosis. Details of the follicle arrangement of the (A) capital, (B) alar, and (C) caudal and dorsopelvic tracts are not shown. A dash line represents the junction between 2 continuous tracts (see text).



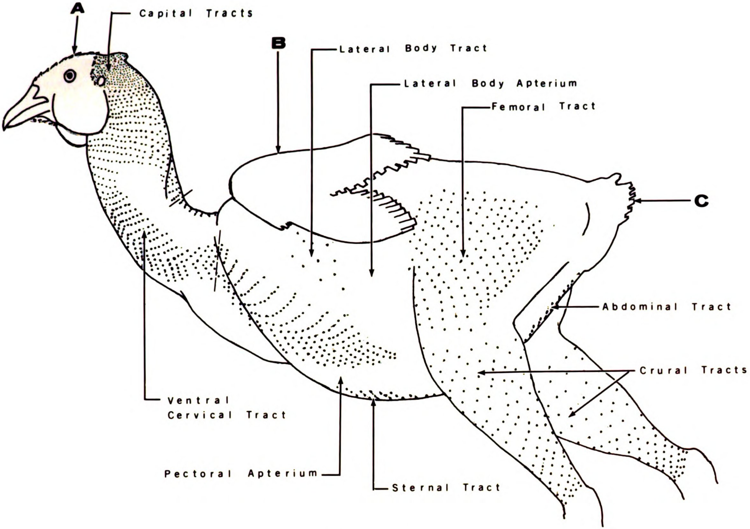

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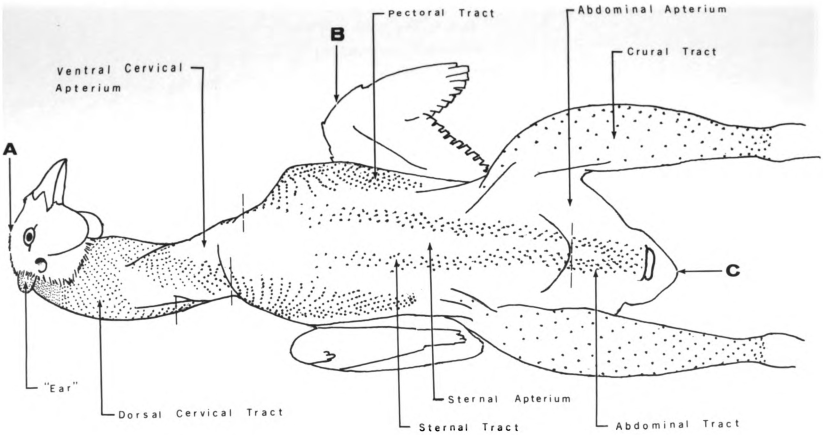
Figure 6

Figure 7.--Ventral view of a male <u>Phasianus colchicus</u> showing pterylosis. Details of the follicle arrangement of the (A) capital, (B) alar, and (C) caudal tracts are not shown. The dash line represents the junction between 2 continuous tracts (see text).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Sternal Tract
Sternal Apterium
Abdominal Tract

Figure 7

Figure 8.--Dorsal view of a male Phasianus colchicus showing pterylosis. Details of the follicle arrangement of the (A) capital, (B) alar, and (C) caudal tracts are not shown. The dash line represents the junction between 2 continuous tracts (see text).

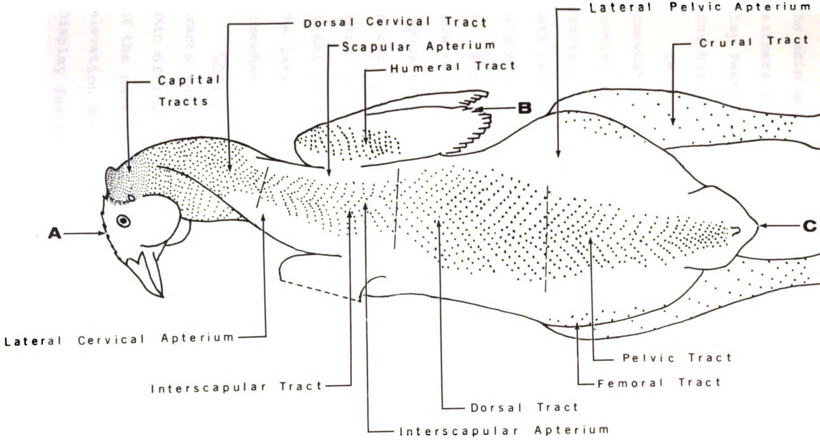
Dorsal Cervical Tract
Scapular Apterium
Humeral Tract
Lateral Pelvic Apterium
Crural Tract
Capital Tracts
B
A
C
Lateral Cervical Apterium
Interscapular Tract
Dorsal Tract
Interscapular Apterium
Pelvic Tract
Femoral Tract

Figure 8

Major differences were noted in the relative thickness of the skin and the relative length of the specialized display feathers in homologous regions. Although specialized display feathers are present in Gallus males, their presence does not alter the basic pattern of follicle arrangement.

In cock Gallus the feathers are longer and the skin is somewhat thicker in the region of the hackles than in hens. Hackles arise from the dorsal cervical and interscapular tracts. Apical feathers in a chevron row are the longest in both sexes. The gross pattern of follicle arrangement in hen ringnecks and hen chickens is similar.

Phasianus cocks, as compared to cock Gallus, appear to have relatively shorter feathers and thinner skin in homologous regions of the dorsal cervical and interscapular tracts. In cock Phasianus long feathers are found on the epidermal "ears" of the dorsal capital tract. These features are absent in Ring-neck hens and in the other representatives. The lateral pelvic apteria in both sexes of Phasianus are somewhat wider, relatively, than in Gallus.

Chrysolophus cocks appear to have narrower dorsopelvic tracts than Phasianus or Gallus. In Chrysolophus males the skin of the dorsal cervical tract in the area of the nape of the neck is thickened mid-dorsally into a goblet-shaped elevation about 3 to 3.5 cm wide and 13 to 16 cm long. Display feathers of the cape arise from this region. These feathers are spatulate-shaped and are much longer than those later

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lateral and posterior to the thickened area which also arise from the dorsal cervical tract.

Feathers of the cape are arranged in chevron-shaped rows with the apex of the chevron pointing anteriorly. Chrysolophus males differ from Gallus and Phasianus males in that the apical feather is the shortest feather in a chevron row and feathers increase in length posteriorly in chevron rows (Table 2). At the posterior border of the cape, feathers are close together transversely. Anteriorly, feathers of the cape merge with feathers of the dorsal capital tract. A central thickening of the skin also occurs in the dorsal occipital region. The long filamentous crest feathers arise from this region. Females of Chrysolophus possess a reduced cape but lack the crest. The ovoid cape feathers of hens are much shorter and the skin is thinner than in males.

Several features are distinct about the pterylosis of Pavo. First, the interscapular apterium which is present in Gallus, Phasianus and Chrysolophus is absent in Pavo. Second, the dorsopelvic tract is linear and of equal breadth in the region just behind the shoulders, but widens considerably over the pelvic region. The thick skin (2.5 to 3 cm) covering the pelvic region corresponds to the area where the long display plumes are found. The junction of the pelvic and dorsal tracts in Pavo may be distinguished by follicle size and by the presence or absence of intercalary downs which are found among the feathers of the pelvic tract but not in

TABLE 3

Lengths of individual consecutive feathers (in mm.) in a chevron arm. From various tracts of male Phasianus colchicus, Gallus gallus, Chrysolophus

TABLE 2

Lengths of individual consecutive feathers (in mm.) in a chevron arm. From various tracts of male *Phasianus colchicus*, *Gallus gallus*, *Chrysolophus pictus* and *Pavo cristatus*.

Abbreviations: cer. = cervical; lat. = lateral; med. = medial; pect. = pectoral.

	Phasianus				*Gallus*	*C. pictus*	*Pavo*
Feather No.	Dorsal Cer.	Pelvic	Pect. (lat. arm)	Pect. (med. arm)	Dorsal Cer.	Dorsal Cer.	Pelvic
0	59	115	85	85	102	41	117
1	48	114	95	80	101	44	184
2	45	103	114	75	100	49	276
3	40	99	121	75	99	53	364
4	33	90	132	72	94	57	446
5	32	82	112	63	90	64	559
6		69		53	87	68	642
7		48		39	80	75	732
8					78	84	793
9					75	87	870
10					73		950
11					68		1054
12							1132
13							1185
14							1263
15							1339

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the dorsal tract (Figure 30). Intercalary downs have been previously described for Pavo (Sager, 1955).

In the pelvic tract of Pavo the apical feather is not the longest feather in a chevron row and feathers increase in length posteriorly in a chevron arm (Table 2). In this respect the feathers of the pelvic tract of Pavo are similar to the feathers of the cape in Chrysolophus. This appears to be related to the fan-shaped form of the feather displays of both representatives.

In peahens the arrangement of follicles in the pelvic tract is similar to that in peacocks but in peahens the thickness of the skin and length of the feathers of the train are greatly reduced. Both sexes possess permanently erected crest feathers arising from the dorsal capital tract covering the frontal bone. The skin of this region is also thickened.

Summary

1. No significant differences were found in the gross pattern of follicle arrangement of the ventral, humeral, crural, femoral or lateral body tracts among males in Gallus, Chrysolophus or Phasianus.

2. An interscapular apterium is present in Gallus, Phasianus and Chrysolophus but is absent in Pavo.

3. The pelvic tract of Pavo is distinctly different from those of the other representatives studied. It is characterized by being wider posteriorly than anteriorly and

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by having small intercalary down follicles interspersed among the follicles of the train feathers. The anterior limit of intercalary downs can be used to delimit the dorsal from the pelvic tract.

4. The presence of enlarged follicles of display feathers does not alter the basic pattern of follicle arrangement.

5. A thickened skin is associated with the presence of enlarged follicles of display feathers. Thickening of the skin in feathered areas may be associated with the development of the smooth muscles found within the dermis.

6. Hackles arise from the dorsal cervical and interscapular tracts in Gallus, cape feathers from a restricted region of the dorsal cervical tract in Chrysolophus.

7. In general, the lengths of feathers within a tract decrease posteriorly along the arm of a chevron row. Thus, apical feathers of a chevron row are usually the longest within the row. Exceptions to this are found in the cape of Chrysolophus and the train of Pavo where feather length increases posteriorly along the arm of a chevron row and the apical feather is the shortest. This appears to be related to the displays of these feathers. Both the cape and the train are fan-shaped when fully displayed.

8. Generally, the lengths of feathers increase posteriorly within feather tracts and from head to tail in continuous tracts. This pattern may be modified in areas where there are display feathers. In males display feathers

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of some particular tracts (e.g., dorsal cervical of Gallus and Chrysolophus) are longer than those feathers of adjacent posterior tracts.

DERMAL MUSCLES

Introduction and Review of the Literature

Dermal muscles (= cutaneous, subcutaneous muscles) are striated muscles which arise from a part of the skeleton or a large body muscle and insert on the undersurface of the skin. The purposes of this section are to describe the gross structure of the striated muscles associated with the skin, to record similarities and differences among several galliform genera, and to make a qualitative evaluation of the differences noted in order to determine their functional implications in feather display. Hopefully, this work will help to stabilize the muscle nomenclature and serve as a basis for detailed comparisons yet to be made for other orders and families of birds. I have selected Phasianus colchicus as a type for comparison with the other forms.

Jacquemin (1836) was apparently the first to describe the striated dermal muscles of the skin. However, his account is brief and inadequate.

Owen (1842) presented the first detailed account of the dermal muscles for a single species, a kiwi (Apteryx australis). He recognized 10 distinct and separate muscles, 6 of which were associated with the skin of the neck.

Of these muscles I have retained the terminology only of his M. constrictor colli.

Viallane (1878) described 2 skin muscles, M. temporo-alaire (= cranial portion of M. cucullaris pars cranialis) and M. frontoiliac (= M. latissimus dorsi pars dorsocutaneus) responsible for elevating the neck feathers in the display of the Superb-bird-of-paradise (Lophorina superba).

Helm (1884; 1886) examined and described the relationships of 15 dermal muscles to the feather tracts in several orders of birds. For the most part his terminology follows that of Owen (1842). He illustrated 8 of these muscles for a "type" waterfowl.

Fürbringer (1888; 1902) was the first to undertake a broad and exhaustive comparative study of the musculature in different families and orders and to bring together in one work the complete synonymy of names used for various muscles. He also was the first to recognize that many dermal muscles which occupy the greater portion of the neck, and which were previously described as separate muscles, conformed to one general plan. He considered these muscles as part of M. cucullaris. The only muscle superficial to it is his M. sphincter colli (= constrictor colli). According to Fürbringer, M. cucullaris has two main divisions. The Kopftheil (pars cranialis) attaches to the skull, spinal pterylae, clavicle, sternum, and propatagium. The cephalic portion of Fürbringer's Kopftheil is considered by George and

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Berger (1965: 272) to be M. complexus, a muscle of the axial skeleton, rather than a dermal muscle. M. complexus is the same as the hatching muscle of Fisher (Fisher, 1958; 1961; 1962). The Halstheil (pars cervicalis) of Fürbringer's cucullaris arises from the neck and is inserted near or in common with pars cranialis.

Fürbringer also noted that many cutaneous muscles corresponded to dermal slips of already well known appendicular muscles. In fact he suggested that the posterior portion of his M. cucullaris dorso-cutaneus (1888: 302), which he found in some birds, be considered as a dermal component of M. latissimus dorsi (= M. lattissimus dorsi pars dorsocutaneus, 1888: 829). In my descriptions of the dermal muscles of the neck I have adoptdd Fürbringer's muscle terminology of the cucullaris system. I found Fürbringer's account of the dermal muscles to be by far the most complete and extensive in the literature.

Shufeldt (1890) was the first anatomist, so far as I know, to study in detail the complete myology of any bird. But numerous errors in his descriptions and findings in the myology of the Raven (Corvus corax sinuatus) have been reported by subsequent investigators (Engels, 1938; Hudson and Lanzillotti, 1955). For this reason I have not used Shufeldt's terminology for the dermal muscles nor have I relied on his descriptions of them. However, his work should not be completely ignored as George and Berger suggest (1966: 225),

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for Shufeldt frequently included the synonymies of Gadow and Selenka (1891) in his footnotes. With reference to the dermal muscles, Shufeldt compared his terminology to that of Fürbringer, Gadow and Selenka, and Owen. However, he still chose to devise his own nomenclature of the 13 dermal muscles he found rather than to adopt Fürbringer and Gadow's concept of the composite M. cucullaris and to follow their classification of the cutaneous components of body muscles.

Gadow and Selenka's monograph (1891), like Fürbringer's, is also a comprehensive study on the comparative myology of birds. Gadow and Selenka provide an extensive list of synonymies for the dermal muscles but omit those of Helm and Shufeldt. They divided M. cucullaris into superficial, deep and propatagial components.

Beddard (1898) surveyed the myology of representatives of many orders and families of birds reported by previous workers. He followed the terminology of Fürbringer for his descriptions of the dermal muscles.

Fisher and Goodman (1955) undertook an extensive study of the myology of the Whooping Crane (Grus americana). They divided M. cucullaris into a caput or capitis part (Kopftheil of Fürbringer) and a hals or cervical part. They also described M. dermotemporalis (Shufeldt) which corresponds to my M. cucullaris pars cranialis as it arises from the skull. Fisher and Goodman's caput portion of M. cucullaris is M. complexus of Gadow and Selenka (1891), Boas (1929), Davids (1935), Zusi (1962), and Lucas and Stettenheim (1965).

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In a recent synopsis of the myology of birds George and Berger (1966: 270-272, 293, 306, 317) reviewed the homologies of the striated dermal muscles of Shufeldt, Fürbringer, and Gadow and Selenka. They stated that there is no evidence for the actual existence of Shufeldt's Mm. dermo-frontalis, circumconcha and dermo-spinalis, that M. cucullaris is not a true muscle of the axial skeleton and that M. complexus is not a part of M. cucullaris but rather a true muscle of the axial skeleton. They retained Shufeldt's terminology of M. dermotemporalis in their descriptions of the cranial attachment of M. cucullaris in the Red-winged Blackbird (_Agelaius phoeniceus_) and Rivoli's Hummingbird (_Eugenes fulgens_).

They also described 4 possible dermal components of M. pectoralis pars thoracicus, 3 of which corresponded to Gadow and Selenka's (1891) pars abdominalis.

Materials and Methods

Specimens for dissection were prepared as described in the Methods section. Complete dissections were made on both sides in the following:

	Total	Males	Females
Gallus gallus			
Single Comb White Leghorn	6	3	3
Rhode Island Red	8	4	4
Araucana	2	1	1
Phasianus colchicus	6	3	3
Chrysolophus pictus	4	3	1
Chrysolophus amherstiae	1	1	0
Pavo cristatus	2	1	1

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In order to ascertain whether striated muscles were attached to the follicles I often examined at 450X teased skin tissue stained with hematoxylin.

In determining the length of dermal muscle slips I measured from the origin to the insertion end on the skin. Information as to the innervation of the dermal muscles has been obtained from numerous sources (Fürbringer, 1888; Gadow and Selenka, 1891; Edgeworth, 1935; Goodman and Fisher, 1962).

Abbreviations

Abbreviations for the dermal muscles are given under the description of each muscle and in the figures. The following are additional abbreviations:

adb. = abdominal, abdominis
ant. = anterior
anterovent. = anteroventral
apt. = apterium, apteria
cap. = capital
cer. = cervical
cov. = coverts
d. = dorsal
ex. = external
ext. = externus
hum. = humeral
interscap. = interscapular
l. = left
m. - musculus
marg. = marginal
mm. = musculi
n. = nerve
op. = opening
pect. = pectoral
post. = posterior
posterovent = posteroventral
reg. = region
sar. = sartorius
sp. = space
tr. = tract
v. = ventral

REVIEW OF THE DERMAL MUSCLES

M. constrictor colli (Con. colli) (Owen)

M. constrictor colli, Owen, 1842: 22. Helm, 1884; 326; 1886: 298. Edgeworth, 1935: 109. Fisher and Goodman, 1955: 27. Goodman and Fisher, 1962: 114.

M. sphincter colli, Fürbringer, 1888: 303. Beddard, 1890: 80.

Oberflachliche Lage M. cucullaris, no. 64 I, Gadow and Selenka, 1891: 214-216, 306.

Description for Phasianus (Figure 9).--M. constrictor colli is the most superficial muscle of the neck. It takes its origin from the ventral median raphe. The fibers encircle the neck transversely, are continuous with one another mid-dorsally, and are firmly attached to the overlying skin throughout their course. The muscle fibers covering the anterior 1/3 of the neck become thinner and more widely separated from each other posteriorly where a few bundles are confluent with the dorsal-medial border of the belly of M. cucullaris pars cervicalis. Anteroventrally a few fibers are confluent with M. mylohyoideus posterior.

Innervation.--Anteriorly by N. accessorius externus and posteriorly by N. vago-accessorius (Fürbringer, 1888: 307); by cervical nerves (Goodman and Fisher, 1962: 115); and by N. facalis (Edgeworth, 1935: 109).

Comparison.--Very similar in *Phasianus* and *Gallus* and least developed in *Pavo*. Dorsally in *Chrysolophus* the anterior boundary is just caudal to the posteriormost follicles of the cape feathers. The muscle surrounds the whole of the neck in *Apteryx* (Owen, 1842: 22) and lies between the posterior ends of the mandibles and the 6th and 7th vertebrae in *Grus* (Fisher and Goodman, 1955: 27). The muscle was not described for any of the gallinaceous birds by Fürbringer (1888) nor for the Raven by Shufeldt (1890).

THE CUCULLARIS COMPLEX (Fürbringer)

M. cucullaris pars cranialis (*Cuc. cran.*)

M. sterno-maxillaris, Owen, 1842: 25.

M. temporo-alaire, Viallane, 1878: 6-12.

M. subcutaneus colli, Helm, 1884: 335; 1886: 298.

M. furculo-cephalicus, Helm, 1884: 357; no. 10, 1886: 339.

Part M. cucullaris, *Kopftheil* (Pars cranialis), Fürbringer, 1888: 304. Beddard, 1898: 80. Part of the Tiefere Lage, M. cucullaris, no. 64, Gadow and Selenka, 1891: 214. Not the capitus portion (caput part) of Fisher and Goodman, 1955: 10, or Goodman and Fisher, 1964: 116.

M. dermo-temporalis, no. 3, Shufeldt, 1890: 5,6. Fisher and Goodman, 1955: 9. Goodman and Fisher, 1964: 115.

Pars cranialis of M. cranio-cervicalis, Edgeworth, 1935: 145.

Dermal component of M. pectoralis, no. 12 (4), George and Berger, 1965: 306.

Description for Phasianus (Figures 9, 10, 11a and 12a).--Whereas the fibers of M. constrictor colli transverse the neck, the fibers of M. cucullaris pars cranialis, which are deep to it, are longitudinal and run the entire length of the neck. Pars cranialis arises fleshy, cranially, from the region of the squamosal bone, just dorsal and anterior to the external ear fossa (Figure 11a). At this point pars cranialis (M. dermo-temporalis, Shufeldt, 1890) is about 6 millimeters wide. Once free of the skull it widens out posteriorly to a flat sheet which overlies M. complexus and the superficial muscles of the neck. It receives a few fibers from the auricular cartilage and from the posterior part of M. constrictor colli. The major portion of pars cranialis meets its partner mid-dorsally, but does not connect with it. It then courses posterolaterally and ventrally to merge with the like muscle from the opposite side as a single broad muscle sheet overlying the crop (Figure 10). It eventually narrows and attaches to the ligament (posteroventral portion of Membrana sterno-coraco-clavicularis, Gadow and Selenka, 1891; Woolfenden, 1961: 124) which unites the hypocleidium and the sternal spine, and to fascia covering M. pectoralis thoracia (Figure 12a).

At about mid-length of the neck some of the fibers fan out laterally and terminate at the anterior end of the thoracic region which is marked by the under marginal coverts of the prepatagium (Figure 10). Here pars cranialis is most firmly bound to the overlying skin and it is difficult to separate the two. The muscle is also thinnest at this point.

The posterior portion of pars cranialis (= dermal component of M. pectoralis, George and Berger, 1965: 306) which covers the crop is not intimately bound to the skin, except mid-ventrally in a transverse line drawn between the under marginal coverts of the prepatagium.

M. cucullaris pars cranialis does not conform directly to the pattern of pterylosis. It passes diagonally and posterolaterally beneath the dorsal cervical tract and lateral cervical apterium and then courses ventrally to the anterior cervico-thoracic region. In the ventral cervico-thoracic region, fibers from both dorsal fasciculi form a ventral muscle sheet which at its widest extent lies beneath the ventral cervical apterium, between the medial (innermost) 7 follicles of the right and left pectoral tracts.

The maximum width of the dorsal faciculi ranges from 38 to 45 millimeters, the single ventral fasciculus covering the crop, 48 to 52 millimeters, and the attachment of the latter to the sternal region 8 to 15 millimeters. Pars cranialis is relatively thicker than M. constrictor colli, and its length corresponds to the length of the neck.

Comparison.--The cranial attachment of M. cucullaris pars cranialis is relatively thicker in male *Gallus* and *Chrysolophus*, especially where it passes beneath the follicles of the display feathers found on the dorsal cervical tract (hackles of *Gallus*, cape feathers of *Chrysolophus*). However, the shape, origin, and course of the muscle does not differ significantly from that of *Phasianus*. The posterior portion of pars cranialis covering the crop is similar in all the forms I examined.

M. cucullaris pars dorsocutaneus

Anterior part of M. fronto-iliaque, Viallane, 1878: 6-17.

M. cucullaris dorso-cutaneus, no. Ib, Fürbringer, 1888: 302.

M. dermo-dorsalis, no. 4, Shufeldt, 1890: 6.

This paired dorsal slip of M. cucullaris pars cranialis is present in *Chrysolophus* and *Pavo* and absent in *Gallus* and *Phasianus*. Pars dorsocutaneus leaves pars cranialis at its most dorsal aspect, as the latter turns laterally and ventrally. Pars dorsocutaneus, about 2 millimeters wide in both *Chrysolophus* and *Pavo*, courses directly caudally, maintaining a uniform width until it reaches its most posterior extent where it diverges slightly to insert by thin fascia onto the integument. The caudal connection to the skin is just cranial to the anteriormost attachment of the cervical component of M. cucullaris pars cervicalis in the anterior interscapular region of Chrysolophus, and just anterior to the caudalmost attachment of pars cervicalis in Pavo (although not diagrammed, refer to Figure 9).

Pars dorsocutaneus is not firmly bound to the skin along its length, except where it terminates caudally, nor does it connect with M. constrictor colli or M. cucullaris pars cervicalis. In relation to pterylosis the caudal attachment of pars dorsocutaneus underlies the two outermost follicles of the interscapular tract. In a more extensive condition pars dorsocutaneus may meet with M. latissimus dorsocutaneus (e.g., Alca, Uria, most Limicolae) or fuse to a common tendon with it which passes to the pelvis (e.g., Meiglystes, and the majority of the passerine birds--Fürbringer, 1888: 305).

M. cucullaris pars propatagialis

M. temporo-alaire, Viallane, 1878: 6-17.

M. tensor cutis brachialis anterioris, Helm, 1886: 299.

M. cucullaris propatagialis, no. Ic, Fürbringer, 1888: 302. Pars propatagialis M. cucullaris, no. 64 III, Gadow and Selenka, 1891: 216.

M. dermo-tensor patagii, no. 6, Shufeldt, 1890: 4, 7.

This muscle, which splits off laterally from M. cucullaris pars cranialis in the cervico-thoracic region and goes to the propatagium, was not present in Phasianus, Gallus, Chrysolophus or Pavo.

M. cucullaris pars omocutaneus

Perhaps M. humero-spinalis, no. 13, Helm, 1886: 341.

M. cucullaris omo-cutaneus, no. Id, Fürbringer, 1888: 303.

Fürbringer gave this name to a muscle he found in Apteryx, Columbidae, Anatidae, many Limicolae and a few Galli. It departs from M. cucullaris pars cranialis and inserts onto the integument of the humeral tract (Fürbringer, 1888: 307). I did not find pars omocutaneus in Phasianus, Gallus, Chrysolophus or Pavo.

M. cucullaris pars metapatagialis

M. cucullaris metapatagialis, Fürbringer, 1888: 302.

Pars metapatagialis, a slip of pars cranialis, which goes to the metapatagium and was described for Uria (Fürbringer, 1888: 305), was not present in any of the forms I examined.

M. cucullaris pars cervicalis (Cuc. cer.)

M. dermo-transversalis, Owen, 1842: 25. Helm, 1884: 326, 349: no. 3, 1886: 300.

Perhaps M. sterno-cervicalis, Owen, 1842: 23.

M. dermo-furcularis, no. 9, Helm, 1886: 339.

M. dermo-spinalis, Owen, 1842: 24.

M. cucullaris, Halstheil (Pars cervicalis), Fürbringer, 1888: 306. Beddard, 1898: 80. Part of the Tiefere Lage, M. cucullaris, no. 64, Gadow and Selenka,

1891: 214. Hals part of M. cucullaris, Fisher and Goodman, 1955: 49.

M. dermo-cleido dorsalis, no. 7, Shufeldt, 1890: 8.

Pars cervicalis of M. cranio-cervicalis, Edgeworth, 1935: 146.

Description for Phasianus (Figures 9, 11b, and 12a).--M. cucullaris pars cervicalis in Phasianus consists of two separate components, one which arises from the lateral surface of the neck, the other from the dorsal medial border of the clavicle.

Cervical component.--This muscle (= M. dermo-transversalis, Owen, 1842: 25; Helm, 1886: 300) consists of 3 to 5 thin slips, each about 3 millimeters wide. They originate by a thin aponeurosis from the lateral surface of cervical vertebrae 7 to 11 where the ventral root of each cervical spinal nerve emerges from between Mm. longus colli ventralis and intertransversarii (Figure 11b).

The slips, once free of the neck, course obliquely posterodorsally beneath the lateral cervical apterium and then diverge slightly to insert by thin fascia onto the integument beneath the lateral follicles of the interscapular tract (Figure 9).

Clavicular component.--This paired muscle is termed M. dermo-cleido dorsalis by Shufeldt and M. dermo-furcularis by Helm. It arises by fascia from the anteromedial surface

of the dorsal one-fifth of the clavicle (Figures 11b, 12a, and 12b). The muscle then courses dorsally and posteromedially beneath the lateral cervical apterium to insert by thin fascia onto the integument beneath the lateral follicles of the posterior region of the interscapular tract. The insertion is caudal to the most posterior slip of the cervical component of pars cervicalis and just anterior to the insertion of M. latissimus dorsi pars dorsocutaneus (Figure 9).

Comparison.--Both the cervical and clavicular components of M. cucullaris pars cervicalis are well developed and similar in *Chrysolophus*, *Gallus*, and *Pavo*. The slips from the lateral surface of the neck generally number 4 or 5 and may vary as to the cervical vertebrae from which they arise. The cervical slips arise most frequently from cervical vertebrae 7 to 11, less often from 8 to 12, and 6 to 10. For the purpose of this investigation I do not consider these differences to be significant.

The cervical component arises from the inferior transverse processes of the 6th to the 12th cervical vertebrae inclusive in *Apteryx* (Owen, 1842: 24), from the 7th to the 11th in *Gallus*, and from the 4th to the 11th in *Nothura maculosa* (Helm, 1884: 349).

According to Fürbringer (1888: 306) pars cervicalis can show many grades of development in its attachment to the spinous processes of the cervical vertebrae, to the skin, and to the clavicle. In cases of considerable development pars cervicalis extends as a broad sheet in direct connection with pars cranialis over the distal five-sixths to one-half of the neck (e.g., one-half in Meleagris). In the case of little development it is represented by a thin bundle at the end of the trunk (e.g., Argus).

Pars cervicalis is strongly developed in Anas (Helm, 1886: 341) and Grus (Fisher and Goodman, 1955: 49). Fisher and Goodman described pars cervicalis (= their hals part of M. cucullaris) as a muscle, some 9 centimeters wide, which overlies the anterior part of the cervico-thoracic region and extends to the shoulder. In Grus it arises from the neural crests of vertebrae 18, 17, and 16 and inserts on the scapular head, furculum, and the clavicular air sac. There is no mention of its attachment to the overlying skin and its relationship to the feather tracts. I did not find any attachment to the neural spines in the forms I examined.

Innervation.--The anteriormost region of M. cucullaris pars cranialis is innervated by branches of N. hypoglosso-accessorius, accessorius externus and the vagoaccessorius; the remaining part of M. cucullaris pars cervicalis by numerous branches from cervical nerves and nerves from the brachial plexus (Fürbringer, 1888: 307; Edgeworth, 1935: 146; Goodman and Fisher, 1962: 115).

DERMAL COMPONENTS OF M. LATISSIMUS DORSI (Fürbringer)

M. latissimus dorsi pars dorsocutaneus (Lat. d. dc.)

M. dermo-spinalis, Owen, 1842: 24. Helm, 1884: 326; 1886: 337.

Posterior part of M. fronto-iliaque, Viallane, 1878: 6-12.

Posterior part of M. cucullaris dorso-cutaneus, No. Ib, Fürbringer, 1888: 302.

M. Latissimus dorso-cutaneus, Fürbringer, 1888: 829.

M. dermo-iliacus, Shufeldt, 1890: 12.

M. latissimus dorsi dorso-cutaneus, Beddard, 1898: 79. Gadow and Selenka, 1891: 230.

M. latissimus dorsi pars dorsocutaneus, George and Berger, 1966: 294.

Description for Phasianus (Figures 9 and 12b).--M. latissimus dorsi pars dorsocutaneus is a thin, fleshy muscle, about 2 millimeters wide and 65 millimeters long, which arises from the superficial surface of the posterior end of M. latissimus dorsi pars posterior and from the neural spines of the last thoracic vertebra. At its origin pars dorsocutaneus fuses with the like muscle on the opposite side and partially covers M. latissimus dorsi pars metapatagialis (Figure 12b). The thin band runs diagonally anterolaterally beneath the dorsal feather tract and diverges slightly to insert by fascia onto the integument beneath the lateralmost follicles of the interscapular tract just caudal to the insertion of the clavicular component of M. cucullaris pars cervicalis (Figure 9). Medial fibers of pars dorsocutaneus course superficial to fibers of the latter without connecting with it. Pars dorsocutaneus is most firmly bound to the skin at its anterior termination.

Innervation.--By a branch of N. latissimus dorsi (Fürbringer, 1888: 568, 572).

Comparison.--Pars dorsocutaneus is equally developed and similar in Chrysolophus, Gallus and Pavo. Fürbringer (1888: 566) stated that in galliform birds pars dorsocutaneus shows all possible gradations in development (e.g., weak in Argus), in separation from M. latissimus dorsi pars metapatagialis (e.g., incomplete in Argus, Numida), and in union with M. cucullaris pars dorsocutaneus (e.g., united in Tetraonidae). In Chrysolophus and Pavo I found the insertions of M. cucullaris pars dorsocutaneus and M. latissimus dorsi pars dorsocutaneus to be separated by the insertion of the clavicular slip of M. cucullaris pars cervicalis.

Hudson and Lanzillotti (1964) did not describe pars dorsocutaneus for Gallus, Phasianus, or Pavo. The posterior portion of their unlabeled muscle in Gallus (1964, Figure 1, p. 94) appears to correspond to my pars dorsocutaneus, their cranial portion to my clavicular component of M. cucullaris pars cervicalis. They figured a uniform band of muscle which courses from the origin of M. lattissimus dorsi pars metapatagialis and passes cranially over the shoulder.

<u>M</u>. <u>latissimus</u> <u>dorsi</u> <u>pars</u> <u>metapatagialis</u> (<u>Lat</u>. <u>d</u>. <u>mpt</u>.)

M. dermo-iliacus, Owen, 1842: 24. No. 6, Helm, 1886: 337.

M. latissimus dorsi pars metapatagialis, Fürbringer, 1888: 563. No. 68 III, Gadow and Selenka, 1891: 228. George and Berger, 1966: 288.

M. latissimus dorsi metapatagialis, Beddard, 1898: 79. Hudson, 1955: 7. Hudson and Lanzillotti, 1964: 8. Lucas and Stettenheim, 1965: 14.

<u>Description for Phasianus</u> (Figures 9 and 12b).--This dermal slip, 55 millimeters long and 3 millimeters wide, arises from the superficial surface of M. latissimus dorsi pars posterior and the neural spines of the thoracic vertebrae. Its origin is deep and slightly posterior to the origin of M. latissimus dorsi pars dorsocutaneus (Figure 12b). Pars metapatagialis is about 2 millimeters wide at its origin. The uniform belly passes obliquely anterolaterally beneath the scapular apterium and narrows to a small tendon which unites with the tendon of M. serratus superficialis pars metapatagialis. The two muscles insert onto the metapatagial membrane just caudal to the posteriormost follicles of the humeral tract (Figure 9). Pars metapatagialis is not firmly bound to the integument except at its insertion (fold of the metapatagium).

Innervation.--By a branch from N. latissimus dorsi (Fürbringer, 1888: 568, 572).

Comparison.--Pars metapatagialis is equally developed in Chrysolophus, Gallus and Pavo where its origin, course, and insertion are very similar to those of Phasianus.

An accessory slip arising from the lateral surface of pars metapatagialis was present, unilaterally, in one specimen of Gallus (Single Comb White Leghorn). This slip, about 2 millimeters wide, passed directly ventrally over the surface of M. serratus superficialis pars metapatagialis to attach to the skin just anterior to the insertion of M. pectoralis thoracica pars subcutaneus thoracicus.

Both pars metapatagialis and pars dorsocutaneus are about the same width in Phasianus, Chrysolophus, Gallus and Pavo. Pars metapatagialis arises from the last thoracic vertebra, fascia of the linea alba, and the first presacral vertebra (synsacrum) in Meleagris gallopavo, Lyrurus tetrix (Tetrao tetrix) and Crax nigra (Crax alector) (Fürbringer, 1888: 571). The muscle is broad but weak in Numida and Acryllium; broad and somewhat stronger in Opisthocomus (Hudson and Lanzillotti, 1964: 8).

M. latissimus dorsi-omocutaneus (Lat. d. omocut.)

This muscle, located between Mm. latissimus dorsi pars dorsocutaneus and metapatagialis in Argus and Numida (Fürbringer, 1888: 566), is not present in Phasianus, Chrysolophus, Gallus or Pavo.

DERMAL COMPONENTS OF M. SERRATUS SUPERFICIALIS
(Fürbringer)

M. serratus superficialis pars metapatagialis (*Ser. s. mpt.*)

M. dermo-costalis, Owen, 1842: 24.

M. tensor cutis brachialis posterioris, no. 7, Helm, 1866: 338.

M. serratus superficialis metapatagialis, Fürbringer, 1888: 378. No. 66b, Gadow and Selenka, 1891: 221. Beddard, 1898: 81. Hudson, 1955: 11. Hudson and Lanzillotti, 1964: 11. Lucas and Stettenhaim, 1965: 14.

M. dermo-ulnaris, no. 11, Shufeldt, 1890. Not of Owen, 1842: 24.

M. serratus metapatagialis, Berger, 1966: 299.

Description for Phasianus (Figures 9 and 12b).--Pars metapatagialis, 60 millimeters long, typically arises from the lateral surface of the vertebral member of the third thoracic rib, just ventral to the uncinate process, and sometimes from the third to the fourth thoracic ribs inclusive. In the latter case the muscle also originates from an aponeurosis between the ribs. The two fasciculi fuse to form a common belly some 4 to 6 millimeters wide. The muscle passes forward and upward beneath the lateral body apterium, narrows to about 2 millimeters, and inserts as a cord-like tendon in common with the tendon of M. latissimus dorsi metapatagialis onto the metapatagial membrane. M. serratus superficialis pars metapatagialis is stronger and more cord-like than Mm. latissimus dorsi pars dorsocutaneus and pars metapatagialis. It is not firmly bound to the skin except at its insertion.

Innervation.--By N. serratus superficialis metapatagialis which branches off from N. serratus superficialis posterior (Fürbringer, 1888: 381).

Comparison.--Very similar in all the forms I examined. The most frequent origin is from the third thoracic rib just ventral to the uncinate process. Variation in the origin of pars metapatagialis is given for numerous galliform genera by Hudson and Lanzillotti (1964: 12).

M. serratus superficialis pars dorsocutaneus

M. serratus superficialis dorso-cutaneus, Fürbringer, 1888: 378.

Fürbringer (1888:381) gave this name to an additional muscle he found in *Apteryx* which courses dorsally to insert onto the undersurface of the skin covering the scapula. I did not find it in *Phasianus*, *Gallus*, *Chrysolophus* or *Pavo*.

DERMAL COMPONENTS OF *M*. PECTORALIS

M. pectoralis thoracica pars subcutaneus thoracicus
(*Pect*. *t*. *sub*. *th*.)

Anterior part of M. dermo-humeralis, Owen, 1842: 24.

No. 12, Shufeldt, 1890: 13.

M. subcutaneus thoracicus, no. 4, Helm, 1886: 301.

M. pectoralis abdominalis pars anterior, Fürbringer, 1888: 450. Beddard, 1898: 79. Hudson and Lanzillotti, 1964: 14.

M. pectoralis abdominalis pars subcutaneus thoracicus, no. 73 III, Gadow and Selenka, 1891: 242.

Dermal component of M. pectoralis, no. 12 (2), George and Berger, 1966: 306.

Description for Phasianus (Figures 10 and 12a).--M. pectoralis thoracica pars subcutaneus thoracicus is a dermal muscle covering the lateral thoracic region. It arises by a narrow tendon and a strong sheet of fascia bridging the insertion of M. pectoralis pars thoracica. The wide but thin belly courses posteriorly and ventrally to diverge and insert by fascia onto the integument beneath the outermost follicles of the posterior seven to ten feather rows of the pectoral tract (Figure 10). Pars subcutaneus thoracicus is firmly bound to the skin beneath the posterior boundary of the lateral body tract and the lateral body apterium which it crosses.

Innervation.--By a branch of N. pectoralis pars thoricica (= N. pectoralis abdominalis; Fürbringer, 1888: 453).

Comparison.--The major portion of M. pectoralis thoracica pars subcutaneus thoracicus is similar in Gallus, Chrysolophus, and Pavo. However, I found one abberation in Gallus.

Sometimes fibers of pars subcutaneus thoracicus continue directly from the pectoral tract to the integument beneath several outer follicles of the sternal tract (unilateral in one specimen, bilateral in another).

M. pectoralis abdominalis metapatagialis (Fürbringer)

The muscle which departs from pars subcutaneus thoracicus and goes to the metapatagium in some birds (Fürbringer, 1888: 453; 1902: 440) was not present in the forms I examined. This muscle of Fürbringer appears to correspond to a minute slip which Hudson and Lanzillotti found in most American quails they examined. They stated that it passes from the insertion of pars subcutaneus thoracicus toward the insertion of M. latissimus dorsi pars metapatagialis (Hudson and Lanzillotti, 1964: 14).

M. pectoralis thoracica pars subcutaneus abdominalis (Pect. th. sub. abd.)

Posterior part, M. dermo-humeralis, Owen, 1842: 24.

M. pectoralis abdominalis pars subcutaneus abdominalis, Helm, no. 8, 1886: 338. Gadow and Selenka, 1891: 245.

M. petoralis abdominalis pars posterior, Fürbringer, 1888: 450. Beddard, 1898: 79. Hudson and Lanzillotti, 1964: 14.

M. dermo-pectoralis, no. 13, Shufeldt, 1890: 14.

Dermal component, M. pectoralis, no. 12 (3), George and Berger, 1966: 306.

Description for Phasianus (Figures 10 and 12a).--M. pectoralis thoracicus pars subcutaneus abdominalis is a dermal muscle covering the ventrolateral abdominal region. Pars subcutaneus abdominalis arises by a strong sheet of fascia which attaches to the dorsal border of M. obliquus abdominis externus, Os pubis, and the integument beneath and slightly lateral to the sternal and abdominal feather tracts. The belly (maximum width of about 40 millimeters at its origin) narrows and courses anteriorly passing just lateral to the abdominal and sternal tracts. The muscle then crosses the pectoral apterium to insert onto the skin beneath the posterior and medialmost three to four follicles of the pectoral tract. The belly, along its medial border, is firmly connected to the skin by fascia.

Innervation.--By a branch of N. pectoralis pars thoracica (= N. pectoralis abdominalis; Fürbringer, 1888: 453).

Comparison.--The facial origin, course, and insertion of pars subcutaneus abdominalis in Chrysolophus, Gallus, and Pavo is similar to that of Phasianus. The muscle apparently is equally developed in most Galliformes, except for Coturnix where it is extremely reduced (Hudson and Lanzillotti, 1964: 14).

OTHER STRIATED MUSCLES ASSOCIATED WITH THE SKIN

M. gastro-lumbalis (Helm)

This thin but wide (about 40 millimeters) dermal muscle is present in Gallus, absent in Chrysolophus, Phasianus and Pavo. The muscle was apparently first described in Gallus by Helm (1884: 352; 1886: 341). M. gastro-lumbalis lies between the anteroventral border of the femoral tract, where the muscle is firmly bound to it by dense fascia, and the posterolateral border of the sternal tract, where the muscle is bound to it by the fascial sheet of M. obliquus abdominis externus. The fibers course ventrally beneath the lateral body apterium and some may unite with fibers of M. pectoralis thoracica pars subcutaneus abdominalis.

M. gastro-lumbalis appears to be a modification of the origin of M. pectoralis thoracica pars subcutaneus abdominalis (M. pectoralis pars abdominalis, George and Berger, 1966: 311). They stated that depending upon the degree of development pars abdominalis arises from the subcutaneus tissue of the pelvic region or from the thoracoabdominal region near the knee. The latter origin corresponds to M. gastro-lumbalis. I found both origins present in Gallus. George and Berger did not give any examples of representatives in which the muscle was present nor did they give any reference which could be examined. This particular condition was not mentioned by Fürbringer or by Gadow and Selenka. I have retained the terminology of Helm until further investigations can be made in more birds.

<u>M</u>. <u>mylohyoideus</u> <u>posterior</u>

Probably M. platysma myoides, Owen, 1842: 24. No. 5, Shufeldt, 1890: 6.

Posterior portion of M. triangularis juguli, Helm, 1884: 336; 1886: 300.

Posterior portion of M. mylohyoideus anterior, Mudge, 1903: 247.

M. gularis, Edgeworth, 1935: 109.

<u>Description for Phasianus</u> (Figure 11a).--This is a transverse triangular sheet of muscle covering the posterior ventral floor of the throat. The muscle is superficial to the deeper hyoid muscles. It arises fleshy from the postarticular process, at the posterior end of the lower jaw, ventral and posterior to the origin of Mm. stylohyoideus and serpihyoideus. M. mylohyoideus posterior, about 2 millimeters wide at its origin, conceals the insertion of M. depressor mandibulae. It then fans out ventrally to join the same muscle from the opposite side at the mid-ventral line. Posteroventrally muscle fibers merge with the anterior part of M. constrictor colli. Mid-anteroventrally M. mylohyoideus posterior inserts on the interramal fascia in common with the posterior border of M. mylohyoideus anterior. M. mylohyoideus posterior is about 1.5 centimeters wide at its insertion. It is not attached to the hyoid bones nor to the deeper tongue muscles.

Innervation.--Branch of N. facialis (Gadow and Selenka, 1891: 307; Edgeworth, 1935: 109).

Comparison.--The muscle is equally well developed in *Chrysolophus* and *Gallus*. It is least developed in *Pavo*, where the origin, insertion and thickness of the muscle sheet are extremely small.

I do not consider M. mylohyoideus posterior to be a dermal muscle. However, I found it necessary to describe it since it adhered to the overlying skin in some of my specimen preparations. For this reason the muscle could have been easily overlooked by previous investigators studying the tongue muscles or it may have been considered a dermal muscle by others (e.g., Helm, 1884: 1886).

A muscle described as M. mylohoideus posterior is figured for *Rhea darwini* (Gadow and Selenka, 1891: 306). It is confluent anteriorly with M. mylohyoideus anterior and posteriorly with M. constrictor colli. Gadow and Selenka divide M. mylohyoideus posterior into two parts: an anterior M. stylo-hyoideus and a posterior M. serpi-hyoideus. This terminology has also been adopted by Mudge (1903), Fisher and Goodman (1955), Goodman and Fisher (1962), and Weymouth *et al*. (1964). However, M. mylohyoideus posterior in the representatives I examined does not correspond to M. mylohyoideus posterior of Gadow and Selenka, nor does it correspond to Mm. stylohyoideus or serpihoideus of the investigators cited above. These muscles are also present in *Phasianus*,

Gallus, Chrysolophus, and Pavo (Figure 11a).

Mudge (1903: 248, 252) stated that the most primitive condition of M. mylohyoideus posterior (= his posterior portion of M. mylohyoideus anterior) is exhibited in Strigops habroptilus where it takes the same origin as Mm. stylohyoideus and serpihyoideus. Mudge figured this muscle for Strigops (Plate 26, Figure 2). Furthermore, he traced the step by step regression of M. mylohyoideus posterior to its complete disappearance in Nestor notabilis and Probosciger (Microglossus) (Mudge, 1903: 253).

Edgeworth (1935: 107) described and figured (Figure 619) M. gularis which corresponds to M. mylohyoideus posterior. He stated that the muscle is simple in Gallus but that in some birds (e.g., Anas, Opisthocomus, Buteo and Passer) the muscle is separated into 2 parts, Mm. gularis anterior and gularis posterior. He apparently failed to recognize that Mm. serpihyoideus and stylohyoideus were also present in Gallus. I agree with George and Berger (1966: 252) who consider Mm. serpihyoideus and stylohyoideus homologous to the posterior and anterior parts, respectively, of M. gularis.

An equally comprehensive study of the tongue musculature on the Galliformes, as done by Mudge for the parrots, would no doubt reveal some interesting relationships among these muscles. At any rate this study has disclosed that the derivatives of the primitive constrictor sheet (Mm. constrictor colli, mylohyoideus anterior, mylohyoideus posterior,

Figure 9.--Internal view of the skin of male *Phasianus* colchicus showing the course, distribution and attachment of the striated dermal muscles associated with the dorsal pyerylae excluding the extreme anterior region of the dorsal capital tract. The solid lines within pterylae represent feather muscles which are superficial to the dermal musculature. Drawn from a photograph of a whole mount. Bouin fixation, unstained and partially cleared. The dash line represents the boundary of the cut skin.

Abbreviations of the Dermal Muscles: (see page 71 for other abbreviations)

con. colli = Constrictor colli

cuc. cran. = Cucullaris pars cranialis (left side cut at cranial attachment and mid-cervical region; right side partially removed to show superficial M. constrictor colli.

cer. c. cuc. cer. = Cervical component of M. cucullaris pars cervicalis (cut).

cl. c. cuc. cer. = Clavicular component of M. cucullaris pars cervalis (cut).

lat. d. dc. = M. latissimus dorsi pars dorsocutaneus (cut).

ser. s. mpt. = M. serratus superficialis pars metapatagialis (cut).

lat. d. mpt. = M. latissimis dorsi pars metaptatgialis (cut).

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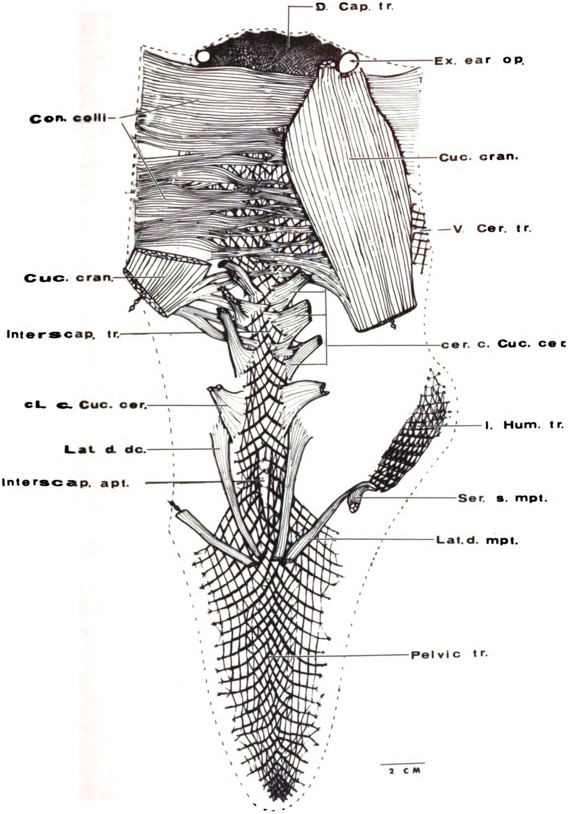

Figure 9

Figure 10.--Internal view of the skin of male Phasianus colchicus showing the course, distribution and attachment of the striated dermal muscles associated with the ventral pterylae excluding the anterior region of the capital and ventral cervical tracts. The solid lines within pterylae represent feather muscles which are superficial to the dermal musculature. Drawn from a photograph of a whole mount. Bouin fixation, unstained and partially cleared. The dash line represents the boundary of the cut skin.

Abbreviations of the Dermal Muscles (see page 71 for other abbreviations).

cuc. cran. = M. cucullaris pars cranialis (cut in the mid-cervical region).

f. cuc. cran. = M. cucullaris pars cranialis (cut at the furcular attachment).

pect. th. sub. th. = M. pectoralis thoracica pars subcutaneus thoracicus (cut).

pect. th. sub. abd. = M. pectoralis thoracica pars subcutaneus abdominalis (cut).

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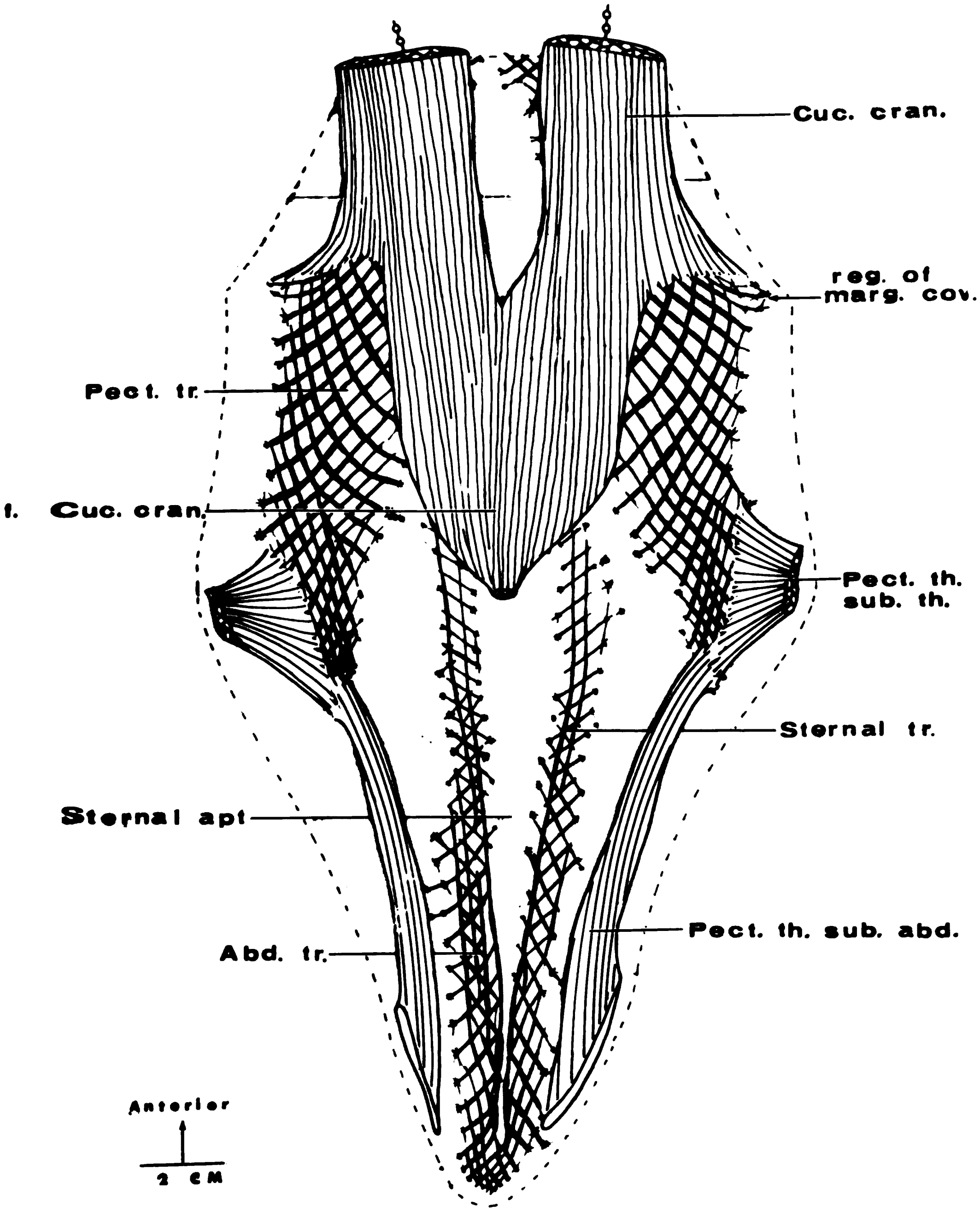

Figure 10

Figure 11.--Left lateral view of the head and neck of male *Phasianus colchicus* showing the superficial musculature and the origin of the dermal muscles.

A. Head

M. *cucullaris cranialis*, *cr*. = the cranial attachment of M. cucullaris pars cranialis (cut).

B. Neck

Mm. *cucullaris cervicalis*, *cer*. = the cervical attachment of Mm. cucullaris pars cervicalis.

M. *cuc*. *cerv*., *cl*. = the clavicular attachment of M. cucullaris pars cervicalis (retracted and cut).

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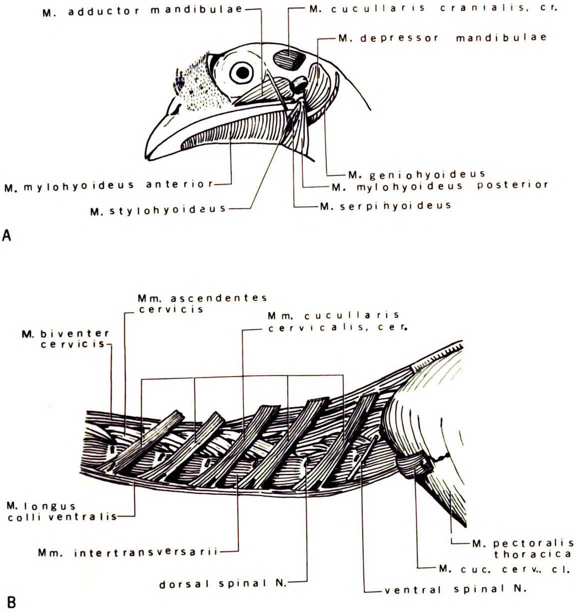


Figure 11

Figure 12.--Dermal and superficial muscles of the trunk of male *Phasianus colchicus*. The skin is not removed from the distal portion of the right arm. (a) ventral view, (b) dorsal view.

Abbreviations for the Dermal Muscles (see page 71 for other abbreviations).

cuc. *cer*. = M. cucullaris pars cervicalis (clavicular component).

cuc. *cran*. = M. cucullaris pars cranialis (furcular attachment).

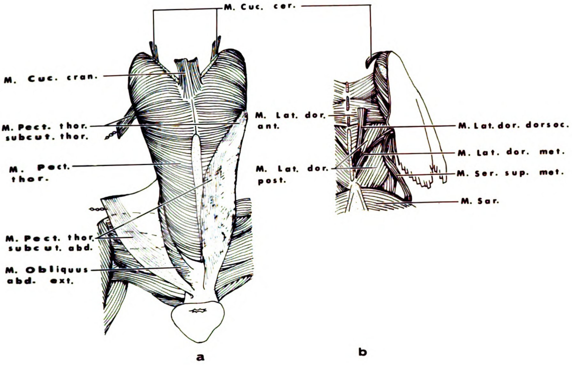
pect. *thor*. *subcut*. *thor*. = M. pectoralis thoracica pars subcutaneous thoracicus.

pect. *thor*. *subcut*. *abd*. = M. pectoralis thoracica pars subcutaneus abdominalis.

lat. *dor*. *dorsoc*. = M. latissimus dorsi pars dorsocutaneus.

lat. *dor*. *met*. = M. latissimus dorsi pars metapatagialis.

ser. *sup*. *met*. = M. serratus superficialis pars metapatagialis.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M. Cuc. cran.
M. Pect. thor. subcut. thor.
M. Pect. thor.
M. Pect. thor. subcut. abd.
M. Obliquus abd. ext.
M. Lat. dor. ant.
M. Lat. dor. post.
M. Lat. dor. dorsoc.
M. Lat. dor. met.
M. Ser. sup. met.
M. Sar.
a
b

Figure 12

stylohyoideus, and serpihyoideus) are well developed in *Phasianus*, *Chrysolophus* and *Gallus*, and weak in *Pavo*.

Mm. occipitalis, frontalis, dermo-frontalis, circumconcha and dermo-spinalis

Several investigators have found dermal muscles associated with the forehead and crown in some birds. Helm (1884: 347, 357; 1886: 340) described *M. occipitalis* which he found only in the Crowned Pigeon *Goüra cristata* (*Goüra coronata*) and *M. frontalis* which he found in some gallinaceous birds and also in the Crowned Pigeon. Shufeldt (1890: 2, 4) described a muscle similar to the latter, *M. dermo-frontalis*, which he found only in the male Raven. These muscles were absent in the forms I examined. Also, I did not find any muscles which corresponded to Shufeldt's *Mm. circumconcha* and *dermo-spinalis*.

Microscopic Examination of Teased Dermal Muscle

In most instances sheets of dermal muscles could be easily stripped from the undersurface of the skin. However, in certain regions portions of the dermal muscles firmly adhered to the skin beneath the feather follicles suggesting the possibility that striated muscle might be attached to the follicle walls. In order to determine whether or not this were true, muscles attached to the follicles were teased free, removed, stained with hematoxylin and examined at 450X. Tissue from the following areas was selected for examination:

(i) Mid-region of the dorsal cervical tract (hackle region of *Gallus*, *Phasianus*) where transverse fibers of M. constrictor colli are firmly attached.

(ii) The insertion end of M. cucullaris pars cranialis at the point where a transverse line connecting the follicles of the marginal coverts intersects with a longitudinal line drawn through the mid-region of the ventral cervical tract (*Phasianus*, *Gallus*).

(iii) M. cucullaris pars cranialis where it attaches to the skin beneath the follicles of the cape feathers in *Chrysolophus pictus* and *C. amherstiae*.

(iv) The insertion ends of the cervical component of M. cucullaris pars cervicalis (*Phasianus*).

(v) The insertion end of M. pectoralis thoracica pars subcutaneus thoracicus (*Phasianus*).

In all instances the only type of muscle I found connected to the feather follicles was non-striated. Petry (1951) made a histological examination of the skin in the pigeon. He did not report finding striated muscle attached to feather follicles. He did find an interlacing of smooth muscle (musculoelastic tissue) and striated muscle present in the lateral cervical apterium. However, he did not state the source of the striated muscle fibers. I assume they were from the cucullaris complex.

Significant Morphological Findings

M. mylohyoideus posterior, though found connected to the skin in some preparations, should not be regarded as a dermal muscle but probably rather as a "tongue" muscle. M. mylohyoideus posterior is described for *Phasianus*, *Gallus*, *Chrysolophus*, and *Pavo*.

Tables 3 and 4 summarize the dermal muscles found in *Phasianus*, *Gallus*, *Chrysolophus* and *Pavo*. M. cucullaris pars dorsocutaneus is present in *Chrysolophus* and *Pavo* and absent in *Phasianus* and *Gallus*. M. gastro-lumbalis is present only in *Gallus*. Many dermal muscles described by previous investigators for other birds are not present in *Phasianus*, *Gallus*, *Chrysolophus* and *Pavo*.

M. cucullaris is the most complex of the dermal muscles having attachments to the skin, skull, neck, appendicular muscles, and to the clavicle. It is not attached to the spinous processes of cervical vertebrae.

The cranial component of M. cucullaris pars cranialis is relatively more developed in male *Gallus* and *Chrysolophus* than in females of these genera. This may be related to the fact that display feathers overlie the muscle in males.

M. constrictor colli is present beneath the hackle follicles of *Gallus* and absent beneath the follicles of the cape feathers in *Chrysolophus*.

Except for the differences noted above, the course, origin and insertion of the dermal muscles do not differ

TABLE 3

Occurrence of dermal muscles in 4 genera of pheasants. An X indicates presence in adult males and females, (-) indicates absence.

	Phasianus	*Gallus*	*Chrysolophus**	*Pavo*
Constrictor colli	X	X	X	X
Cucullaris pars cranialis	X	X	X	X
Cucullaris pars dorsocutaneus	-	-	X	X
Cucullaris pars propatagialis	-	-	-	-
Cucullaris pars omocutaneus	-	-	-	-
Cucullaris pars metapatagialis	-	-	-	-
Cucullaris pars cervicalis (cervical component)	X	X	X	X
Cucullaris pars cervicalis (clavicular component)	X	X	X	X
Latissimus dorsi pars dorsocutaneus	X	X	X	X
Latissimus dorsi pars metapatagialis	X	X	X	X
Latissimus dorsi pars omocutaneus	-	-	-	-
Serratus superficialis pars metapatagialis	X	X	X	X
Serratus superficialis pars dorsocutaneus	-	-	-	-
Pectoralis thoracica pars subcutaneus thoracicus	X	X	X	X
Pectoralis thoracica pars subcutaneus abdominalis	X	X	X	X
Pectoralis abdominalis metapatagialis	-	-	-	-
Gastro-lumbalis	-	X	-	-
Dermo-spinalis	-	-	-	-
Occipitalis	-	-	-	-
Frontalis; Dermo-frontalis	-	-	-	-
Circumconcha	-	-	-	-

**Chrysolophus pictus* and *C. amherstiae*.

TABLE 4

Origin, insertion and course of the dermal muscles.

	Origin			Insertion onto the Skin				Course
	Skin	Skel- eton	Body muscle	Along entire length	At one end	Beneath pterylae	At the border of pterylae	Apterium crossed
Constrictor colli	X			X^1		X		none
Cucullaris								
p. cranialis		X		X^2	X^3	X^2	X^3	l. cer., v. cer.
p. dorsocutaneus	X^4				X		X	none
p. cervicalis								
cervical component			X				X	l. cer.
clavicular component		X			X		X	l. cer.
Latissimus dorsi								
p. dorsocutaneus			X		X	X		none
p. metaptatgialis			X		X		X	scap.
Serratus superficialis								
p. metapatagialis			X		X		X	l. body
Pectoralis thoracica								
p. subcutaneus abd.			X	X			X	pect.
p. subcutaneus thor.			X	X			X	l. body
Gastro-lumbalis	X				X^1		X	l. ster.

(1) connected to the skin at both ends; (2) anterior half; (3) posterior half; (4) see text; abd. = abdominalis; cer. = cervical; l. = lateral; p. = pars; pect. = pectoral; scap. = scapular; ster. = sternal; thor. = thoracicus; v. = ventral. Refer to text descriptions for details.

significantly between Phasianus, Gallus, Chrysolophus, and Pavo, nor between males and females of these genera.

Although differences exist in the course, origin, distribution and site of attachment to the skin between individual muscles, common characteristic features of the dermal muscles as a group are:

(i) They are striated muscles.
(ii) They are in the form of thin sheets or bands.
(iii) They do not attach to individual feather follicles.
(iv) Some portion of the muscle attaches to the undersurface of the skin by connective tissue or fascia.

Some dermal muscles are confined solely to the skin; that is, they have both their origin and insertion restricted to the skin (e.g., Mm. constrictor colli, cucullaris pars dorsocutaneus, gastro-lumbalis). Of these only M. constrictor colli is bound to the skin along its entire length.

With respect to origin some dermal muscles arise from the skeleton (e.g., M. cucullaris pars cranialis, the clavicular component of cucullaris pars cervicalis). Other dermal muscles arise from a body muscle (e.g., the cervical component of M. cucullaris pars cervicalis, Mm. latissimus dorsi pars dorsocutaneus and pars metapatagialis, Mm. serratus superficialis pars metapatagialis, pectoralis thoracica pars subcutaneus thoracicus and pars subcutaneus abdominalis).

At their insertions, some dermal muscles are firmly bound to the skin along most of their length (e.g.,

M. constrictor colli, the anterior portion of M. cucullaris pars cranialis, Mm. pectoralis thoracica pars subcutaneus thoracicus and pars subcutaneus abdominalis). M. pectoralis thoracicus pars subcutaneus abdominalis is firmly attached along its medial border.

Most dermal muscles are firmly bound to the skin at the insertion end only (e.g., M. cucullaris pars dorsocutaneus, the posterior half of M. cucullaris pars cranialis, the clavicular component of M. cucullaris pars cervicalis, Mm. latissimus dorsi pars dorsocutaneus and pars metapatagialis, M. serratus superficialis pars metapatagialis).

Attachments to the skin are beneath the follicles of feather tracts (e.g., M. constrictor colli, the anterior half of M. cucullaris pars cranialis), or at the edge of feather tracts, generally beneath groups of feathers bordering feather tracts (the posterior half of M. cucullaris pars cranialis, Mm. cucullaris pars dorsocutaneus and pars cervicalis, latissimus dorsi pars dorsocutaneus and pars metapatagialis, pectoralis thoracica pars subcutaneus abdominalis and pars subcutaneus thoracicus, serratus superficialis pars metapatagialis).

All dermal muscles except Mm. constrictor colli and cucullaris pars dorsocutaneus course beneath apteria. This may be significant in aerodynamics. The action of such a muscle may draw the borders of two feather tracts closer together thus making the feathers of one tract overlap more with those of an adjacent tract. This would probably result in a more uniform contour of the plumage which allows for a smoother passage of air over the surface of the body during flight.

In the birds I studied dermal muscles are not associated with all feather tracts. They are not attached to the skin beneath follicles of the dorsal, capital, crural and pelvic tracts, nor are they attached to the skin bordering these tracts. The common feature is that in these regions the skin is tightly bound to the body. In contrast to this situation 6 dermal muscles are associated with the loose skin of the neck.

Action of the Dermal Muscles

Morphological evidence.--The action of the dermal muscles must first be determined before their relationships to feather display can be ascertained. My deductions of muscle action are based primarily upon morphological evidence obtained from analyses of their structure, form, origin, insertion, course and distribution. Some of the morphological findings were reported in the previous section and summarized in Tables 3 and 4.

It is possible that in regions of the body where the skin is loose one function of the dermal muscles (particularly M. cucullaris pars cranialis) may be to regulate the tension of the skin. Another possible function may be to support the skin and its epidermal derivatives. For example, the muscle may become rigid during contraction and thus be capable of supporting a load acting at right angles to the longitudinal axis of the muscle fibers. In other words the muscle may resist shearing stresses. This type of action appears to be related to the greater development of M. cucullaris pars cranialis in the dorsal neck of males of Gallus and Chrysolophus as compared to females of these genera. I have previously shown that females of these forms lack the display feathers found in males. Thus the dorsal neck of males appears to be subjected to more shearing stresses than in females.

My morphological evidence supports the conclusions of Langley (1904) who suggested that dermal muscles function principally to control the position of the skin and groups of feathers rather than to regulate the degree of elevation of individual feathers. It appears that when a muscle contracts several actions may take place, depending upon the origin, course, insertion of the muscle(s) contracting and upon the elastic nature of the skin within pterylae and apteria. The following generalized actions are hypothesized.

Some dermal muscles appear to tense the skin over a particular body region. Regions within pterylae may be drawn together, or the border of one feather tract may be drawn toward another feather tract. Apteria may be folded and shortened. A muscle which arises from the skeleton or a body muscle may draw the skin toward the origin when it contracts, thus tensing the skin and possibly tightening it to the body.

As pointed out previously, the cucullaris complex has attachments to the skull, skin, neck, clavicle and furculum. Thus, the muscle complex may have numerous functions. Pars cranialis probably serves to tighten the skin between the skull and the thoracic region.

The cranial component of pars cranialis which covers the anterior dorsal and the posterior ventral region of the neck may aid in resisting shearing stresses. Tightening of the skin by this muscle may also aid in passing food down the esophagus and in regulating the expulsion of air through the trachae and the cervical air sacs. The neck and head of gallinaceous birds is highly mobile. It appears that the development of pars cranialis may be related to the mobility of the neck and head. The cranial component of pars cranialis apparently is present in all birds, but is more developed in long-necked forms (Fürbringer, 1888: 303). Combined contraction of both paired components and the resultant tightening of the skin may help to retract the head and neck; unilateral contraction may aid in bending the head to one side.

The development of the cranial portion of pars cranialis may be related to the movement and positioning of the head in hummingbirds (e.g., Eugenes fulgens) where the muscle takes a different origin from the skull (Weymouth et al., 1964: 256). Pars cranialis arises from the dorsal surface of the skull medial to, and just caudal to the midpoint of the orbit.

The posterior mid-ventral component of pars cranialis attaches to the skin and furculum. This muscle overlies the crop. Tightening of the skin in this region may serve to pass food from the esophagus into the crop. A more plausible function appears to be for support against shearing stress. This would especially seem true when the crop is full. Fürbringer (1888: 305) stated that the muscle is more developed in those forms with a highly developed crop and that the muscle is either reduced or takes a different origin from the clavicle in those forms in which the crop is less developed.

The cervical component of M. cucullaris pars cervicalis arises as 3 to 5 slips from the lateral surface of the cervical vertebrae. It passes dorsally beneath the lateral cervical apterium and posteriorly to insert on the skin beneath the lateralmost follicles of the interscapular tract. The contraction of this muscle probably tightens the skin to the lateral posterior region of the neck. Tightening of the skin may aid in the expulsion of air in the cervical air sacs and in controlling the contour of the body by shortening the apterial distance between the dorsal and ventral cervical tracts which probably would result in a greater overlap of feathers and allow for a freer flow of air over the body during flight.

The clavicular component of M. cucullaris pars cranialis passes from the clavicle to the lateral border of the interscapular tract. Contraction of this muscle may tighten the skin between the clavicle and the interscapular region permitting a smooth flow of air over this region of the body during flight.

M. latissimus dorsi pars metapatagialis is a dermal component of an appendicular muscle which crosses beneath the scapular apterium to the poasterior medial border of the humeral tract. The action of this muscle probably tightens the skin between the back and upper arm which may play a role in regulating the flow of air over this region.

The preceding account has been a general discussion on the possible action and function of some of the dermal muscles described previously. Morphological evidence suggests that the action of the dermal muscles is to tighten the skin in particular regions of the body. It appears that the striated dermal muscles are not responsible for producing the <u>fanned</u>, <u>depressed</u>, <u>ruffled</u> and <u>sleeked</u> feather postures observed during display. Other functions relating to the functioning of the esophagus, crop, air sacs, mobility of the head and neck and flight were presented.

<u>Physiological evidence</u>.--In order to test my hypotheses of muscle action based upon morphological evidence, some

muscles and nerves associated with the skin were stimulated electrically. The 6 Single Comb White Leghorn chickens used in the experiments were anesthetized according to the methods previously described.

Using a Harvard model 935B stimulator, a 0.1 volt 250 cycle stimulus was applied for about 1 second directly to the dermal muscle or to the peripheral end of cut nerves according to the procedure of Langley (1904). When the muscle contracted, movements of the skin and feathers were noted at low magnification with a dissecting microscope and the stimulus was then stopped. This stimulus was selected arbitrarily over others (ranging from 0.1 volts to 500 volts and from 1 to 500 cycles per second) which also caused the muscles to contract.

Three muscles were selected for stimulation. The cranial component of M. cucullaris pars cranialis was chosen because of its relationship to the display feathers of the dorsal cervical tract. It arises from the skull and the belly closely adheres to the skin beneath the hackles. Contraction of this muscle should tighten the skin in this region and draw it toward the skull. The action should occur without elevating or depressing the feathers.

The cervical component of M. cucullaris pars cervicalis was selected because it courses beneath the lateral cervical apterium and is attached to the neck at one end and to the lateral border of the interscapular tract at the other. Contraction of this muscle should pull the skin inward toward the lateral region of the neck. Folding of the skin in the lateral cervical apterium should occur.

M. latissimus dorsi pars metapatagialis courses beneath the scapular apterium. Stimulating this muscle should result in the folding of the scapular apterium and a tightening of the skin of the back and upper arm.

The stimulus was applied to M. cucullaris pars cranialis at a point about one centimeter distal to its origin from the skull. This point was chosen because it can be easily exposed. Also, posterior to this M. cucullaris is covered by M. constrictor colli. Thus in the latter site it would be difficult to stimulate the cucullaris without stimulating M. constrictor colli. The cranial attachment was exposed and stimulated from the dorsal external surface.

The cervical portion of M. cucullaris pars cervicalis was exposed by making a longitudinal incision in the posterior half of the skin of the ventral neck. Cervical spinal nerves and slips of pars cervicalis on one side of the neck were freed from adjacent tissue. The muscle was stimulated about midway between its origin and insertion.

The origin of M. latissimus dorsi pars metapatagialis was exposed by making an incision lateral to the mid-dorsal line on the opposite side of the back. The flap of skin was carefully freed from the back to expose the muscle. Pars metapatagialis was stimulated at its origin.

Muscle response to the stimulus was similar in all three cases. When the muscle was stimulated it contracted, the skin twitched and folded. Four or five trials were made for each muscle. The skin twitched and remained folded as long as the stimulus was applied (1-5 sec.). Folding of the skin was at right angles to the long axis of the muscle and occurred in numerous places so that the skin between the origin and insertion was thrown into many fine wrinkles.

During contraction of M. cucullaris pars cranialis the skin of the dorsal neck moved cranially and groups of hackle feathers around the site of the stimulus moved closer together lengthwise (corresponding to the long axis of the muscle). The feathers neither elevated nor depressed.

When fibers of M. cucullaris pars cervicalis were stimulated, the skin of the lateral cervical apterium folded and groups of feathers along the lateral border of the interscapular tract were drawn sharply toward the neck.

Folding and twitching of the skin was less noticeable when M. latissimus dorsi pars metapatagialis was stimulated.

Stimuli for the nerve experiments were the same as those for the muscles. When peripheral ends of cut cutaneous nerves of the pectoral and femoral regions were stimulated individually, neither the feathers nor the skin moved. However, stimulation of individual cutaneous branches of dorsal cervical spinal roots produced twitching and folding of the skin which caused groups of feathers in the interscapular region to draw closer together. Again the feathers neither elevated nor depressed. Folding and twitching of the skin were most noticeable in the region of the lateral cervical apterium when ventral cervical roots were stimulated. This is because ventral roots innervate the cervical component of M. cucullaris pars cervicalis. When the muscle contracts, a region of the skin corresponding to the insertion is tightened and pulled inward toward the origin at the neck.

These findings support my deductions of muscle action based upon morphological data, suggesting again that the action of the dermal muscles is to move the skin rather than to control elevation of the feathers. In general, my preliminary physiological experiments verify some of the findings of Langley (1904). He found that stimulating ventral cervical roots produced a sharp twitch of the striated muscles associated with the neck. Langley found that stimulating peripheral nerves produced depression of the feathers. This response is similar to that produced when the sympathetic system is stimulated. I could not produce feather depression when I stimulated peripheral nerves.

<u>Evidence from muscle extirpations</u>.--Before I present the experiments in muscle extirpation I shall review the morphological factors that may play a role in the action of M. cucullaris pars cranialis.

This complex muscle is composed of two components (Figures 9 and 10). The cranial component is attached to the skull and to the skin of the dorsal, lateral and lateroventral neck. The posterior component attaches to the furculum and to the skin of the ventral neck. Fibers of both muscles merge in the ventral posterior region of the neck. Both components are most firmly attached to the skin in a transverse line connecting the under marginal coverts of the prepatagium. The cranial component, just posterior to the skull, is covered superficially by M. constrictor colli and some fibers of the cranial component merge with it. Both muscles are attached to the undersurface of the skin but not to the feather follicles. The foregoing account illustrates the complexity of the gross morphology of pars cranialis.

An attempt to explain muscle action is further complicated when the innervation of pars cranialis is considered. It is reported to be innervated by the accessorius externus, vago—accessorius, hypoglosso-accessorius nerves, cervical nerves and nerves from the brachial plexus (Fürbringer, 1888: 307; Edgeworth, 1935: 146; Goodman and Fisher, 1964: 115).

The cranial component of M. cucullaris pars cranialis is of particular interest since it lies beneath the hackles of _Gallus_ and the cape feathers of _Chrysolophus_. The muscle is more developed in males than in females of these forms. However its greater development in males may not be functional as far as display is concerned. The possibility of resistance against shearing stresses has already been discussed.

I previously demonstrated that stimulating the cranial origin of pars cranialis caused the skin to twitch and fold. Hackle feathers moved closer together, anteriorly, without erecting or depressing. However, the response was restricted to the vicinity of the stimulus; the whole muscle did not appear to contract, for the response was not along the entire course of the muscle.

In order to test further the hypothesis that M. cucullaris pars cranialis does not regulate the degree of elevation of the hackles in Gallus (bamtum Rhode Island Red chickens), the muscle was extirpated at its origin. Such muscle extirpations have been used to determine the role of M. depressor caudae and M. caudofemoralis in flight (Fisher, 1957). I know of no studies involving extirpations of dermal muscles.

Two weeks prior to muscle extirpations 9 cock and 4 hen Rhode Island Red chickens were allowed to create a social situation in which the peck order was altered each day by removing, isolating and resubmitting cock birds. The purpose of this was to determine the dominant males which could then be paired later to provoke agonistic displays. All cocks were color marked with leg bands so participants in agonistic encounters could be identified.

When isolated cocks were reintroduced into the flock in the presence of hens there was an apparent attempt to establish a new peck order. This was characterized by an exchange of displays between the intruder and the flock, and also within the flock. Lateral displays as well as shaking of the body were numerous and occurred between all members. Frontal displays, which followed the lateral display, were most frequent between the dominant bird and the new intruder. Submissive actions of introduced cocks were characterized by numerous lateral displays followed either by retreat or displacement activities. Only those males which most frequently raised their hackles, either during the body shake or frontal display, were selected for further experimentation. I felt that males which were consistently submissive prior to the operation would be submissive postoperatively. Three such submissive males were eliminated from the study.

Before the operation all birds were anesthetized intravenously with Equi-Thesin® (1.9 to 3.5 ml/kg body weight). In the experimental birds a one and one-half centimeter segment of M. cucullaris pars cranialis was removed, bilaterally, from its cranial attachment. Only the skin superfical to the muscle was cut in sham-operated birds.

The skin was sutured and the birds were allowed to recover. All birds apparently recovered completely. In general, they exhibited normal behavior patterns associated with feeding, crowing and body maintenance, 24 hours after the operation. One noticeable difference in postoperative birds appeared to be a slight drooping of the head. This may have been due to the destruction of pars cranialis, which in its intact form may help to keep the head in an upright position, or it could be attributed to the lingering effects of anesthesia. Drooping of the head diminished 24 hours after the operation.

Muscle extirpations were not made in all cocks on the same date (Table 5). Some birds served as controls early in the experiment but after 21 days all cocks had had the operation, at which time the experiment was terminated.

After a period of isolation (1 to 5 days) experimental birds were reintroduced into the flock and observed for 10 minutes. If the experimental cock was submissive it was isolated again and reintroduced at another time, sometimes into the pairing territory of another breed (Araucana). The Araucana was selected because it always provoked agonistic displays when it was introduced into the territory of experimentals.

Table 5 shows that shaking of the body, <u>frontal</u> display or submissive behavior was performed by introduced cocks; the response apparently depended upon the social structure of the flock. <u>Frontal</u> displays were frequent between bird 2 and bird 3. These birds ranked 1 and 2 respectively in the hierarchy before and after muscle extirpation. All birds were submissive when introduced into the breeding territory of a foreign bird (Araucana). When the Araucana was introduced into the flock, all 6 birds challenged him with <u>frontal</u> displays.

FOOTNOTES TO TABLE 5

(1) The first column is the date birds were resubmitted to rivals. In the second column the number on the left refers to the number of days subsequent to muscle extirpation; the number in parentheses is the number of days the birds were isolated prior to resubmitting to rivals.

(2) + indicates the hackles elevated;
0 indicates hackles not elevated.

(3) Birds were considered submissive when they did not challenge rivals with a frontal display. Shaking of the body was recorded since it involves the movement of feathers.

(4) A cock Araucana introduced into the territory of Rhode Island Reds.

(5) Bird introduced into the territory of paired Araucanas.

TABLE 5

Responses of cock Rhode Island Red chickens to rivals after partial removal (1.5 cm) of M. cucullaris pars cranialis from its cranial attachment*.

	Operation		Exposed to	Behavior		
Bird	Type	Date	rivals[1]	Hackles[2]	Display[3]	Directed toward
1	Sham	3/7	3/11 4(4)	+	Body shake	Flock
	Bilateral	3/23	3/28 5(5)	0	Submissive	Flock
			3/28 5(5)	+	Frontal	Araucana[4]
2	Bilateral	3/7	3/11 4(4)	+	Body shake	Flock
			3/14 7(1)	0	Submissive	Araucana[5]
			3/15 8(2)	+	Frontal	Bird three
			3/22 15(0)	+	Frontal	Bird three
			3/26 19(1)	+	Body shake	Flock
			3/28 21(0)	+	Frontal	Araucana
3	Control	3/7	3/11 (4)	+	Body shake	Flock
			3/15 (0)	+	Frontal	Bird two
	Bilateral	3/17	3/18 1(1)	0	Submissive	Flock
			3/22 5(4)	0	Submissive	Araucana[5]
			3/22 5(4)	+	Frontal	Bird two
			3/23 6(1)	0	Submissive	Flock
			3/28 11(1)	0	Submissive	Flock
			3/28 11(1)	+	Frontal	Araucana[4]
4	Control	3/17	3/18 (1)	0	Submissive	Flock
	Bilateral	3/21	3/22 1(3)	0	Submissive	Araucana[5]
			3/22 1(3)	+	Frontal	Hen
			3/23 2(1)	0	Submissive	Flock
			3/27 6(1)	0	Submissive	Flock
			3/28 7(0)	+	Frontal	Araucana[4]
5	Control	3/17	3/18 (1)	0	Submissive	Flock
	Control	3/17	3/22 (4)	0	Submissive	Araucana[5]
	Bilateral	3/23	3/26 3(3)	+	Body shake	Flock
			3/27 4(1)	0	Submissive	Flock
			3/28 5(1)	+	Frontal	Araucana[4]
6	Bilateral	3/23	3/25 2(2)	+	Frontal	Hen
			3/27 4(1)	0	Submissive	Flock
			3/28 5(1)	0	Submissive	Flock
			3/28 5(1)	+	Frontal	Araucana[4]

*Refer to the key to Table 5, page 123 for details.

During frontal display both the experimental and the control birds elevated their hackles (Figure 4; the banded bird is bird 2, eight days after the operation). Hackles appeared to raise as quickly and as high in experimentals as in controls. The remaining body feathers were strongly depressed in both birds. Movements of the body and feathers did not appear to differ among experimentals and controls.

Experiments were terminated on 28 March, 1967 and each bird was anesthetized and reexamined for the degree of regeneration of M. cucullaris pars cranialis. I found no apparent adhesion of the muscle to the skull 5, 7, 11 and 21 days after the cranial portion had been extirpated.

Results from these experiments demonstrate that partial destruction of M. cucullaris pars cranialis does not affect the degree of elevation of the hackles in Rhode Island Red chickens. Thus, morphological and physiological evidence, and evidence from muscle extirpations in live birds, support the hypothesis that the action of the striated dermal muscle is to position the skin rather than to regulate the degree of elevation of individual feathers.

Summary and Discussion

Generalizations about the morphology and action of the dermal muscles apply only to the birds I examined.

The gross morphology of 10 striated dermal muscles is described for *Phasianus*, *Gallus*, *Chrysolophus* and *Pavo*.

Mm. constrictor colli, cucullaris pars cranialis, cucullaris pars cervicalis, latissimus dorsi pars dorsocutaneus and pars metapatagialis, pectoralis thoracica pars subcutaneus thoracicus and pars abdominalis are present in both sexes of all representatives. The course, origin and attachments of these muscles do not differ significantly between sexes or among representatives.

Mm. cucullaris pars dorsocutaneus is present only in Chrysolophus and Pavo. M. gastro-lumbalis, present only in Gallus, may be a dermal component of M. pectoralis thoracica pars abdominalis.

M. mylohyoideus posterior is not considered a dermal muscle but rather a "tongue" muscle. It is present in Phasianus, Gallus, Chrysolophus and Pavo.

As a group, dermal muscles may be attached to the skeleton or to appendicular muscles and are always attached to the skin at one end. Mm. constrictor colli, cucullaris pars dorsocutaneus and gastro-lumbalis have both their origin and insertion restricted to the skin.

M. cucullaris pars cervicalis and the clavicular component of M. cucullaris pars cranialis arise from the skeleton.

The cervical component of M. cucullaris pars cervicalis, Mm. latissimus dorsi pars dorsocutaneus and pars metapatagialis, Mm. serratus superficialis pars metapatagialis, pectoralis thoracica pars subcutaneus abdominalis and pars subcutaneus thoracicus appear to be dermal components of body muscles.

Dermal muscles do not attach to individual feather follicles. Rather, they attach by fascia to the undersurface of the skin, generally beneath groups of feathers at the borders of feather tracts. They usually cross apteria.

No dermal muscles are found associated with the dorsal capital, crural or pelvic tracts.

Six dermal muscles are associated with the loose skin of the neck.

Deductions of muscle action were made, based upon morphological evidence and evidence obtained from experiments in muscle and nerve stimulation and muscle extirpations in live birds. Actions of individual muscles are assumed to depend upon the origin, course, and insertion of the muscle(s) contracting and upon the elastic nature of the skin within pterylae and apteria.

The evidence strongly suggests that the action of the dermal muscles is to tense and tighten the skin, not to regulate the degree of elevation of the feathers.

Tensing and tightening of the skin probably serve many functions. Some factors which might play a role in the development and function of M. cucullaris, the most complex of the dermal muscles, were considered and discussed previously. These included multiple innervation, the mobility of the head and neck, the functioning of the esophagus, trachea, crop and cervical air sacs, and the contour of the body as related to flight.

The phylogeny of M. cucullaris may also provide some insight as to its function in birds. Although he does not discuss the functional relationships of M. cucullaris, Edgeworth (1935: 141-153) presents a detailed account of its development among vertebrates.

He stated that it develops as a backward extension of the caudal-most branchial muscle plates in Dipnoi, Elasmobranchii, Teleostomi, Amphibia, Reptilia and Mammalia. In general, the muscle arises from the skull and passes to the scapula, clavicle or to the sternum. Apparently it is absent in limbless forms (e.g., Urodela, Ophidia) and in some teleosts which have a fixed pectoral girdle (e.g., Acipenser sturio). It does not develop in Anura until metamorphosis.

This suggests that M. cucullaris may be related to coordinated movements between the skull and the skeletal components of the pectoral girdle which in turn may be associated with locomotion.

Edgeworth stated that in some forms in which the shoulder girdle is rudimentary most of the fibers of M. cucullaris pass from the skull to the skin (e.g., Amphisbaenid reptiles). This modification in attachment of M. cucullaris may be an adaptation for the fossorial habits of these forms.

In reptiles M. cucullaris develops from the 2nd branchial muscle plate. In birds the 2nd branchial muscle plate is not formed. Edgeworth (pp. 146, 153) does not accept the 1st branchial muscle plate as the source of the cucullaris. He describes M. cranio-cervicalis which develops from occipital myotomes and has the same function as M. cucullaris but is of different development than in reptiles. He does not consider M. cranio-cervicalis homologous to M. cucullaris. I have retained the terminology of M. cucullaris because of its widespread acceptance in the avian literature, and until more evidence is available on the homologies of this complex muscle.

The proposed actions and functions of the dermal muscles found in _Phasianus_, _Gallus_, _Chrysolophus_ and _Pavo_ are sum-summarized below. The first 6 muscles are assumed to interact with one another to control the loose skin of the neck.

_M_. _constrictor_ _colli_ probably tightens the skin around the anterior neck. The action may aid in passing food down the esophagus.

The _cranial_ _component_ _of_ _M_. _cucullaris_ _pars_ _cervicalis_ presumably tightens the skin of the anterodorsal and lateral neck. Since it is relatively more developed in male of _Gallus_ and _Chrysolophus_ than in females of these forms, its development appeared to be related to the displays of these birds. However, experiments in muscle stimulation and extirpation of the cranial attachment in live birds demonstrated that the muscle is not responsible for elevating the hackles in _Gallus_. It may play a more important role in supporting the skin against shearing stresses, aiding in regulating the mobility of the head and neck, and aiding in passing of food down the esophagus or passing of air through the trachea and cervical air sacs.

The *furcular component of M. cucullaris pars cranialis* is intimately associated with the crop. Contraction of the muscle probably tightens the skin over the crop, thus perhaps supporting this organ and possibly aiding the passage of food through it.

M. cucullaris pars dorsocutaneus, a dorsomedial posterior continuation of the cranial component of M. cucullaris pars cranialis, appears to supplement the action of the latter in tightening the skin between the skull and the interscapular tract. It is present only in *Chrysolophus* and *Pavo*.

Slips of the *cervical component of M. cucullaris pars cervicalis* arise from the lateral surface of the neck and pass posterodorsally to insert onto the skin beneath the lateralmost follicles of the interscapular tract. Electrical stimulation of the muscle results in the folding of the skin in the lateral cervical apterium and drawing of the skin inward to the lateral surface of the neck. The action may aid in the expulsion of air from the cervical air sacs or in the control of the flow of air over the thoracic region of the neck.

The *clavicular component of M. cucullaris pars cervicalis* arises from the dorsal medial border of the clavicle and inserts onto the skin beneath the lateralmost follicles of the interscapular tract just posterior to the insertion of the cervical component. The muscle presumably tightens the skin which may aid in controlling the flow of air over the shoulder during flight.

M. latissimus dorsi pars dorsocutaneus acts upon the skin of the interscapular tract and appears to be antagonistic to the action of the cranial component of M. cucullaris pars cranialis and also M. cucullaris pars dorsocutaneus when the latter is present. M. latissimus dorsi pars dorsocutaneus presumably draws the skin beneath the interscapular tract posteriorly.

M. latissimus dorsi pars metapatagialis presumably tenses the skin between the dorsal thoracic region and the metapatagium and *M. serratus superficialis pars metapatagialis* tenses the skin between the lateral thoracic region and the metapatagium. These two muscles may interact to control the flow of air beneath the shoulder.

M. pectoralis thoracica pars subcutaneus thoracicus probably tenses the skin over the anterior thoracic region. The action presumably is to draw the skin of this region dorsally and anteriorly toward the axillary region. The action may be important in controlling the flow of air over the lateral surface of the body.

M. pectoralis thoracica pars subcutaneus abdominalis acts upon the skin of the ventrolateral thoracic and abdominal regions. Its action appears to be antagonistic to M. pectoralis thoracica pars subcutaneus thoracicus (i.e., to draw the skin caudally and ventrally and to tighten it against the ventrolateral thoracic and abdominal wall of the body). The action may play a role in controlling the flow of air over the ventrolateral surface of the body or in the expulsion of air from the abdominal air sacs.

M. gastro-lumbalis is present only in *Gallus*. Its action apparently is to tense the skin between the anteroventral border of the femoral tract and the posterolateral border of the sternal tract.

Relationship of the Dermal Muscles to Feather Display

I have previously described the movements of body feathers during display and during preening. In general, two different types of feather movements were assumed to occur. In the first type, feather shafts appeared to move independently of the movement of the skin. In other words the feathers may move in one direction and the skin may move in another direction or remain stationary.

Observations of movements of the skin and of clipped feathers during preening of the pelvic tract in *Gallus* revealed that the skin of this area did not move as the feathers erected or depressed. Since striated muscles are absent from the pelvic tract in all representatives, some other mechanism must be responsible for raising and lowering the feathers of this area.

I have assumed that some movement of the feathers is dependent upon the movement of the skin. Observations of the skin and of clipped feathers of the dorsal neck of Gallus during preening revealed that the skin and feathers of the dorsal cervical tract may move anteriorly or posteriorly. Integrated movements of the skin and feathers appeared to be coordinated with the extension and retraction of the head and neck.

The presence, location, attachments, contraction and action of the cranial component of M. cucullaris beneath the dorsal cervical tract, and of M. latissimus dorsi pars dorsocutaneus beneath the interscapular tract do explain this type of feather movement, but fail to explain elevation of the hackles during display.

The contraction of the cervical component of M. cucullaris pars cervicalis apparently explains the observed inward folding of the skin of the neck when clipped birds were handled.

Hackle feathers are elevated and remain elevated during the frontal display of Gallus even though the head may take many different positions. Elevated hackles may move closer together or further apart (anteroposteriorly) depending upon the position of the head. This form of feather movement is assumed to be under control of the skin which appears to be activated by M. cucullaris.

I previously mentioned that swelling and shrinking of the body was most conspicuous and was unilateral during the lateral display of Chrysolophus. It may be that control of inflation and deflation of the air sacs, and the size of the thoracic cavity is dependent upon the tension of the skin on the thoracic and abdominal wall of the body. Mm. pectoralis thoracica pars subcutaneus thoracicus and pars subcutaneus abdominalis are positioned over the ventro-thoracic and abdominal region of the body. Activating the skin of the region by these muscles may explain the compressed shape of the body occurring during the courtship display of Chrysolophus.

In the lateral display of Chrysolophus the yellow feathers of the rump appeared to shift toward one side of the body for which I proposed the movement of the skin as an explanation. However, since dermal muscles are not associated with the skin of the pelvic tract, another mechanism must be present to explain the shifting of the plumage of the rump in Chrysolophus.

The gross morphology and action of the dermal muscles, one component of the skin muscles, fail to explain:

1. The movement of feathers independent of the movement of the skin.

2. The elevation and depression of feathers during preening of particular feather tracts.

3. The general fluffing of all body feathers in the courtship display of Phasianus.

4. The inclination and elevation of the "ear" tufts in Phasianus.

5. The ruffling of the hackles and depression of the remaining body feathers in the _frontal_ display of _Gallus_.

6. The extension and elevation of the cape in the lateral display of _Chrysolophus_.

7. The shifting of the plumage of the rump to one side of the body in the _lateral_ display of _Chrysolophus_.

8. The raising and spreading of the train in _Pavo_.

9. The apparent permanence of the erected crest of _Pavo_ and the depressed crest of _Chrysolophus_.

Though the dermal muscles appear to be the mechanism which activates the skin, they fail to explain the mechanism which activates the feathers.

The second component of the skin muscles is the smooth muscles. This system will be examined next in an attempt to determine their role in feather display.

SMOOTH MUSCLES OF THE SKIN

Introduction

While the striated dermal muscles attach to the undersurface of the skin, the non-striated muscles of the skin are confined within the dermis. Within pterylae, bundles of smooth muscle (feather muscles) link adjacent feather follicles. A delicate layer of musculoelastic tissue, characterized by an alternating series of smooth muscle fibers and elastic tendons, spans some apteria. Feather muscles of follicles at the borders of feather tracts and of isolated follicles in apteria unite with the musculoelastic tissue.

Concurrently, but independent of this study, Dr. A. M. Lucas and his associates of the U. S. Department of Agriculture Avian Anatomy Investigations at Michigan State University undertook an extensive investigation of the feather muscles (= their musculi pennati) and the musculoelastic tissue (= their musculi apterii) in the chicken, turkey, coturnix, white Pekin duck and the common pigeon. They investigated the relationship of the smooth muscles to feather type and to patterns of pterylosis. Their studies were made at the gross, subgross and microscopic levels. They also investigated the micro-morphology of the innervation and vascularization of the skin.

Although specific goals differed between their studies and mine, the approaches at the gross and subgross levels were similar. Also since my study concerns the relationship of the feather muscles to contour feathers which are positioned conspicuously during display, feather type and feather pattern could not be ignored. For this reason my findings of noteworthy similarities or differences in the relationship of the smooth muscles to feather type or pterylosis are compared with those of Lucas and Stettenheim (unpublished).[1] The plan in this investigation of the smooth muscles is similar to that used in the examination of the dermal muscles. The basic pattern, distribution, arrangement, attachment, and extent of development are first presented for _Phasianus colchicus_. Similarities and differences in the gross morphology of the feather muscles as found in _Gallus_, _Pavo_, and _Chrysolophus_ when compared with _Phasianus_ are noted and then related to feather display.

Patterns of the muscoloelastic tissue are described but not figured. The arrangement of the feather muscles of the wing and tail was not investigated. For these details the reader is again referred to the descriptions and excellent figures of Lucas and Stettenheim (unpublished).

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[1] The reader is reminded that this citation refers to the manuscript of "Avian Anatomy. Integument," currently in the process of final editing; the manuscript will be published for the U. S. Department of Agriculture by the Government Printing Office.

The basic arrangement, attachment and distribution of the feather muscles are most easily demonstrated in regions of the body where the skin is thin and dermal muscles are absent. The femoral and crural tracts are two such regions, and skin from these areas are examined first.

Femoral Tract

Description for Phasianus (Figures 13, 14, and 15).--The pattern of pterylosis as viewed from the external surface shows the feather follicles arranged in indistinct chevron-shaped rows with the apex of the chevron pointing anteriorly (Figure 6). This pattern is most evident in the middle of the tract and becomes more obscure at the dorsal and posterior boundaries. When a whole mount of the tract is made and the gross pattern of feather muscles and follicle rows is considered, a completely different picture is obtained (Figure 13).

The pattern of chevron-shaped follicle rows is not evident. Using a mid-dorsal longitudinal line as a reference, muscle and follicle rows course anterodorsally and posterodorsally. Anterodorsal and posterodorsal follicle rows are not always in a continuous line across the entire tract. Intercalary rows of follicles frequently interrupt the continuous pattern. An intercalary row is identified by 2 or more follicles aligned in a row which is between, and shorter than, two longer continuous rows of the tract.

Intercalated rows may be irregular (Figure 13A) or uniform (Figure 13B). Although intercalary follicles are a part of the total picture of pterylosis, they do not conform to the unusually clear pattern of follicle row arrangement found in the middle of the tract. Since they are ruptive to the pattern, I consider them different from the rest of the tract follicles.

Anterodorsal and posterodorsal muscle rows are about equally developed except at the posterior part of the tract where posterodorsal rows are dominant. Muscle rows are subsequently considered dominant over other muscle rows when the muscles of one row stain darker than another row. Larger muscles stain darker than smaller muscles.

Intersections of posterodorsal and anterodorsal muscle rows connecting four contiguous follicles form subpatterns consisting of diamonds, squares, or parallelograms. A feather follicle is present at each intersection. Orientation of feather follicles indicates that feathers might overlap the base of a feather diagonally across from it if feathers were present. Longitudinal diagonal muscle rows are infrequently present and if equally developed with respect to the anterodorsal and posterodorsal muscle rows they divide the quadrilateral into two prominent triangles. Closed quadrilaterals and triangles are not present along the outer border except at the caudal region of the tract. Rather, feather muscles radiate and unite with the musculoelastic tissue characteristic

Figure 13.--External view of the skin covering the left thigh of a male Phasianus colchicus showing feather muscles of the femoral tract.

A--The location from which Figure 14 was made.

B--Intercalary follicle rows.

C--A point where diagonal muscles become dominant anteriorly.

This causes a more acute curve in the posterodorsal directed muscle rows. Change in direction of muscle rows results in a slight reorientation of quadrilaterals.

The solid lines within the tract represent feather muscles. Fine lines radiating out from isolated follicles represent feather muscles which connect to the musculoelastic tissue (= apterial muscles) characteristic of most featherless spaces. The pattern of the musculoelastic tissue is not shown. Feather follicles are shown to demonstrate their variation in size, their orientation, and their position relative to the epidermal surface. The drawing was made from a Kodachrome slide taken of a whole mount. Bouin fixation, unstained and partially cleared.

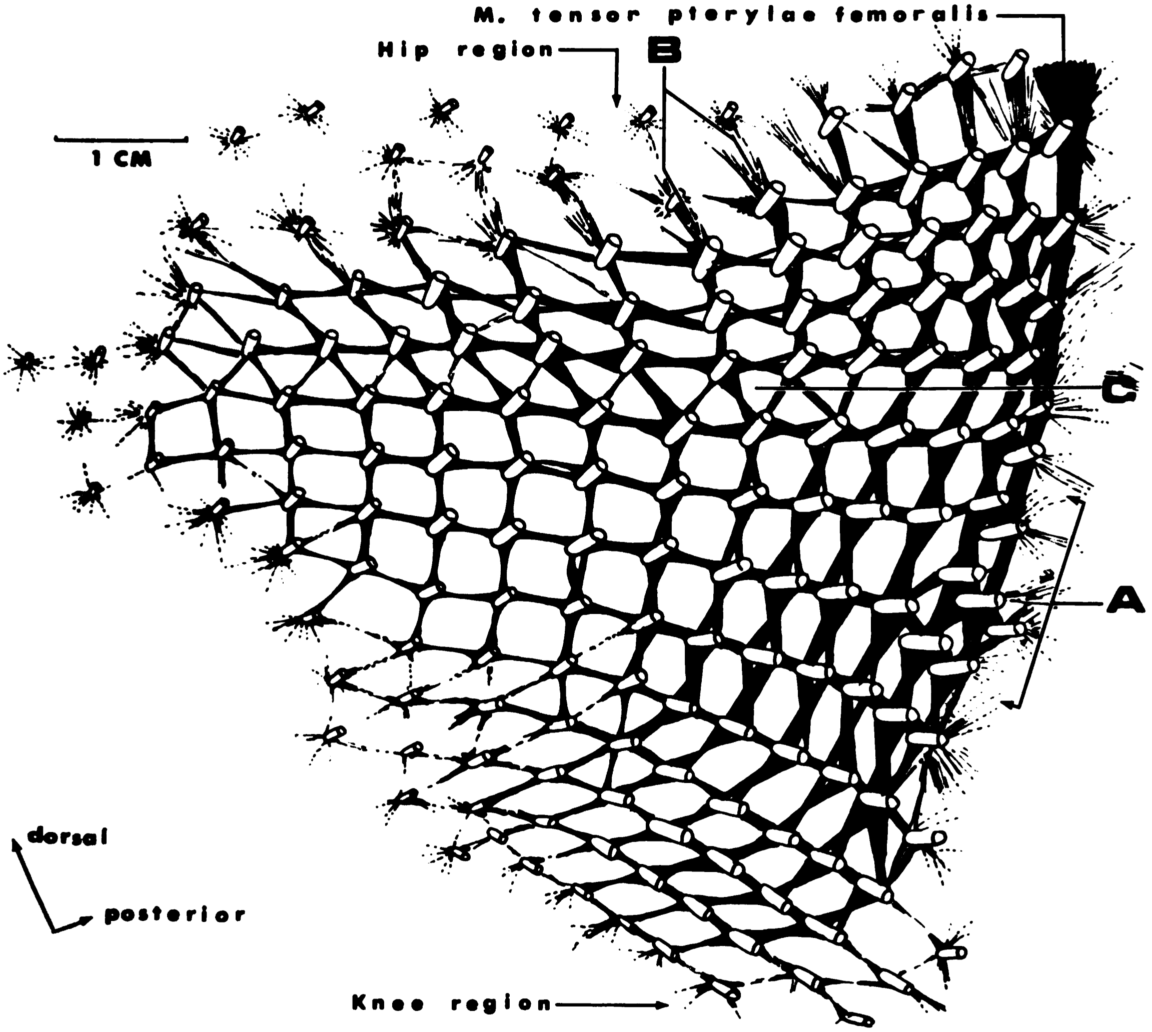
M. tensor pterylae femoralis
Hip region
B
1 CM
C
A
dorsal
posterior
Knee region

Figure 13

Figure 13.--External view of the skin covering the left thigh of a male Phasianus colchicus showing feather muscles of the femoral tract.

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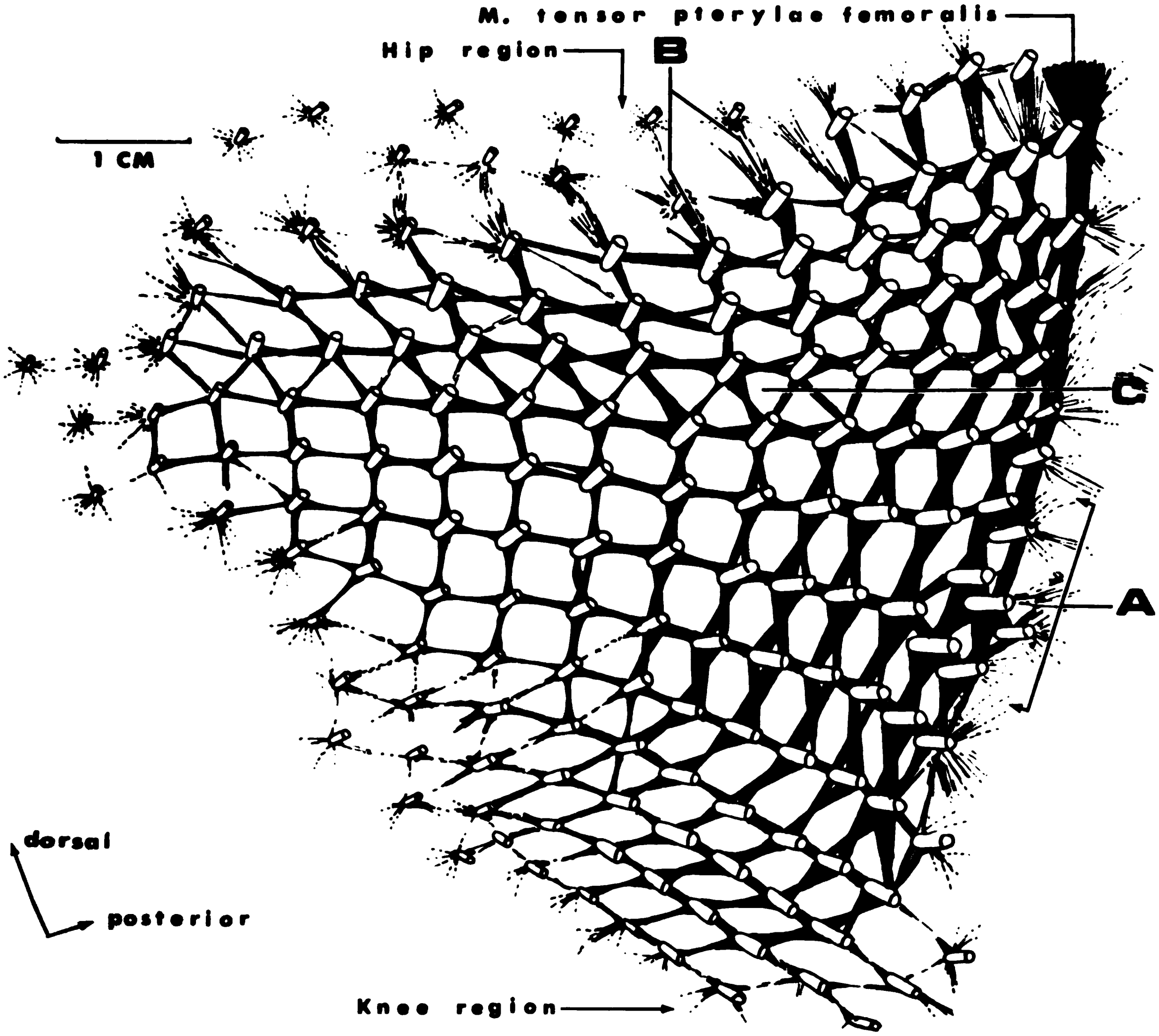
M. tensor pterylae femoralis
Hip region
B
1 CM
C
A
dorsal
posterior
Knee region

Figure 13

of apteria. Musculoelastic tissue is least developed at the caudal border of the tract. Triangles are most noticeable in the anterodorsal region of the tract where intercalary follicle rows are found (Figure 13B).

Analysis of the feather muscles at the gross level indicates that where rows of intercalary follicles occur, a change in the direction of dominant muscle rows also occurs. It appears that the diagonals become progressively stronger anteriorly in such a way that the posterodorsal muscle rows are shifted one-half of a row anteriorly. The diagonal muscle rows then predominate and account for the strongly curved feature of the posterodorsal muscle rows in this region. The former posterodorsal muscle rows become faint diagonals and the former diagonals reform a dominant pattern of new quadrilaterals. Thus, the pronounced presence of triangular subpatterns within a tract may indicate that the direction of muscle rows has changed.

The basic arrangement and attachment of feather muscles connecting four contiguous follicles in the middle of the femoral tract are illustrated in Figure 14. Feather muscles course from the outer end (neck) of one follicle to the inner end (bulb) of adjacent follicles. A smaller band-like elevator muscle passes on each side of the single larger band-like depressor. Depressors are cord-like in the posterior region. Interdigitation of elevator and depressor muscle fibers is infrequent. In the middle of the tract the

Figure 14.--Internal view of a quadrilateral showing the basic arrangement and attachment of the feather muscles to four follicles in the mid-region of the left femoral tract of Phasianus colchicus. The drawing was made from a Kodachrome slide taken at 20X under a dissecting microscope. Bouin fixation, unstained and partially cleared.

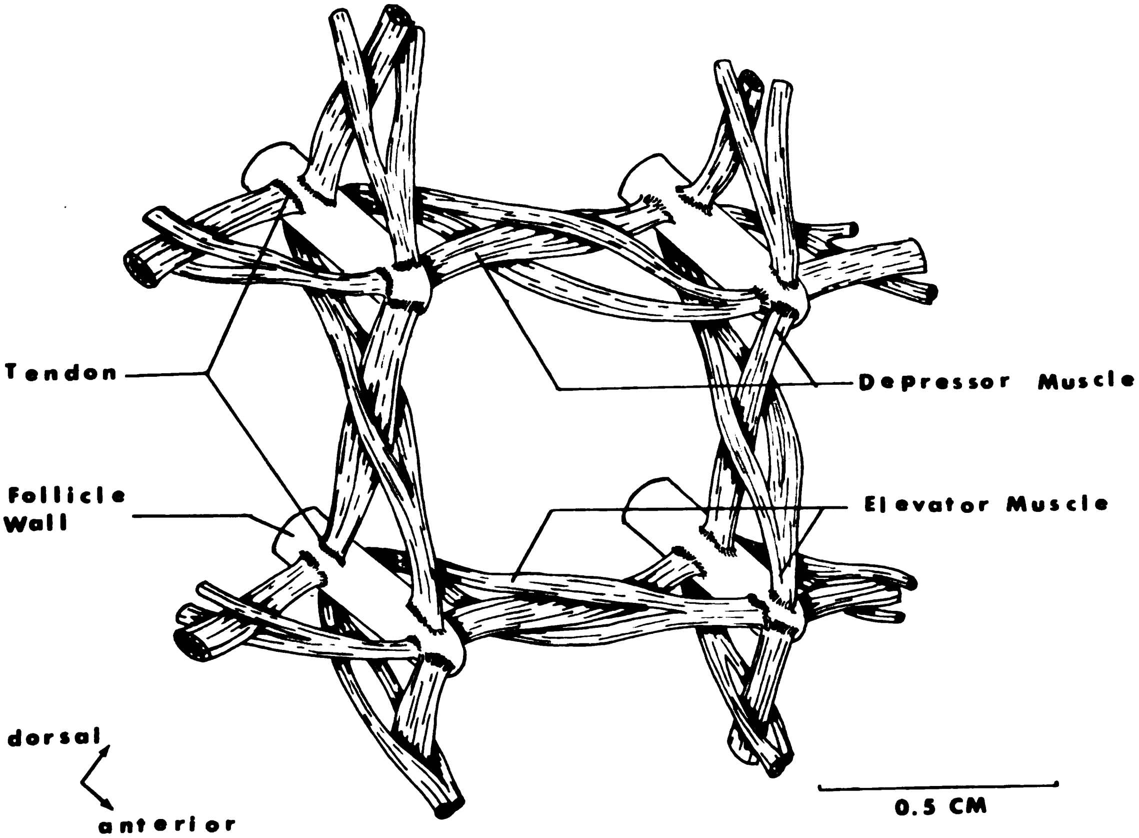
Tendon
Follicle Wall
Depressor Muscle
Elevator Muscle
dorsal
anterior
0.5 CM

Figure 14

non-striated muscles attach perpendicularly to the follicle wall. Attachment is by elastic tendons. Combined contraction of the depressor muscles would probably pull the outer end of the follicle, and the feather shaft extending from it, closer to the epidermal surface. The elevators, would probably move the feather shaft away from the epidermal surface. These actions have been proposed by Langley (1904).

Feather musculature is most dense and complex in the posterior portion of the tract where feather follicles are long and close together in the anterodorsally directed rows. The muscle pattern in this area is further complicated by the presence of several rows of intercalary follicles with 2 to 3 follicles in each row (Figure 13A). A change in the direction of muscle rows of the principal follicles is not evident at the gross level. At the subgross level a basic pattern of quadrilaterals is still evident (Figure 15). Muscle rows course anterodorsally and posterodorsally between four contiguous intercalary follicles and between four contiguous follicles characteristic of the tract. In the latter, elevators and depressors are well developed in both the anterodorsal and posterodorsal rows. In the quadrilateral connecting intercalary follicles both elevators and depressors are found only in the posterodorsal rows. Anterodorsal muscle rows have either depressors only or well developed muscles (retractors) which attach to the neck end of the follicles. Contraction of retractors apparently causes the follicles

Figure 15.--Internal view showing the arrangement and attachment of feather muscles to follicles at the caudal border of the left femoral tract of a male *Phasianus colchicus*. Refer to Figure 13A for the location from which the drawing was made. Intercalary follicles are shaded.

The drawing was made from a Kodachrome slide taken at 15X under a dissecting microscope. Bouin fixation, unstained and partially cleared.

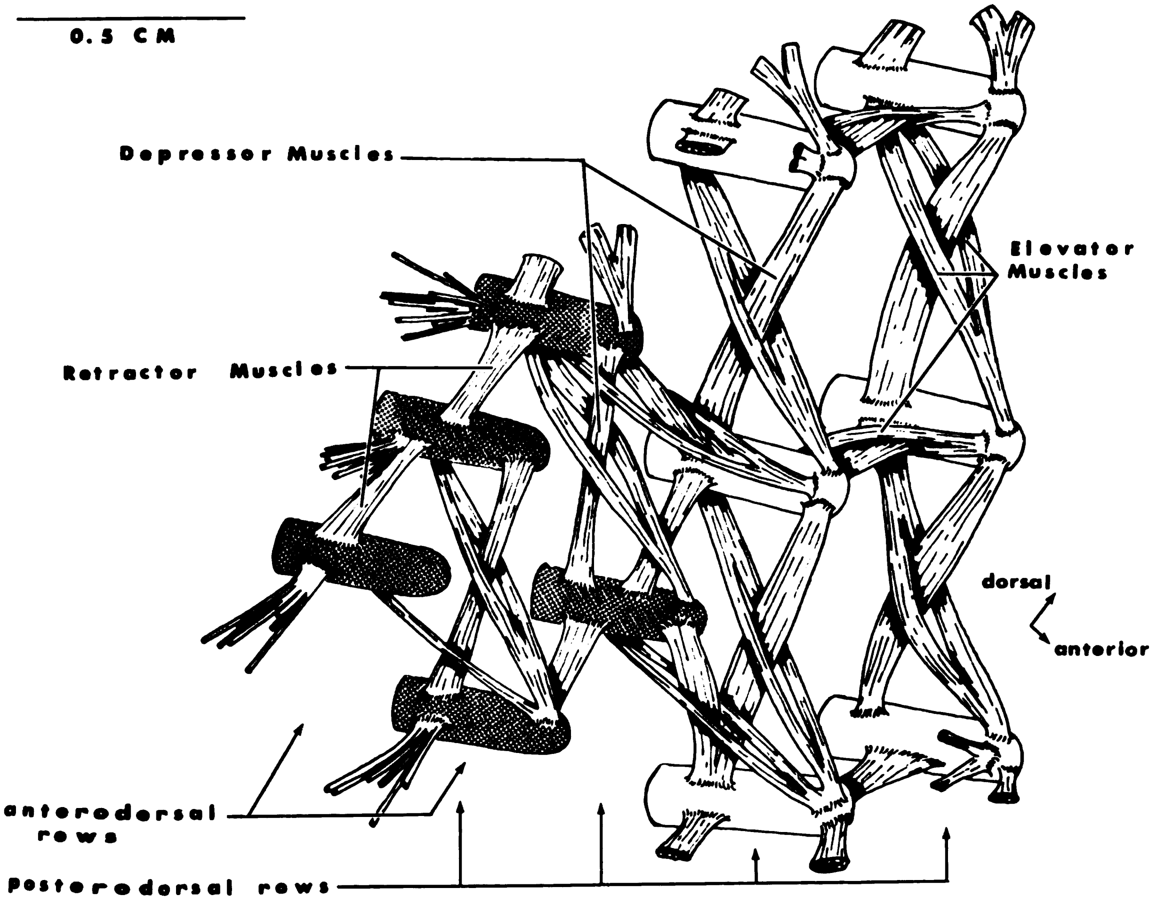
0.5 CM
Depressor Muscles
Elevator Muscles
Retractor Muscles
dorsal
anterior
anterodorsal rows
posterodorsal rows

Figure 15

to move closer together without elevating or depressing the feathers. Since these retractors are attached tangentially to the feather follicle, rotation of the feather probably also occurs.

Muscles connecting one intercalary follicle with two follicles typical of the tract form a triangular subpattern. Examination of one triangle at the subgross level reveals that an intercalary follicle is connected to a regular tract follicle which is anterior and dorsal to it by a retractor muscle only, and connected to a follicle which is anterior and ventral to it by both depressors and elevators. Considering that the presence of both elevators and depressors is characteristic of the tract, it appears that in the caudal region anterodorsal intercalary follicle rows are shifted one-half of a row dorsally.

Retractor muscles are well developed along most of the caudal border of the tract. They cover the outer one-third of each follicle and extend posterodorsally for 5 to 7 follicle rows. Fibers of the retractor muscles widen and then depart from the tract as a thin sheet and cross the pelvic apterium. Lucas and Stettenheim (unpublished), first described the muscle sheet (which they found moderately developed in the chicken and strongly developed in the turkey) as a tensor of the femoral tract (_M_. _tensor_ _pterylae_ _femoralis_). From its attachment to the follicles it appears that contraction of this muscle moves the feathers dorsally along the lateral surface of the thigh but without elevating or depressing them. Lucas first postulated that this muscle might act to reduce the droop of the feathers of the femoral tract. However, after he transected the muscle no drooping of the feathers was observed. He suggested that further experiments were needed.

Comparison.--The general shape of the femoral tract and orientation of muscle rows are similar in Phasianus, Gallus, Chrysolophus and Pavo. Equally dominant muscle rows consisting of flat double elevators and band-like single depressors course antero- and posterodorsally in Phasianus, Gallus and Chrysolophus. Some diagonal muscles are present.

In Pavo posterodorsal muscle rows consisting of thin flat elevators and thin flat depressors are dominant. Generally, depressor and elevator muscle fibers interdigitate with each other. Anterodorsal muscle rows have tendons located mid-way between adjacent follicles. Tendons occupy one-fifth to one-third of the total distance between the follicles and generally are restricted to the depressor uscles. Interdigitation of depressors and elevators, and e presence of tendons mid-way between the follicles, are pical throughout the femoral tract of Pavo except for to 6 follicles of each row at the caudal region. Here d-tendons are absent and muscle arrangement is similar that in Phasianus, Gallus and Chrysolophus.

M. tensor pterylae femoralis is least developed in Pavo, moderately developed in Phasianus and Gallus, and strongly developed in Chrysolophus. Musculoelastic tissue at the caudal end of the tract is virtually absent in Phasianus, Gallus and Chrysolophus, but prominent in Pavo. Musculoelastic tissue spans a greater distance between the femoral and pelvic tracts (lateral pelvic apterium) in Phasianus, Chrysolophus and Pavo than it does in Gallus.

In all forms the musculoelastic sheet spanning the crural apterium is delicate but is well developed anteroventrally.

Crural Tract

Description for Phasianus (Figures 16 and 17).--The crural tract covers the entire surface of the lower leg (Figure 6). With reference to a mid-dorsal longitudinal line, muscle and follicle rows course anterodorsally and posterodorsally. At the gross level, muscle rows are thickest and about equally developed on the anterior and posterior surface, moderately distinct on the lateral surface and faintly distinct on the medial surface. Quadrilaterals and muscle rows are indistinct, vertically, in the midregion of the lateral surface (Figure 16). This pattern was also found in two other preparations. Muscle rows are moderately developed at the ankle on the lateral surface, but not on the medial surface. Muscles end abruptly at the commencement of scales covering the proximal end of the tarsometatarsus.

At the subgross level thin bundles of ribbon-like double elevators and single depressors are present on the anterior surface. On the posterior surface muscle rows consist of double elevators and double depressors. In both regions the depressors are slightly more developed than the erectors. Interdigitation of muscle fibers accompanied by some tendinous anastomoses is characteristic of both regions.

On the medial surface follicles are spaced further apart (Figure 6). Musculature is least developed in this region of the tract. Muscle rows are often indistinct at the gross level. Sometimes only anterodorsal muscle rows are formed and a pattern of quadrilaterals is not evident (Figure 17). Extremely thin depressors and elevators anastomose with each other by tendons mid-way between the follicles. Other fine muscle fibers radiate from different levels of the follicle and terminate within the dermis without linking to adjacent follicles. Longitudinal and transverse diagonals are present within the tract but are indistinct and do not form a continuous pattern. Retractors are most commonly found at the bulb.

Comparison.--The pattern, degree of development and the arrangement of the feather muscles of the crural tract in Gallus and Chrysolophus are similar to that of Phasianus.

Figure 16.--External view of the left crural tract of Phasianus colchicus showing the arrangement of the feather muscles and orientation of the follicles. A line drawn between AA' represents the anterior surface, between PP' the posterior surface. Refer to Figure 13 for techniques in making the drawing. Bouin fixation, unstained and partially cleared.

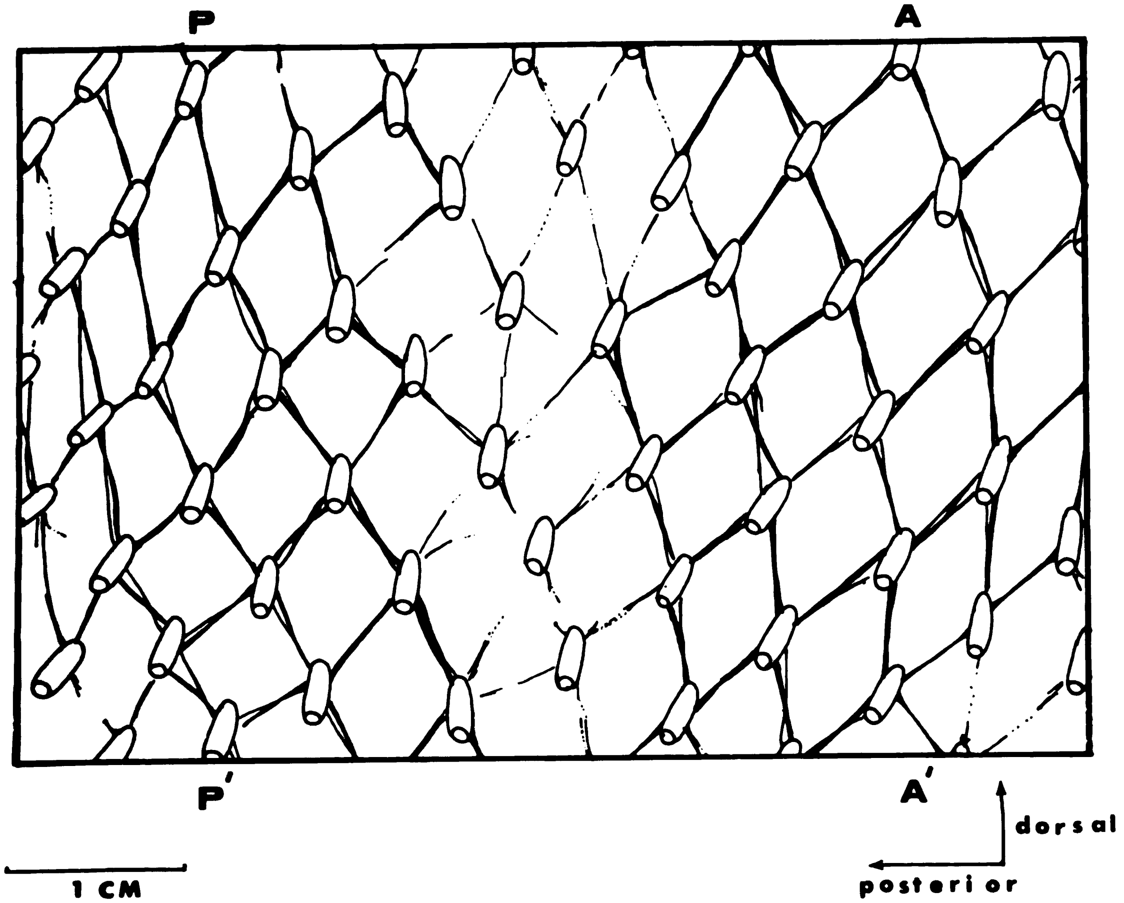

Figure 16

Figure 17.--Internal view showing the arrangement and attachment of feather muscles to four follicles in the mid-region of the medial surface of the left crural tract of *Phasianus* *colchicus*. Refer to Figure 13 for techniques in making the drawing. Bouin fixation, unstained and partially cleared.

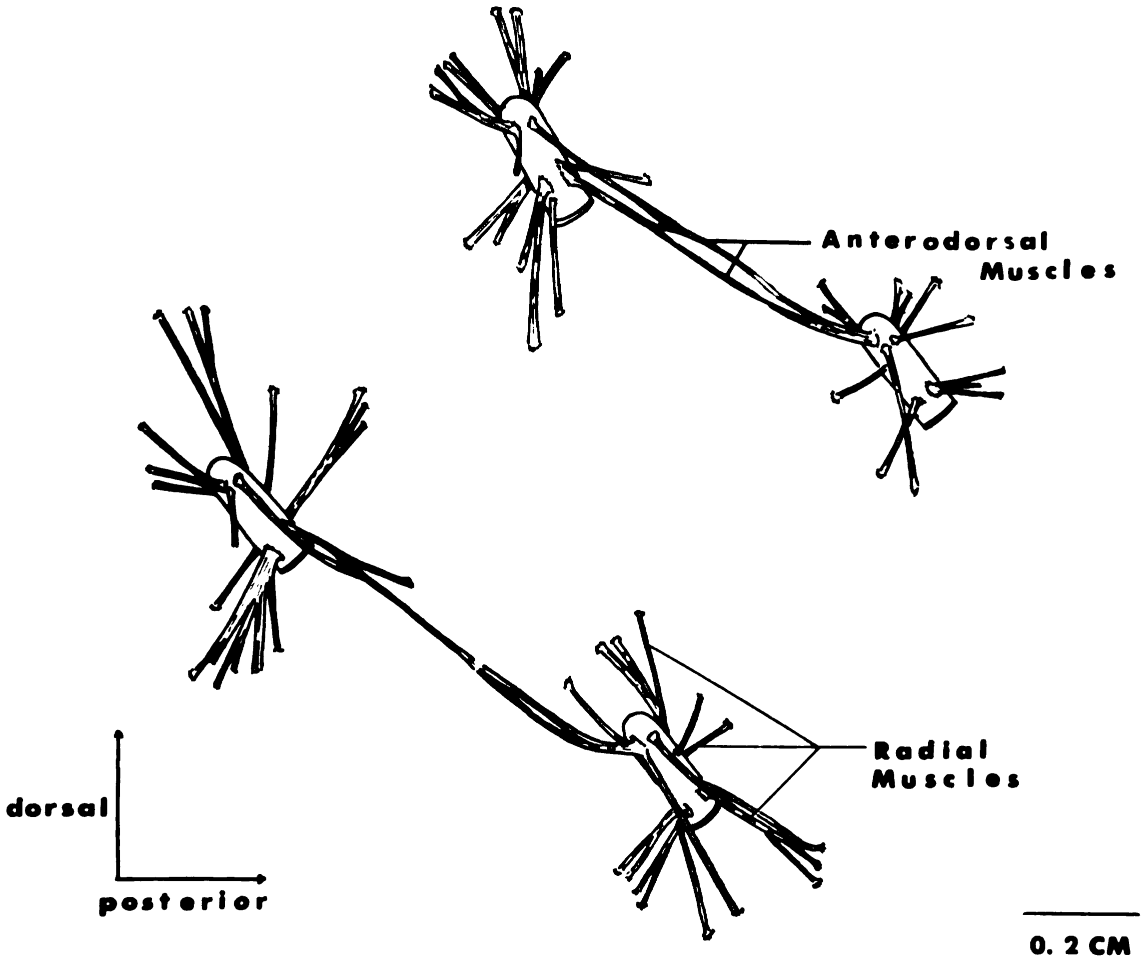
Anterodorsal Muscles
Radial Muscles
dorsal
posterior
0. 2 CM

Figure 17

Musculature is least developed in *Pavo*. Arrangement of the muscles into rows could not be distinguished at the gross level. At the subgross level a pattern of closed quadrilaterals is present on the lateral, anterior and posterior surfaces. Muscle rows course antero- and posterodorsally. These rows are characterized by numerous (4 to 6) thin, flat, loosely arranged bands of muscle. The most prominent features are the extensive amount of tendons and the anastomoses of muscle fibers mid-way between the follicles of all rows. Distinction between elevators and depressors is difficult. This pattern, reduced in development, is also present on the medial surface where there is a greater number of muscle fibers than on the lateral surface. Most of them are radial muscles of semiplumes.

Lateral Body Tract

Description for Phasianus (Figure 18).--The lateral body tract is wedge-shaped with the apex pointing posteroventrally toward the lateral border of the pectoral tract (Figure 6). Follicles are arranged anteroposteriorly into rows with 2 to 4 follicles in each row. Muscle rows course ventrally, posteroventrally and longitudinally with reference to a midventral longitudinal line (Figure 18). Closed quadrilaterals and triangles are present. Incomplete posteroventral muscle rows connecting 3 to 5 follicles are dominant. These rows are comprised chiefly of depressors and retractors

Figure 18.--External view of the skin covering the lateral surface of the body of Phasianus colchicus showing feather muscles of the left lateral body tract. Refer to Figure 13 for techniques in making the drawing. Bouin fixation, unstained and partially cleared.

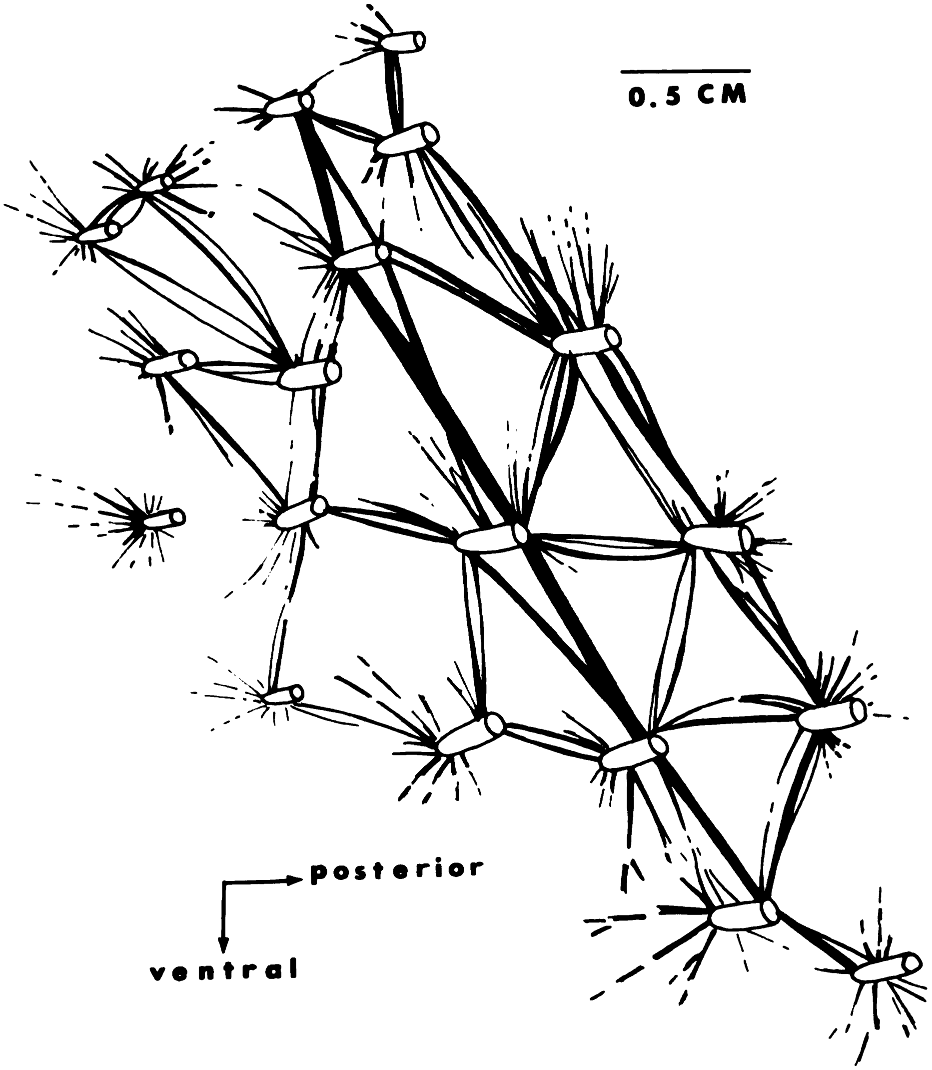

Figure 18

which attach tangently at the neck of the follicle. Musculo-elastic tissue is absent in the lateral body apterium except at the narrow apex of the lateral body tract where a few scattered fibers unite with the muscles of follicles at the lateral border of the pectoral tract.

Comparison.--The shape of the tract is similar in all forms. In general, the tract is characterized by weak musculature seldom arranged into rows. This is especially true for Pavo where radial muscles predominate.

Humeral Tract

Description for Phasianus (Figures 19 and 22).--This is a rectangular tract narrowing and curving medially at the anterior end. Follicles are arranged close together in posteromedial rows across the tract. The pattern of pterylosis suggests that two follicles in adjacent posteromedial rows form the anterior and posterior boundaries for square quadrilaterals (Figure 8). However, a different picture is obtained when the pattern of the feather muscles is examined (Figure 22). Musculature is complex, well developed, and strongest at the caudal end of the tract. Patterns of triangles rather than quadrilaterals are dominant. The pattern is further revealed at the subgross level (Figure 19). Muscle rows course anteromedially, longitudinally and posteromedially with reference to a longitudinal line drawn along the medial border of the tract.

Quadrilaterals are elongated diamonds with the long axis generally oriented longitudinally. Posteromedial muscles, consisting of stronger retractors, are actually diagonals which divide the quadrilateral into two triangles. Smaller retractors are attached tangentially at the neck. In the anteromedial and longitudinal muscle rows single depressors are strong; double erectors are weak. Thin longitudinal retractors may be present at the bulb. They are most common along the medial border and anterior region of the tract.

The previous description is for the pattern found in one specimen. In another preparation the pattern was similar except that retractors were reduced in the posteromedial rows, and erectors and depressors were well developed in the anteromedial and longitudinal rows. In still another preparation only the anteromedial and the posteromedial rows were well developed and diagonals transversing the diamond were absent.

Musculoelastic tissue is absent in the scapular apterium except at the caudal end of the tract where it courses transversely to the lateral follicles of the interscapular tract. It is absent in the humeral apterium except anteriorly where it courses to follicles of the marginal coverts and pectoral tract.

Comparison.--Musculature is strongly developed in all forms. In Gallus, Chrysolophus and Pavo two muscle rows are dominant, anteromedially and posteromedially. Double

Figure 19.--External view showing the arrangement and attachment of the feather muscles to four follicles in the mid-region of the left humeral tract of *Phasianus colchicus*. Refer to Figure 13 for techniques in making the drawing. Bouin fixation, unstained and partially cleared.

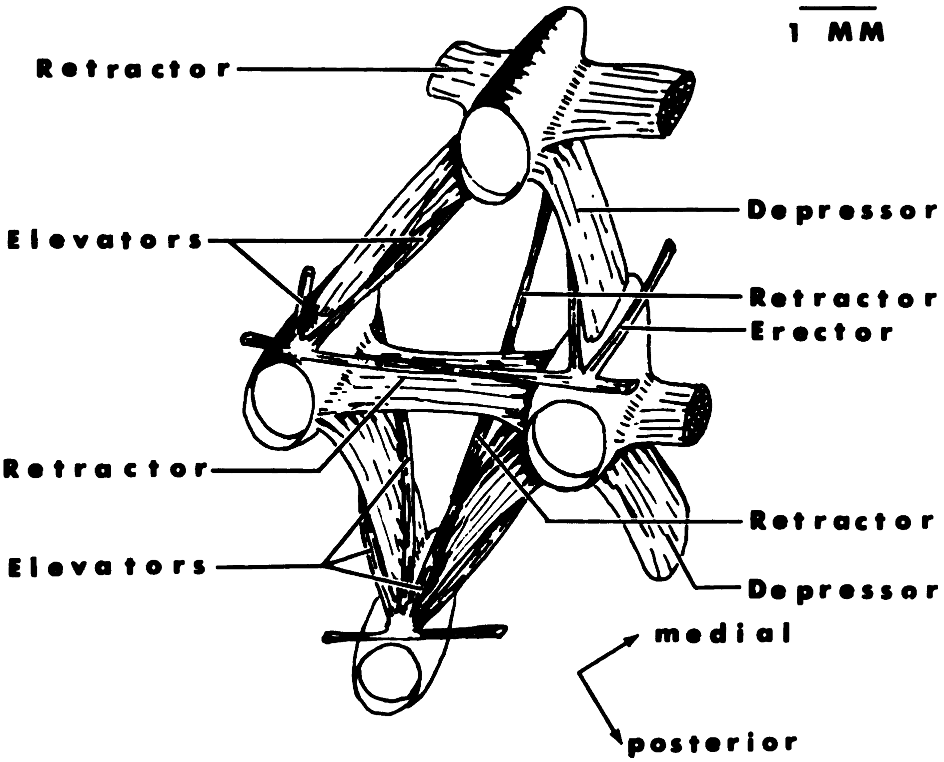
1 MM
Retractor
Elevators
Retractor
Elevators
Depressor
Retractor
Erector
Retractor
Depressor
medial
posterior

Figure 19

erectors and single depressors are about equally developed. Thin retractors can be found at the bulb end of the follicles. Lucas and Stettenheim (unpublished), found that the muscle pattern in Gallus and Meleagris conformed closely to the pattern of pterylosis. I also found this to be true for Gallus.

Ventral Capital, Ventral Cervical, Pectoral, Sternal and Abdominal Tracts; Musculoelastic Tissue

Description for Phasianus (Figures 21 and 22).--A mid-ventral longitudinal line is used as a base for describing the direction of muscle and follicle rows. In the interramal region (not figured) follicles of the ventral cervical tract are arranged close together in chevron-shaped rows. The anteroventrally directed follicle rows meet mid-ventrally and form the apex of the chevrons. Dominant muscle rows course anteroventrally and longitudinally. Thin diagonals course posteroventrally transversing the quadrilaterals. Muscles are arranged into bundles forming very thin bands. In the longitudinal rows depressors are doubly attached at the bulb and singly attached at the neck. All double attachments are tangential to the follicle wall.

In the middle of the ventral cervical tract, just posterior to the external ear opening, follicles are distributed far apart in the anteroventral rows. The chevron pattern is lost, musculature is weak and muscles are infrequently arranged into bundles. Separate fibers become more numerous. Longitudinal muscle rows are slightly more dominant than the other rows and the double attachment of depressors at the bulb is still evident. Interdigitation and mid-tendinous anastomosis of muscle fibers are frequent. Laterally, anteroventral rows are continuous with the posterodorsal rows of the dorsal cervical tract (Figure 22).

Musculature becomes more developed in the middle and posterior regions of the neck where the tract separates from the capital and dorsal cervical tracts to form two tracts (ventral cervical) covering the lateral surface of the neck. Here, chevron-shaped rows of muscles and follicles are again conspicuous (Figure 21). Equally dominant anteroventral and posteroventral muscle rows comprise the arms of the chevron. However, muscle dominance terminates abruptly at the apex of each chevron. The number of follicles is about the same in each arm. Bundles of muscles and patterns of quadrilaterals are well formed. Band-shaped double erectors and cord-shaped double depressors are about equally developed in the two rows. Double erectors attach tangentially to the follicle at the neck, the double depressors tangentially to the bulb. Musculature is weakest in the antero- and posteroventral rows which connect adjacent chevrons. In these rows single depressors and double erectors are thin bands. The depressors are slightly stronger than erectors and attach perpendicularly to the follicle wall. A few longitudinal diagonals may be present laterally. Some retractors are present at the bulb in the antero- and posteroventral rows. Generally, muscle arrangement is weaker, but similar to that of the interscapular tract (Figure 29).

Paired pectoral tracts cover the lateral surface of the breast. It was previously shown that follicles are arranged in chevron-shaped rows (Figures 6 and 7), that chevron arms are unequal in the number of follicles in an arm, and that feathers become progressively longer in the lateral arm, shorter in the medial arm (Tables 2 and 6). A chevron-shaped pattern of muscle rows is distinct (Figure 21). This appears to be due to the gradual increase in muscle development medially in the posteroventral rows and laterally in the anteroventral rows (Figure 21). To test this, the extent of muscle development was examined in two complete chevron rows of the right pectoral tract (Table 6).

The results show that total muscle volume is greater for those follicles of the lateral arm than in the medial arm of the chevron. Apparently this is related to the longer and heavier feathers in the lateral arm (Figure 20; Table 6). Muscle volume decreases posteriorly in the medial arm and increases posteriorly in the lateral arm. The total number of muscle bundles and the number of depressors and erectors are rather constant in a chevron row except at the borders of the chevron where radial type muscles predominate. Using muscle volume as an index of size, depressors are about twice as large as the erectors (e.g., row A mean d/e ratio

TABLE 6

Variation of muscle volume (mm^3), feather length (mm) and weight (gms) of feathers in the pectoral tract of <u>Phasianus</u> <u>colchicus</u>. "A" represents a complete chevron row 3 follicle rows caudal to the undermarginal coverts of the prepatagium, "B" represents a complete chevron row 3 rows caudal to "A." I = lateral follicles, M = medial follicles, O = apical follicle. The asterisk indicates those outermost follicles having a large number of radial muscles, the volume of which was not determined. See Figure 21 for the location of the chevron rows.

		Feather		Erectors (e)		Depressors (d)		Totals of Muscle No. and Volume		
Follicle		Length	Weight (X 10^{-2})	No.	Volume	No.	Volume	No.	Volume (d+e)	Volume (d/e)
A	L-6*	18	1.84	-	-	-	-	-	-	-
	L-5	116	5.20	8	2.8902	5	3.8302	13	6.7204	1.3252
	L-4	111	4.84	8	3.2921	6	3.4370	14	6.4358	1.0440
	L-3	94	4.35	7	3.1728	6	3.3480	13	6.5208	1.0457
	L-2	88	3.86	8	2.2816	6	4.1969	14	6.4785	1.8394
	L-1	81	3.51	8	1.7685	6	4.6826	14	6.4511	2.6477
	O	78	3.52	8	2.0084	7	3.8696	15	5.8780	1.9267
	M-1	74	3.08	8	1.5170	6	3.1491	14	4.6661	2.0758
	M-2	72	3.01	8	1.5745	5	3.4176	13	4.9921	2.1705
	M-3	68	2.84	8	1.4029	5	3.0539	13	4.4560	2.1768
	M-4	65	2.50	8	1.4537	6	3.1391	14	4.5928	2.1593
	M-5	61	2.19	7	0.9570	6	2.8250	13	3.7820	2.9519
	M-6*	56	1.75	5	0.4050	5	0.6060	10	1.0110	1.4962
	M-7*	42	0.92	2	0.1058	2	0.2082	4	0.3140	1.9678
Means--do not include outermost follicles									5.5431	1.9412

B	L-5*	112	3.94	1	1.1040	2	0.7731	3	1.8350	0.7002
	L-4	132	7.10	8	3.6023	6	5.3164	14	8.9187	1.4758
	L-3	121	6.69	10	3.2649	6	4.7870	16	8.0519	1.4662
	L-2	114	5.73	8	2.3256	5	3.8375	13	6.1631	1.6501
	L-1	95	4.52	8	2.1423	6	5.4898	14	7.6321	2.5625
	O	85	3.91	8	1.8685	6	4.2449	14	6.1134	2.2718
	M-1	80	3.40	8	1.4235	6	4.3146	14	5.7381	3.0309
	M-2	75	3.25	8	1.1330	6	4.1694	14	5.3024	3.6799
	M-3	75	3.05	8	1.3989	5	3.9081	13	5.3070	2.7936
	M-4	72	2.74	8	1.5936	5	3.8935	13	5.4871	2.4432
	M-5	63	2.04	8	1.1167	6	2.4883	14	3.6050	2.2282
	M-6	53	1.32	7	1.1104	6	2.0373	13	3.1477	1.8347
	M-7*	39	0.77	3	0.5974	4	0.2680	7	0.9654	0.4503
Means--do not include outermost follicles									5.9424	2.3122

Figure 20.--Relationship of muscle volume to (A) feather weight and (B) feather length of contour feathers in the right pectoral tract of Phasianus colchicus. "a" represents a complete chevron row 3 follicle rows caudal to the under-marginal coverts of the prepatagium; "p" a complete chevron row 3 rows caudal to "a." L = lateral follicles, M = medial follicles. Black symbols refer to length or weight of feathers and open symbols to volume of muscles.

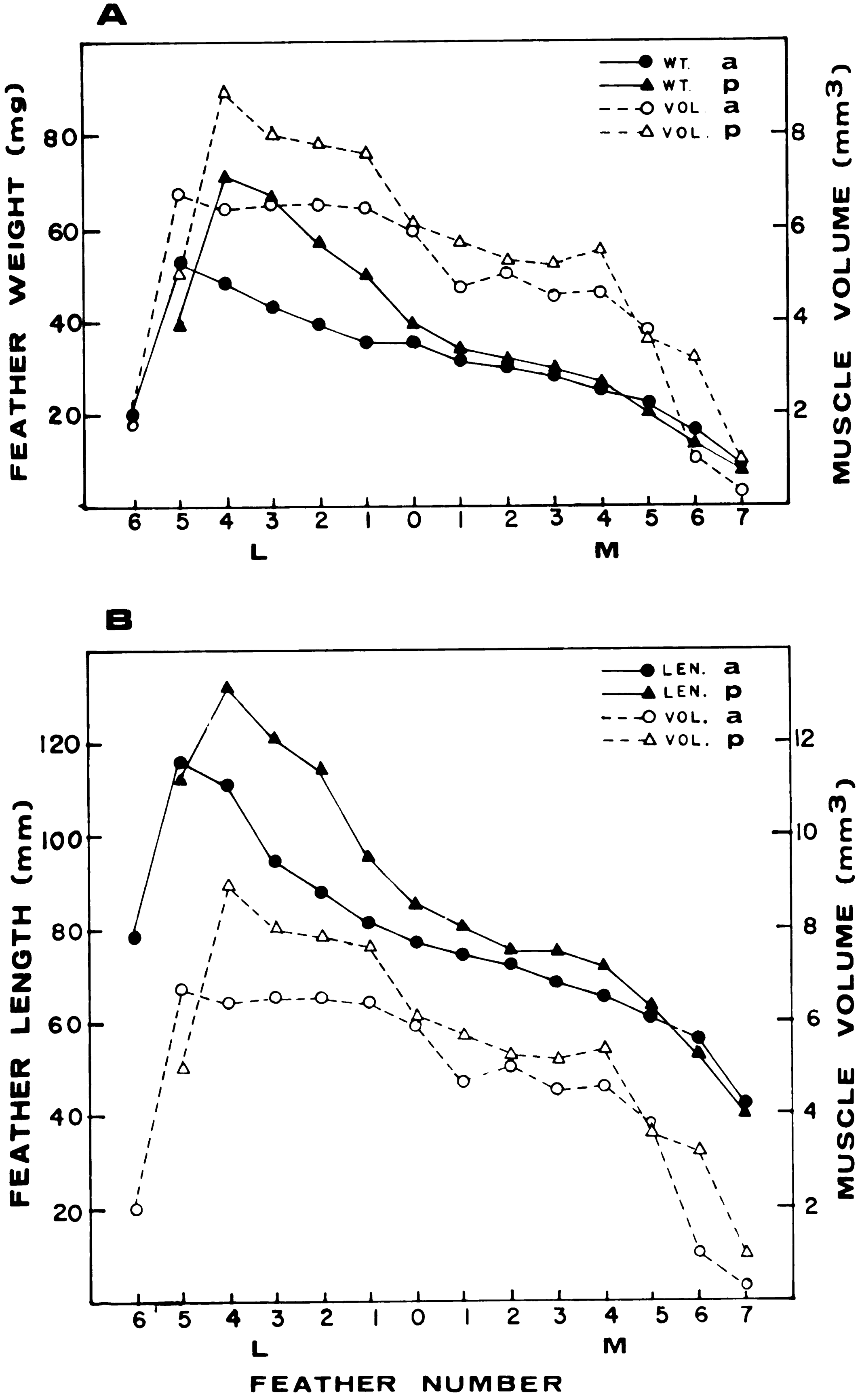
A
WT. a
WT. p
VOL. a
VOL. p
FEATHER WEIGHT (mg)
MUSCLE VOLUME (mm^3)
20
40
60
80
2
4
6
8
6
5
4
3
2
1
0
1
2
3
4
5
6
7
L
M
B
LEN. a
LEN. p
VOL. a
VOL. p
FEATHER LENGTH (mm)
MUSCLE VOLUME (mm^3)
20
40
60
80
100
120
2
4
6
8
10
12
6
5
4
3
2
1
0
1
2
3
4
5
6
7
L
M
FEATHER NUMBER

Figure 20

1.9; range $1.0mm^3$-$2.65mm^3$). In relation to total volume, and assuming that a d/e ratio of 1.9 is normal for the tract, depressors appear to be appreciably reduced (or the erectors enlarged--small d/e ratio) in the long feathers of the lateral arm (e.g., row A d/e ratio of 1.0 and 1.3). A small depressor-erector ratio may be an indication of a possible greater ability for raising feathers, or a lesser ability for lowering them.

A few longitudinal diagonals are present, but only along the lateral border. Longitudinal rows consist of two erectors which pass on each side of a single depressor. Both erectors and depressors are band-shaped. Double cord-shaped depressors and double band-shaped erectors are the most frequent type found in the antero- and posteroventral rows.

To summarize, musculature on the ventral skin of the head, neck and anterior body is least developed in the interramal region, and progressively more developed, caudally, in the pectoral tract. The extent of muscle development seems to be related to the length and weight of the feathers.

Narrow paired sternal and abdominal tracts cover the ventrolateral surface of the body (Figure 7). The tracts are continuous with each other. From the pattern of musculature no apparent distinction can be made as to the point where the sternal tract ends and the abdominal tract begins (Figure 21). Musculature becomes progressively more developed caudally. A strong longitudinal muscle row is

Figure 21.--Internal view of the skin from the ventral side of the body of male Phasianus colchicus showing the feather muscles. The ventral capital and the extreme anterior region of the ventral cervical tracts are not shown. All dermal muscles are removed. Musculoelastic tissue is not shown.

The short dashed lines represent boundaries of the cut skin. The long dashed lines represent the arbitrary boundary between 2 continuous tracts. A-A', B-B' represent 2 chevron rows whose feather lengths, weights and muscle volume were determined in Table 6. The drawing was made from a series of Kodachrome slides taken of whole mounts. Bouin fixation, unstained and partially cleared.

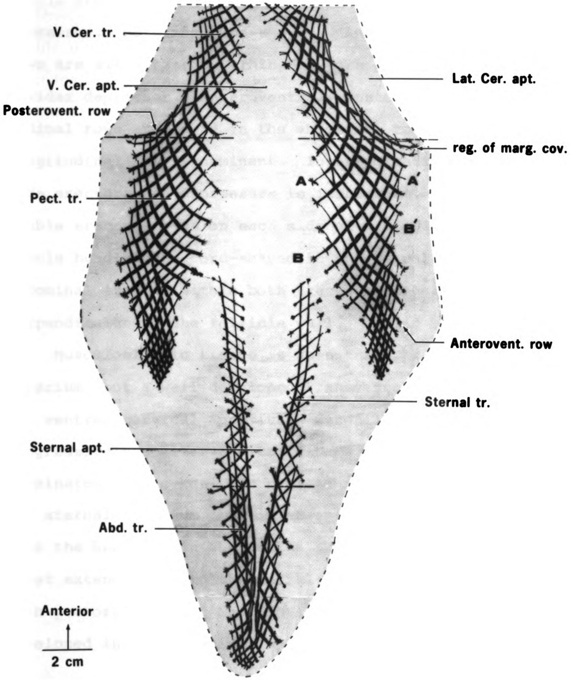
V. Cer. tr.
V. Cer. apt.
Posterovent. row
Lat. Cer. apt.
reg. of marg. cov.
A
A'
Pect. tr.
B'
B
Anterovent. row
Sternal tr.
Sternal apt.
Abd. tr.
Anterior
2 cm

Figure 21

present along the medial border of both tracts. In the sternal tract the medial longitudinal row consists of thin double erectors which pass around each side of a wide single depressor. Both are band-shaped. Anteriorly, posteroventral rows are also present. Thin erectors pass on each side of a wider depressor. Anteroventral, posteroventral and longitudinal rows are found in the abdominal tract. The medial longitudinal row is dominant. Interdigitation of equally wide erectors and depressors is infrequent. Generally, double erectors pass on each side of a single depressor. All muscle bundles are cord-shaped in the caudal region of the abdominal tract. Within both tracts attachments are usually perpendicular to the follicle wall.

Musculoelastic tissue is absent in the lateral cervical apterium, but a well developed transverse sheet is present in the ventral cervical apterium. Caudally, this sheet becomes progressively smaller and the fibers more scattered. It terminates at the keel, is present in the anterior region of the sternal apterium, but is absent in the skin directly over the keel and in the median abdominal apterium. The sheet extends beneath the medial-most 3 to 4 follicles of each pectoral tract. Musculoelastic tissue is also well developed in the abdominal apteria.

Comparison.--The gross pattern of muscle rows in Gallus, Chrysolophus, and Pavo is similar to that of Phasianus. Most differences were found in Pavo which is characterized by relatively weaker musculature in all ventral tracts. In the interramal region elongated diamond-shaped quadrilaterals are present in *Gallus* and *Chrysolophus* but not in *Pavo*, which has muscles of the radial type, a few of which link adjacent follicles. Most of the latter are longitudinal. Mid-ventrally, just posterior to the skull, musculature is small in *Gallus* and *Chrysolophus* and a pattern of quadrilaterals is not evident. Longitudinal rows are dominant, consisting of thin flat bundles of interdigitating erectors and depressors. The pattern is similar in *Pavo*.

In the mid-region of the neck, musculature is least developed in *Pavo*, strongest in *Chrysolophus*. Quadrilaterals are present in all representatives. In *Pavo* muscle bundles are thin flat bands, the depressors usually attach tangently, double at the bulb. In *Chrysolophus* erectors are thick bands, the depressors cord-shaped. Also, where the follicles are close together in the anteroventral rows thin retractors are present at the bulb. Quadrilaterals and muscle bundles are well formed in the pectoral tract of all representatives. Musculature is weakest in *Pavo*. Retractors, at the bulb, are present in the anterior 1/3 of the tract in *Gallus* and *Chrysolophus*, but only along the lateral region in *Pavo*. Musculature consisting of erectors, depressors and retractors is most developed at the caudal region of the pectoral tract in all representatives.

In the sternal tract the medial longitudinal muscle row is absent in *Chrysolophus*, weakly developed in *Pavo* and well developed in *Gallus*. It is present and as equally developed as the anteroventral and posteroventral rows in the abdominal tract of *Chrysolophus* and *Pavo*. In the caudal region of the abdominal tract erectors and depressors are cord-shaped in *Phasianus*, *Gallus* and *Chrysolophus*, band-shaped in *Pavo*.

In all representatives musculoelastic tissue is absent in the lateral cervical and median abdominal apteria, strongly developed in the ventral cervical and lateral sternal apteria, weakly developed in the pectoral apteria, abdominal apteria, and the anterior 1/3 of the sternal apteria. Generally, musculoelastic tissue appears to be less developed in *Pavo* and about equally developed in *Phasianus*, *Gallus* and *Chrysolophus*.

Both dermal muscles and musculoelastic tissue co-exist in some apteria, but not in others. However, in a few instances some reduction of musculoelastic tissue occurs at places where part of a dermal muscle is firmly attached to a portion of the skin beneath an apterium. This is true for the insertion ends of *M*. *pectoralis thoracica pars subcutaneus abdominalis* and *pars subcutaneus thoracicus*. The complete absence of musculoelastic tissue in the lateral cervical apteria may be explained by the presence of *M*. *cucullaris*. It may be that the presence of well developed dermal muscles (e.g., *M*. *constrictor colli*, *M*. *cucullaris*) in the anterior neck region indicates a greater ability than that of musculoelastic tissue alone for controlling the elasticity of the neck.

Dorsal Capital, Dorsal Cervical, Interscapular, Dorsal and Pelvic Tracts; Musculoelastic Tissue

Dorsal capital tracts

Description for Phasianus (Figure 22).--A mid-dorsal longitudinal line is used here as a base for describing the direction of muscle and follicle rows in all dorsally located pterylae. Musculature is fairly well developed mid-dorsally between the "ears." Muscle rows course anterodorsally, posterodorsally and longitudinally. The longitudinal rows are dominant. They consist of flat loosely arranged bundles of interdigitating erectors and depressors which appear about equally developed. A pattern of triangles is strongly evident. This pattern ends abruptly, laterally, where a short apterium (5 to 6 mm wide and devoid of follicles) separates this region from the follicles of the "ear." A thin longitudinal sheet (6mm long and 2mm wide) of loosely arranged parallel muscle fibers arises from the dorsal capital tract, tranverses beneath the apterium, and courses to the posteromedial border of the "ear." This muscle, part of the feather muscle complex, may act as a tensor muscle of the "ear" and the dorsal region of the capital tract. As far as I know the muscle has not been reported before. I have named it M. tensor pterylae capitalis dorsalis (Figure 23A).

Feather muscles are also associated with the follicles of the "ear." I previously described the "ear" as an elevation of the skin above the head. Dissections from the internal surface disclose that the "ears" are highly vascularized. Due to the curved nature of the skin, the high degree of vascularization and the extensive amount of mucoid-like tissue, dissections were tedious and the pattern of feather musculature was difficult to determine. Quadrilaterals or triangles were not evident. Small flat depressors and erectors connect adjacent follicles. One interesting feature is the presence of well developed retractors at the bulb and neck, some of which course longitudinally along the entire length of the "ear." Posteromedially some retractors are continuous with the _M_. _tensor pterylae capitalis dorsalis_.

It is quite conceivable that erection of the "ear" tufts during display results from the combined interaction of the feather muscles and the "flushing" of arteries and sinusoidal capillaries which extend into the "ear." _M_. _tensor pterylae capitalis_ dorsalis probably aids in compression of the "ear" which would result in the flattening of it. Bundles of erectors and depressors, although reduced in comparison with those in the mid-dorsal capital tract, appear to be sufficiently developed to account for the erection and depression of individual feathers implanted on the "ear."

Small bristles, interspersed between fleshy papillae, are implanted on the facial wattle of _Phasianus_. The facial area is flushed bright red during the breeding season. Dissection revealed that this region is highly vascularized. Extremely thin and delicate muscle fibers of the radial type are attached to bristle follicles but not to the fleshy papillae. Stiff auricular feathers have well developed erectors and depressors.

Comparison.--In general, musculature is least developed in Pavo, moderately developed in Phasianus and Gallus and well developed in Chrysolophus. Significant morphological differences exist between representatives and between sexes. Most differences appear to be related to specialized structures which may serve a signal function. Greatest similarities in muscle pattern, arrangement and attachment exist between females of Phasianus and Gallus and between males and females of Pavo. M. tensor pterylae capitalis dorsalis is present only in male Phasianus, the only representative to possess accessory integumentary "ears."

Gallus.--Small contour feathers are present, but papillae and bristles are absent from the wattle and ear lobe. Small contour feathers located on the face have delicate narrow strands of muscle connecting adjacent follicles. Mid-dorsally, muscle rows course chiefly longitudinally. Musculature becomes more prominent caudally, somewhat diminished until it terminates at the comb anteriorly, and gradually weaker laterally, where musculature transforms

Figure 22.--Internal view of the skin from the dorsal side of the body of male <u>Phasianus colchicus</u> showing the feather muscles. The extreme anterior region of the dorsal capital tract and the right humeral tract are not shown.

All dermal muscles are removed. Musculoelastic tissue is not shown. The short dashed lines represent boundaries of the cut skin, the dash-dot lines where sketching of the pattern was terminated. The long dashed lines represent the arbitrary boundary between 2 continuous tracts. The drawing was made from a series of Kodachrome slides taken of whole mounts. Bouin fixation, unstained and partially cleared.

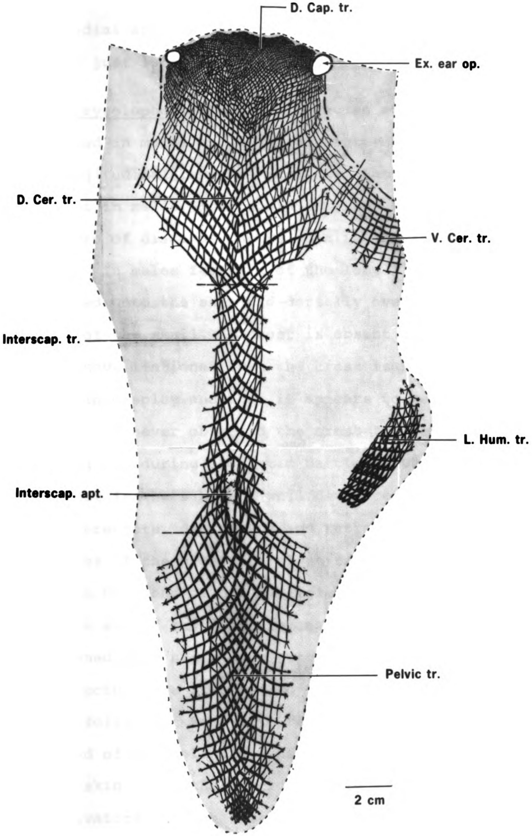
D. Cap. tr.
Ex. ear op.
D. Cer. tr.
V. Cer. tr.
Interscap. tr.
L. Hum. tr.
Interscap. apt.
Pelvic tr.
2 cm

Figure 22

to a radial arrangement and finally to typical apterial muscles just lateral to the eye.

Chrysolophus.--In the mid-region musculature is well developed in males and females. Anterodorsal, posterodorsal and longitudinal rows are present. Longitudinal rows are distinct in males, less so in females, with the result that a pattern of diamonds can be seen in the latter, not in the former. In males feathers of the long flowing crest are implanted onto the skin mid-dorsally over the parietal region of the skull. A crest is absent in females.

I have mentioned that the crest is not elevated in courtship display and that it appears to be permanently depressed. I never observed the crest to elevate during preening nor during agonistic battles with other males. Yet, the crest feathers have a well developed musculature consisting of erectors, depressors and retractors (Figure 23B). Follicles of the crest are close together transversely so that the bulb end of one follicle is practically touching the neck end of the follicle anterior to it. This distance is spanned by a stout double cord-like depressor. Thin band-like erectors are attached to the bulb and to the mid-region of the follicle. Band-like retractors are present near the neck end of the follicle. Assuming the epidermal surface of the skin to be the fulcrum, it appears that attachment of the elevators is such that feather erection would be less than normal. It is possible that the retractors help to

Figure 23A.--Diagrammatic representation of M. tensor pterylae capitalis dorsalis of a male *Phasianus colchicus*.

Figure 23B.--Dissection of feather muscles associated with 4 crest follicles of a male *Chrysolophus pictus* as viewed from the internal surface. Retractors are thick at the neck end of the follicle but absent at the bulb end. Muscle attachment is limited to the upper 2/3 of the follicle.

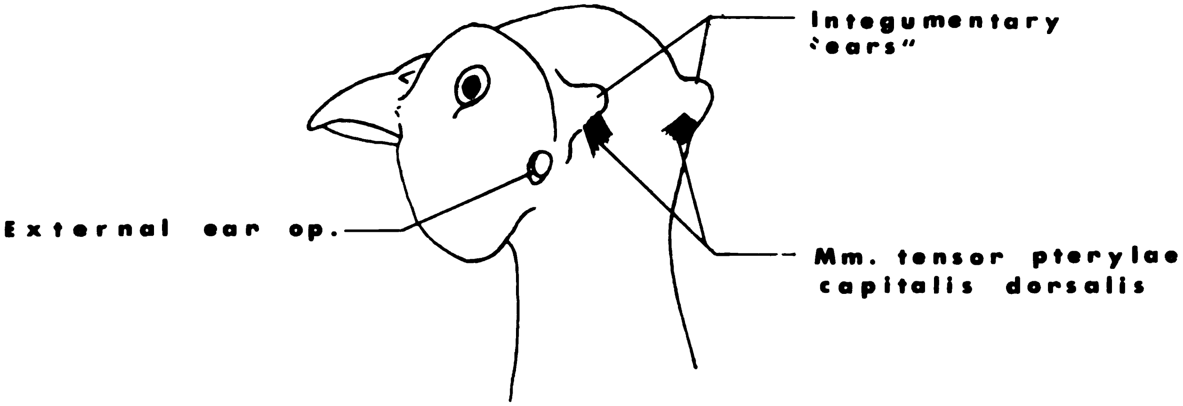

Figure 23A

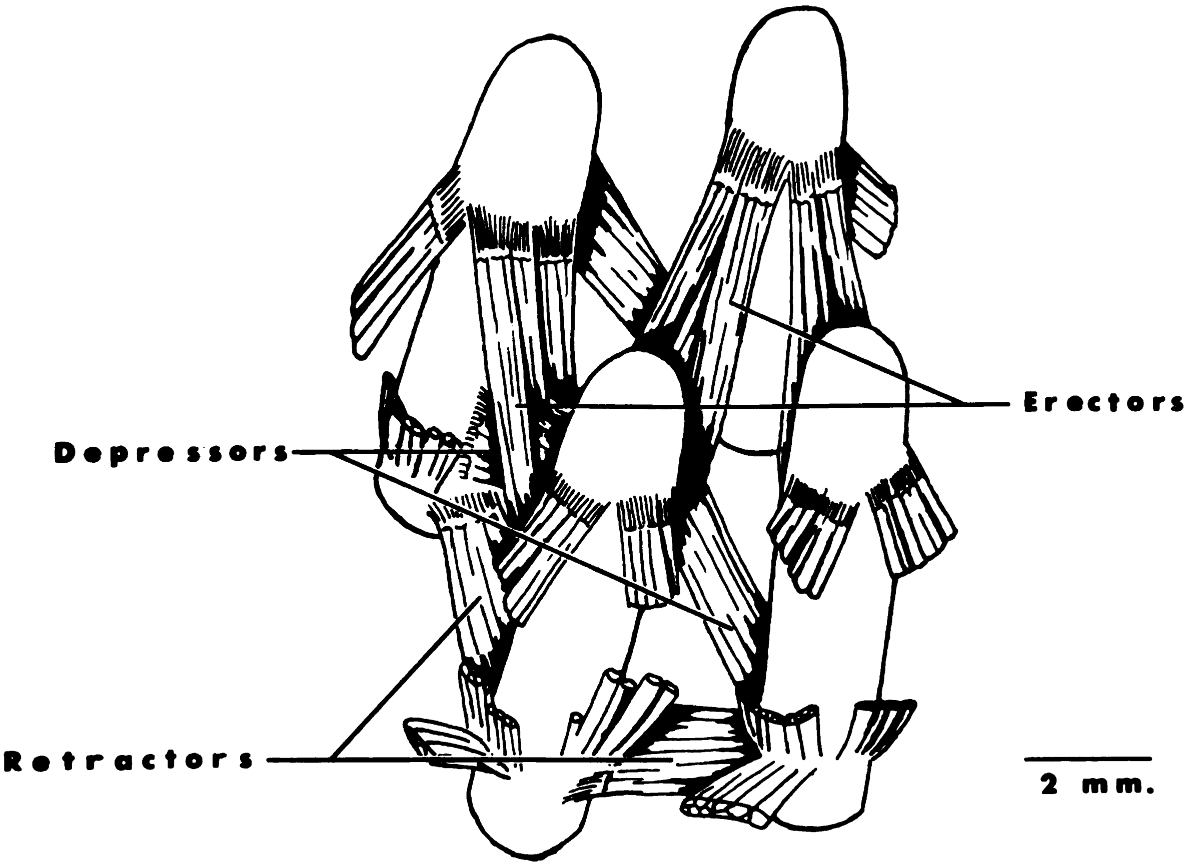

Figure 23B

maintain crest feathers in a relatively constant position. Judging from the attachment of muscles, it appears that movement, if any, of the crest feathers in Chrysolophus is stronger in the direction of depression than of elevation.

Pavo.--Except for the crown, musculature of the dorsal capital tract is less developed in Pavo than in the other forms studied. Musculature is so reduced that a pattern of quadrilaterals is not evident at the gross level. At the subgross level very delicate bundles course anterodorsally, posterodorsally and longitudinally. Dominance of a particular row is not apparent. One significant difference is that muscle attachment is limited to the neck end of the follicle. Although delicate erectors, depressors and retractors are present, their size and attachment suggest that these feathers are capable of very limited movement.

Males (Figure 5) and females possess a narrow fan-shaped crown consisting of 20 to 22 feathers which are implanted onto the skin mid-dorsally over the frontal region of the skull. Follicles of these feathers are crowded together in an 8 by 11 millimeter area. Small intercalary down feathers and semiplumes are interspersed between follicles of the crown feathers. As far as I know, the presence of downs and semiplumes among crown feathers has not been reported before in Galliformes. The condition may be unique for Pavo.

The length of crown feather follicles is about 3½ times longer than other follicles of the capital tract. Implantation of crown feathers is perpendicular to the surface of the skin with the result that feathers appear to be in a permanent state of erection. I did not observe feathers of the crown to move during display or preening.

Upon dissection I found the musculature extremely well developed (Figure 24). The outer follicles of the crown are connected to each other by strong retractors which attach tangentially to each follicle and occupy most of its length; some muscles completely cover the bulb end. Interior crown follicles are interconnected by retractors which cover 2/3 of the outer end of the follicle. Depressors and erectors are totally absent. Follicles appear to be arranged randomly rather than into rows. Similarly, muscle bundles do not course in any one well-defined direction. Since most of the muscle mass is confined to the outer end of the follicle these muscles apparently function to maintain the feathers of the crown in a relatively fixed position (i.e., elevated).

Dorsal cervical tract

Description for Phasianus (Figure 22).--The pattern of feather musculature shows that the junction of the dorsal cervical and the dorsal capital tract is not distinct. Follicles and muscle rows gradually become spaced further apart laterally over the neck. Posterodorsal muscle rows

Figure 24.--External view of the skin of the dorsal surface of the head of a male Pavo cristatus showing feather musculature of the crown feathers. Refer to Figure 13 for techniques in making the drawing. Bouin fixation, unstained and partially cleared.

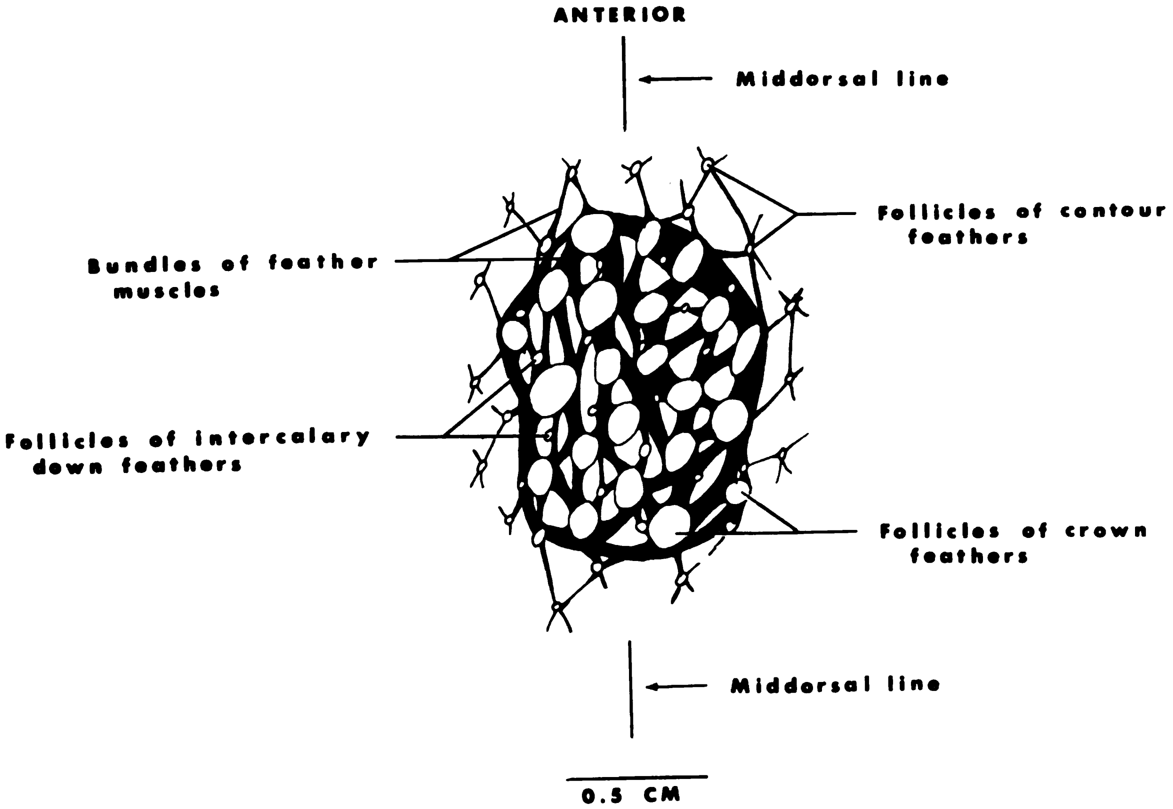
ANTERIOR
Middorsal line
Follicles of contour feathers
Bundles of feather muscles
Follicles of intercalary down feathers
Follicles of crown feathers
Middorsal line
0.5 CM

Figure 24

are slightly more dominant than are the anterodorsal rows. The latter often approach a longitudinal course in the anterior region of the neck. Faint longitudinal diagonals infrequently transect the conspicuous quadrilaterals. Anteriorly and laterally, posterodorsal rows are continuous with the anterodorsal rows of the ventral cervical tract. Erector and depressor muscle bundles are flat bands which frequently interdigitate with each other in the mid-region. Retractors are absent from the bulb and neck ends of the follicle.

Lucas and Stettenhaim (unpublished) determined in the chicken that the junction of the dorsal cervical and interscapular tracts can be characterized by a change in direction of the dominant muscle rows. They did not find this to occur in common coturnix, turkey, domestic duck and common pigeon. In these birds the two tracts were continuous with each other and the junction was arbitrarily placed. In _Phasianus_ I found the junction of the dorsal cervical and interscapular tract to be similar to that of _Gallus_. At the junction, muscle row dominance changes from the posterodorsal rows of the dorsal cervical tract to the anterodorsal rows of the interscapular tract (Figure 22).

Comparison.--Musculature is extremely well developed in _Chrysolophus_, strong in _Gallus_, moderately developed in _Phasianus_ and least developed in _Pavo_. Greatest differences in muscle pattern, arrangement and attachment occur among males and appear to be related to their feather displays. Greatest similarities exist between females of *Phasianus* and Gallus and between males and females of *Pavo*. The pattern and arrangement of feather musculature are similar in hen and cock *Chrysolophus* but are much more developed in the latter.

Gallus.--My findings for *Gallus* agree with those of Lucas and Stettenheim (unpublished) who described and figured at the gross and subgross level musculature of the hackles in the male Single Comb White Leghorn chicken. The gross pattern of feather musculature in *Gallus* and *Phasianus* is similar. However, I found some noteworthy differences when males were compared (Tables 7, 8 and 9). In general, musculature of the hackles of cock chickens is much more developed than in cock or hen ringnecks (Table 7). Musculature of *Gallus* is characrerized by dominant rows running posterodorsally and longitudinally, while in *Phasianus* dominant muscle rows course posterodorsally and anterodorsally. Longitudinal diagonal muscles are numerous and thick in *Gallus*, few and weakly developed in *Phasianus*. The presence of strong longitudinal diagonals in *Gallus* produces a dominant subpattern of triangles which is not typical of *Phasianus*.

Hackles of male *Gallus* are longer and heavier and have a greater weight per millimeter of feather length (feather ratio) than do homologous feathers of male *Phasianus*

TABLE 7

Differences in the feather musculature of the dorsal cervical tract in males of *Phasianus colchicus* and *Gallus gallus*. Mean values are given and the numbers in parentheses are ranges.

	Gallus[1]	*Phasianus*[2]
Dominant muscle rows	Posterodorsal, longitudinal	Posterodorsal, anterodorsal
Diagonals	Longitudinal, strong and numerous	Longitudinal, weak and few
Subpattern	Triangles	Quadrilaterals
No. of muscles/feather	18 (16-21)	15 (14-16)
No of erectors/feather	8 (6-10)	8 (6-8)
No. of depressors/feather	7 (6-8)	8 (6-12)
No. of retractors/feather	4 (4-6)	None

[1] Values from 52 follicles representing 8 individuals.

[2] Values from 36 follicles representing 6 individuals.

TABLE 8

Mean weight and length of 6 feathers from the mid-region of the dorsal cervical tract of adult male *Phasianus colchicus*, *Gallus gallus* and *Chrysolophus pictus*. Ranges are in parentheses.

	Phasianus	*Gallus*	*Chrysolophus*
Feather weight (mg)	1.7 (1.3-2.2)	33.0 (27-42)	30.9 (25.1-35.7)
Feather length (mm)	22.0 (15-29)	135.0 (112-152)	62.7 (42-84)
Feather ratio (mg/mm)	0.07 (0.06-0.09)	0.25 (0.21-0.29)	0.4928 (0.38-0.49)

TABLE 9

Weight of muscles of 6 feathers from the mid-region of the dorsal cervical tract of adult male *Phasianus colchicus*, *Gallus gallus* and *Chrysolophus pictus*. Values in milligrams are combined weights for musculature of 6 feathers.

	Phasianus	Gallus	Chrysolophus
Erectors	1.7	2.3	3.0
Depressors	1.8	1.9	2.7
Retractors	-	1.3	1.8
Depressor-Retractor	-	-	0.5
Total muscle mass	3.5	5.5	8.1
Depressor-erector ratio	1.1	0.8	0.9

(Table 8). Hackles also have more muscles (Table 7) and a greater total mass of muscle per feather (Table 9). This is apparently due to the presence of well developed diagonals and retractors. A smaller depressor-erector muscle ratio in _Gallus_ suggests that hackles may either have a greater ability for erection, or a lower ability for depression than do homologous feathers of _Phasianus_.

Retractors are present at the neck end of the follicles and are best developed in the posterodorsal and longitudinal rows. They comprise about 24 per cent of the total muscle volume (Table 9). Retractors in _Gallus_ may aid in keeping the hackles uniformly spaced during erection.

Chrysolophus.--Cape feathers of male _Chrysolophus_ _pictus_ and _C_. _amherstiae_ are large spatulate-shaped feathers arising from a goblet-shaped region of the dorsal cervical tract. Analyses of pieces of skin from this region reveal that musculature associated with follicles of these display feathers is much more developed than musculature of adjacent feathers (Figure 25). There is an abrupt transition from the well developed musculature of the cape to the less developed musculature of the dorsal cervical and capital tracts. Also, the gross pattern and arrangement of the muscles is much different from the other forms studied (compare Figure 25 with Figure 22).

It was previously shown in _Phasianus_ that muscle size (muscle volume and muscle mass) appeared to be related to the length and also to the weight of the feathers with which they are associated (Table 6, Figure 20). However, feather length or feather weight alone may not be the best index of the load that a set of muscles is required to move. This may be especially true when feathers of different shapes and from different birds are being compared. Some short stout feathers with a thick shaft may be heavier than a long slender feather with a thin shaft. Thus, the weight of a feather per unit of feather length may be a better estimate of load. This point is further demonstrated when hackles of Gallus and cape feathers of Chrysolophus are compared (Table 8). Feathers of both weigh nearly the same but have different lengths. Using feather weight as an index one would expect the weight of muscle associated with the hackles of Gallus and with the cape feathers of Chrysolophus to be similar. Using feather length, hackles should have a much greater weight of muscle than do the cape feathers. Neither appears to be true. Cape feathers apparently have a greater weight of muscle than do hackles (Table 9). This would be expected when the weight of the feather per unit length (feather ratio) is considered (Table 8).

Another method of estimating load (suggested by P. Stettenheim, pers. comm.) considers the distance along the shaft to the feather's center of gravity. This distance multiplied by the weight of the feather should give a value that includes length, weight and shape of the feather.

This method was not used in this study, but might prove of value in subsequent investigations.

Except for the protractors, which will be discussed shortly, musculature of the cape feather follicles is confined to a goblet-shaped area. Within this area anterodorsal, posterodorsal, longitudinal, and transverse muscle rows are present. They vary in degree of development in different regions of the goblet.

Both anterodorsal and posterodorsal muscles are dominant in the mid-region. Posterodorsal muscles approach a transverse course medially and become much thicker caudally. In the mid-region erectors, depressors and retractors are well developed (Table 9). Although not shown in the table, muscle development is greatest in the posterodorsal rows where erectors are cord-like and retractors are thick bands at the neck of the follicle. Erectors, depressors and retractors are thin bands in the anterodorsal rows. A low (0.9) depressor-erector ratio suggests that cape feathers may have a high ability for being erected (Table 9). But, this apparently is not a good criterion for ascertaining muscle action in <u>Chrysolophus</u>, for the cape feathers are not elevated away from the epidermal surface during display (Figure 2). It is possible that retractor muscles may be important. They make up about 30 per cent of the total muscle weight of the feathers in the mid-region. Another significant feature is the absence of longitudinal muscles in this region. This indicates that there may be limited movement of the feathers in the anteroposterior direction.

Musculature is very thick and complex in the caudal region, where posterodorsal and transverse muscles are the dominant rows. Transverse muscles consist only of retractors which are found at the neck. Posterodorsal rows are by far the thicker of the two. They are characterized by well-developed cord-like erectors and retractors. Depressors are somewhat thinner. Retractors may occupy as much as 2/3 of the outer end of the follicle. At the neck end some retractor bundles of the posterodorsal rows are continuous with retractor muscles in the transverse rows. Erectors in the posterodorsal rows are attached laterally to the follicle at the bulb end, medially to the follicle at the neck end. Attachment of depressors is just the reverse.

Musculature is also very well developed laterally where it courses principally in two directions, longitudinally and posterodorsally (Figure 25).

In addition to the typical feather muscles, a most significant feature concerning the cape feathers, is a smooth feather muscle in the form of a well-developed plexiform sheet of anastomosing bundles. It extends from the follicles of the cape across to the external ear opening and then anteriorly and ventrally to converge as a tendon at the angle of the jaw (principally to the posterior part of the quadratojugal bone). As far as I know the muscle has not been described before. I have named it *M. protractor pennati cervicalis dorsalis* (= cape protractor).

The muscle is firmly attached to a tendon at the angle of the jaw, at the medial border of the external ear opening and at the lateral follicles of the cape. It is not firmly attached to the undersurface of the skin nor is it attached to the small superficial follicles of the capital tract (Figure 26). The muscle plexus has its greatest development caudal to the external ear opening. Its course is posterodorsally toward the cape where it attaches to the outer ends of the lateral-most follicles (Figure 27). Microscopic examination of teased muscle showed it to be composed of smooth muscle.

On the basis of morphological arrangement and attachment, the action of the feather muscles on the cape feathers during display can now be postulated.

I have shown that musculature is most developed in the posterodorsal rows. My first hypothesis is that only the erectors in the posterodorsal rows of the cape region contract during display. If they do, feather shafts would move anteriorly and ventrally but not away from the epidermal surface. This theory assumes, as we have previously, that the surface of the skin acts as a fulcrum. However, this action could occur without the presence of the strong muscle plexus at the lateral border of the cape.

A second hypothesis is that *M. protractor pennati cervicalis dorsalis* tightens the skin of the cape and that this

Figure 25.--Internal view of the skin from the dorsal surface of the neck of male _Chrysolophus_ _pictus_ showing feather musculature of the cape feathers, dorsal cervical tract and parts of the capital and interscapular tracts. Musculature associated with the cape feathers is most highly developed. Cape protractors (= _Mm_. _protractor_ _pennati_ _cervicalis_ _dorsalis_).

The shaded area represents the skin which is cut along the lateral cervical apteria. All dermal muscles have been removed. Musculoelastic tissue is not shown. Refer to Figure 13 for techniques in making the drawing. Bouin fixation, unstained and partially cleared.

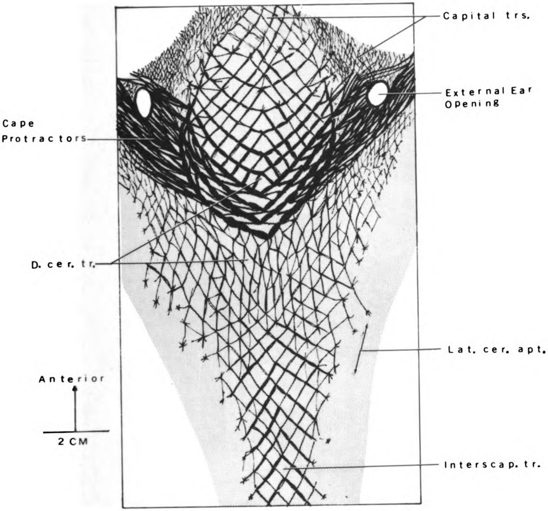
Capital trs.
External Ear Opening
Cape Protractors
D. cer. tr.
Lat. cer. apt.
Anterior
2 CM
Interscap. tr.

Figure 25

Figure 26.--Internal view of the skin between the right external ear opening and follicles of the cape feathers showing the arrangement of the cape protractor muscles (= *Mm. protractor pennati cervicalis dorsalis*). A section of the cape protractors has been removed to reveal the course of the delicate superficial feather musculature of the lateral capital tract.

The dash line represents the cut boundary of the skin. Anterior follicles of the capital tract are not shown. From a male *Chrysolophus pictus*. Refer to Figure 13 for techniques in making the drawing. Bouin fixation, unstained and partially cleared.

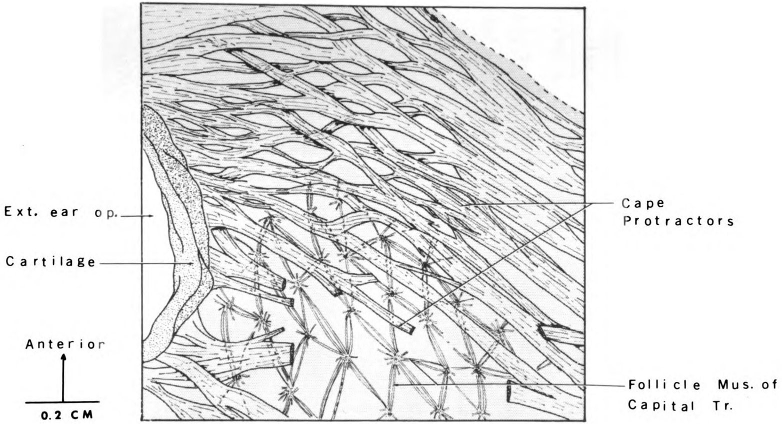
Ext. ear op.
Cartilage
Anterior
0.2 CM
Cape Protractors
Follicle Mus. of Capital Tr.

Figure 26

Figure 27.--Dissection of feather muscles associated with one of the outermost follicles of the left lateral cape of *Chrysolophus pictus*. Viewed laterally from the internal surface. Attachment of retractors and protractors is at the neck end of the follicle. Protractors (= *Mm. protractor pennati cervicalis dorsalis*).

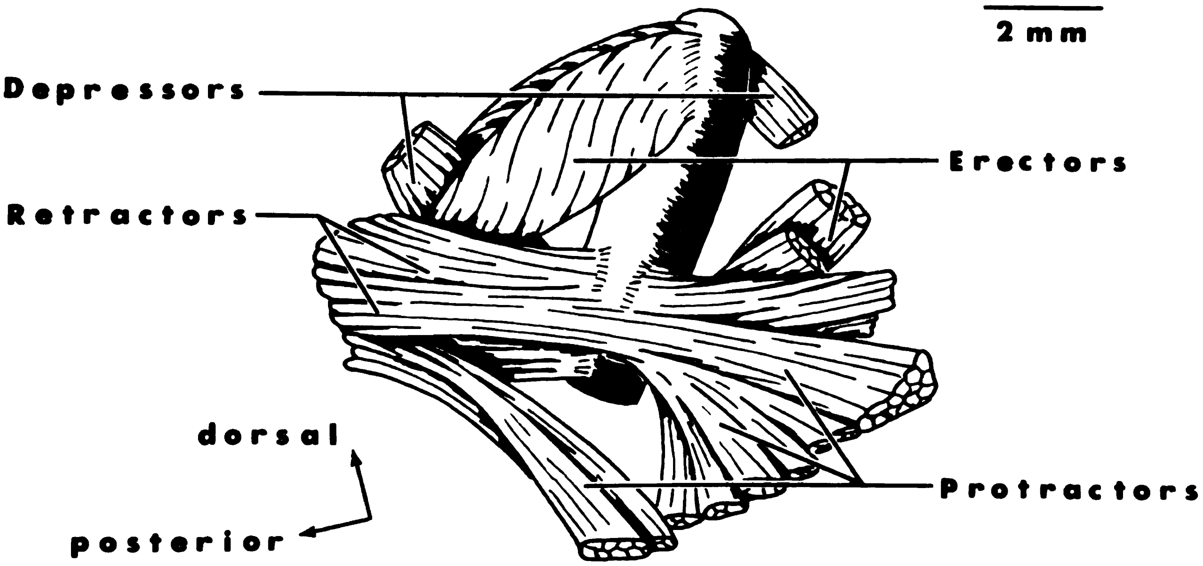
2 mm
Depressors
Erectors
Retractors
dorsal
posterior
Protractors

Figure 27

tightening is a prerequisite to contraction of the erectors.

My third hypothesis is that M. protractor pennati cervicalis dorsalis alone functions to move the feathers to a display position. In this theory it is assumed that the bulb end of the follicle acts as the fulcrum.

The action of the M. protractor pennati cervicalis dorsalis was deduced from the following experiment. Unilateral transections of the skin were made in 4 anesthetized male Golden Pheasants. A longitudinal incision was made between the ear and the cape severing M. protractor pennati cervicalis dorsalis. Care was taken not to cut the underlying cranial attachment of M. cucullaris pars cranialis. The wound was sutured and after recovery overnight males were resubmitted to hens.

Males did not perform courtship displays until two days after the operation. During display feather movement was drastically reduced on the operated side, while feathers of the control side were fully extended. Positioning of the feathers on the operated side reached 1/4 the maximum height after 6 to 7 days and full extension was attained after 11 to 12 days.

These results strongly suggest that neither M. cucullaris pars cranialis nor the erector muscles of the cape are responsible for extension of the feathers during display. Rather, it appears that the display position of the cape feathers results from the contraction of M. protractor pennati cervicalis dorsalis. The proposed action of the cape protractors is illustrated in Figure 28.

The above evidence negates the first hypothesis. The second does not seem feasible. It seems that the third hypothesis which presupposes a third class lever system best explains movement of the cape feathers in the courtship display of Chrysolophus. This is further supported by the presence of strong retractors at the neck in the posterodorsal and transverse rows. It appears that contraction of these muscles would return cape feathers back to a nondisplay position.

Pavo.--Musculature of the dorsal cervical tract is least developed in Pavo cristatus. The pattern and extent of development are similar in males and females. Flat bundles of muscle which link adjacent feathers in the dominant anterodorsal and posterodorsal rows produce diamond-shaped quadrilaterals. A few delicate longitudinal muscles may be present but in general they are absent from the tract. Unlike the chicken and the Ring-necked Pheasant, there is no distinct junction between the dorsal cervical and interscapular tracts. In this regard, the pattern is similar to that described by Lucas and Stettenheim (unpublished) for the turkey.

Interscapular tract

Description for Phasianus (Figures 22, 29 and 30).--The junction of the dorsal cervical and interscapular tracts has

Figure 28.--Schematic representation of the course of the protractor muscles (= *Mm. protractor pennati cervicalis dorsalis*) and the movement of one cape feather from a non-display position (solid outline) to a display position (dashed outline). Male *Chrysolophus amherstiae*.

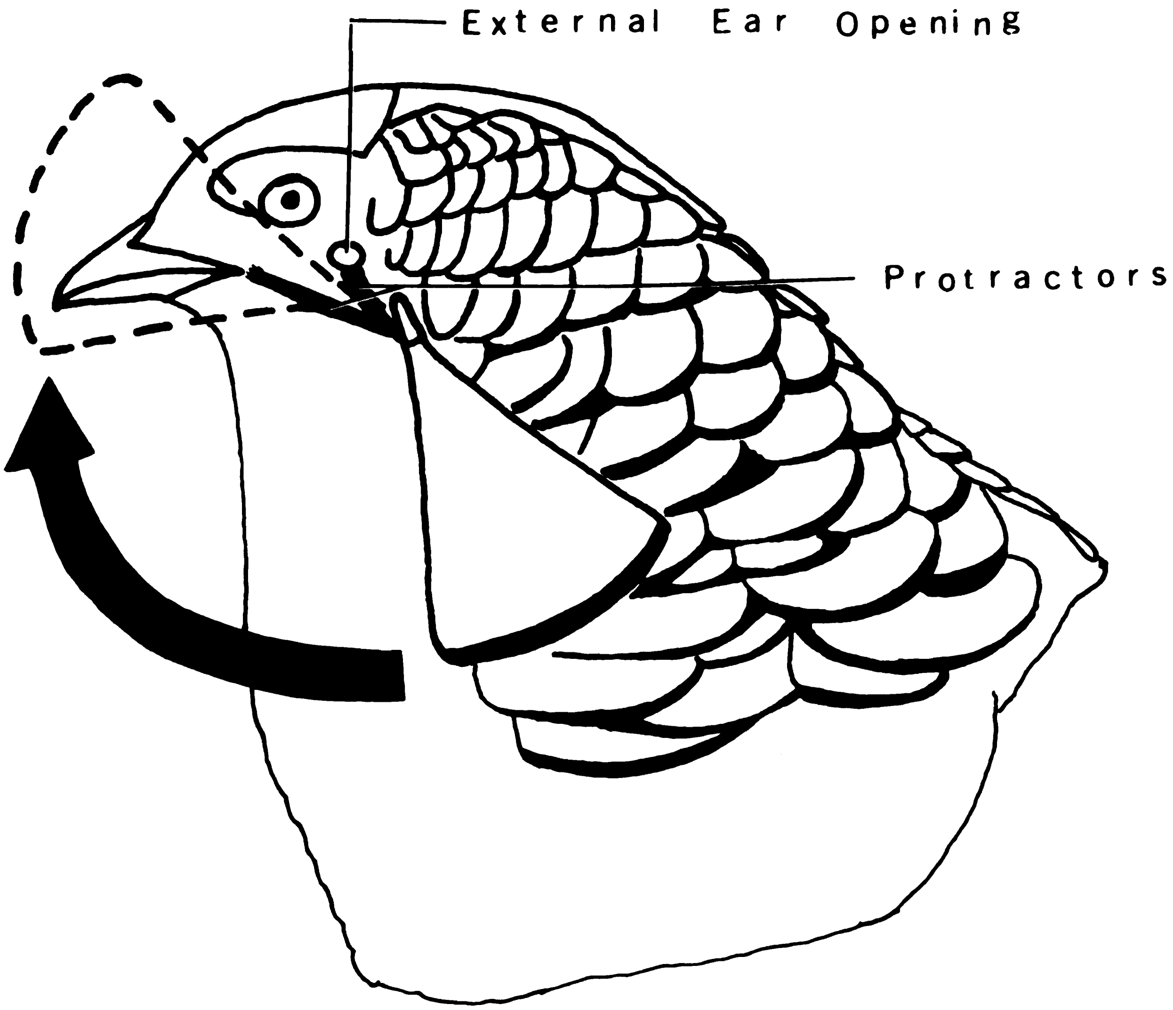

Figure 28

been discussed previously. The interscapular tract differs from the dorsal cervical tract in having different muscle rows which are dominant and being much narrower in width (Figure 22).

The interscapular tract is uniform in width throughout its length. In the anterior region muscle rows course principally posterodorsally and anterodorsally, the latter being more dominant. The anterodorsal rows correspond in direction to the chevron-shaped arrangement of the follicles. The latter is best illustrated in Figure 29. Dominance of the anterodorsal rows diminishes at the mid-dorsal line. Laterally these muscle rows are less developed and are directed posterodorsally (Figure 22). Longitudinal muscles are present but are not arranged into distinct rows except lateral to the interscapular apterium.

A dissection of the muscles associated with several follicles of the mid-region of the interscapular tract of Phasianus shows that muscle bundles are well developed (Figure 30). In the anterodorsal rows, where follicles are close together, a stout depressor-retractor muscle is present. This passes through 2 band-like erectors which generally attach tangentially to the neck end of the follicle. Delicate single or double retractors at the bulb end may act to spread the feathers. Erectors and depressors are flat bands in the posterodorsal and longitudinal rows.

The interscapular tract of Phasianus is characrerized by the presence of a median dorsal apterium about 3

Figure 29.--External view of part of the interscapular tract of male <u>Phasianus</u> <u>colchicus</u> showing the gross pattern of the feather muscles. Musculature of the anterodorsal rows is not illustrated in order to show the pattern of follicle arrangement. Follicles of a chevron arm are numbered consecutively, laterally, from the apical feather (0). Dermal muscles have been removed. Musculoelastic tissue and muscles of the radial type found at the lateral borders of the tract are not shown. Refer to Figure 13 for techniques in making the drawing.

Figure 30.--Dissection of feather muscles associated with 7 medial follicles of 2 left chevron arms of the interscapular tract. Internal view. From a male *Phasianus colchicus*. Refer to Figure 29 for the method in numbering the follicles.

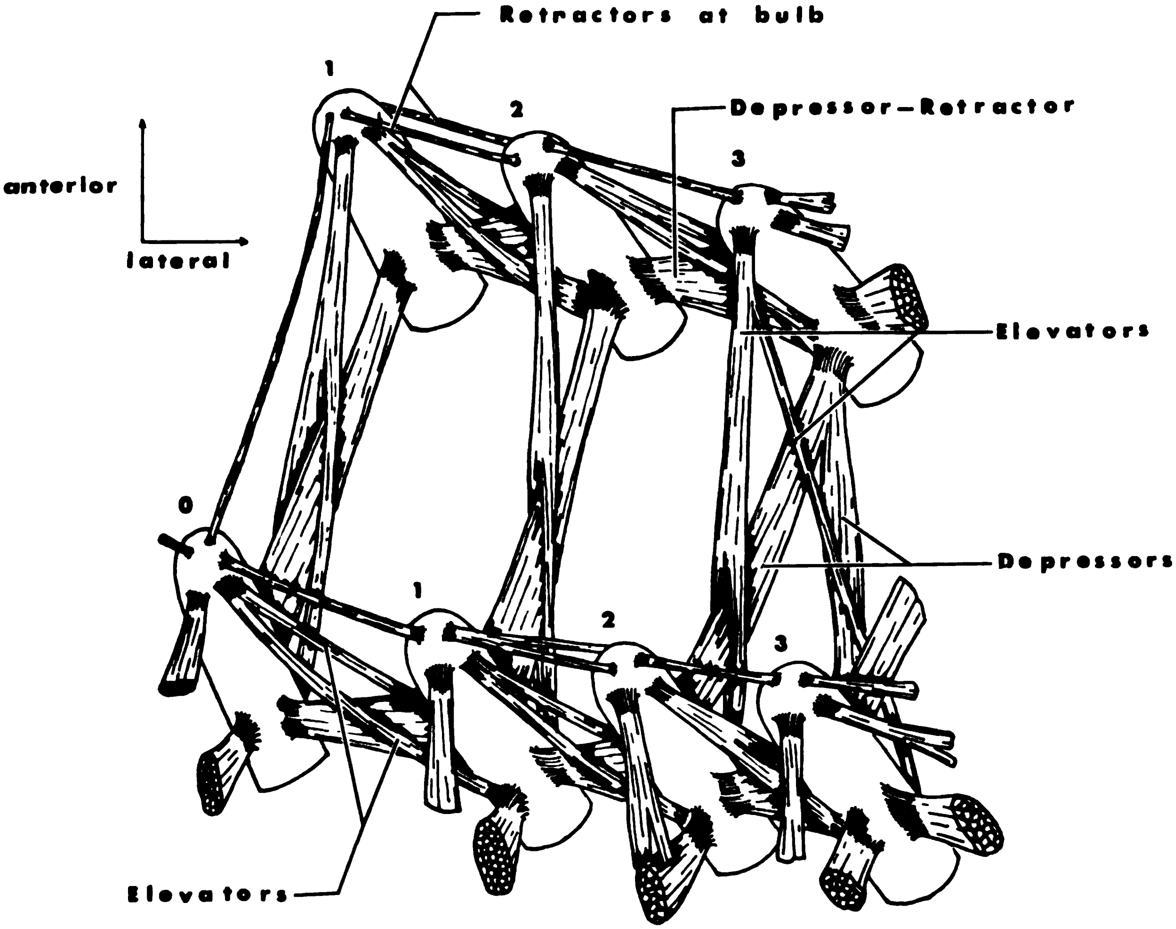
Retractors at bulb
1
2
Depressor–Retractor
3
anterior
lateral
Elevators
0
Depressors
1
2
3
Elevators

Figure 30

centimeters long in adults. I found a similar apterium in a day old chick. In the description of pterylosis the posterior end of this apterium was used to delimit the junction of the interscapular and dorsal tracts (Figure 8). In most of the specimens of Phasianus I examined the apterium was restricted to the interscapular tract. However, in one preparation the apterium extended into the dorsal tract (Figure 22). One or several centrally located follicles may be present anteriorly in the apterium. Musculoelastic tissue is absent within the apterium but delicate depressors, erectors or retractors cross the apterium in such a way as to connect the lateral arms of the gapped chevron-shaped follicle rows. The anterior boundary of the interscapular apterium is just posterior to the insertion of the clavicular component of M. cucullaris pars cervicalis and M. latissimus dorsi pars dorsocutaneus (Figure 9). Musculature is well developed lateral to the interscapular apterium. Rows course chiefly anterodorsally and longitudinally.

Comparison.--The gross pattern and arrangement of feather muscles of the interscapular tract are most similar in Phasianus and Chrysolophus. Musculature appeared to be slightly less developed in Pavo, slightly stronger in Gallus. No significant differences were noted in muscle development between males and females of the same species.

Greatest differences in muscle arrangement seem related to differences in patterns of pterylosis. The interscapular apterium was absent in Pavo, present in Chrysolophus and variable in Gallus. In one preparation of Gallus in which the apterium was absent, longitudinal muscle rows were more dominant than the anterodorsal rows. Also, longitudinal rows connected adjacent apical follicles, a feature not found in the anterior region of the tract (Figure 29). However, musculature associated with the apical follicles was generally weak. Mid-dorsal musculature was further reduced in another preparation. Small longitudinal muscles connected apical follicles but anterodorsal rows were absent. In a third preparation of Gallus apical feathers were absent and thin delicate muscles crossed the apterium in a pattern similar to that described previously for Phasianus. In all instances the apterium or area of reduction of mid-dorsal musculature was located in a 3 centimeter long region at the posterior end of the interscapular tract and corresponded in length and location to the apterium found in Phasianus and Chrysolophus.

The junction of the dorsal cervical and the interscapular tracts in Chrysolophus is similar to that of Phasianus and Gallus. But the change in dominant rows from posterodorsal and longitudinal to anterodorsal appears to be more gradual in Chrysolophus (compare Figure 25 with Figure 22).

Dorsal and pelvic tracts

Description for Phasianus (Figure 22).--The dorsal tract can be differentiated from the interscapular tract by the fact that it is wider (Figure 22). However, it is continuous caudally with the pelvic tract and there is no distinct separation between the two. For this reason in the description on pterylosis an arbitrary line was drawn between the trochanters of the two femurs. Collectively, both tracts are subsequently referred to as the dorsopelvic tract.

Muscle rows are directed anterodorsally, posterodorsally and longitudinally. An anterodorsal muscle row is composed of muscles which connect follicles of a chevron arm. Posterodorsal and longitudinal rows connect adjacent chevrons. Anterodorsal rows are dominant throughout the dorsopelvic tract.

In the mid-region, intersection of dominant anterodorsal and posterodorsal muscle rows produces a pattern of diamond-shaped quadrilaterals. A different pattern is formed laterally. Parallelograms result from the intersection of anterodorsal and longitudinal muscle rows. The gradual change in dominance, laterally, from posterodorsal to longitudinal rows is a characteristic feature of the tract.

Just anterior to the oil gland all three rows are well developed and triangles are formed.

In the dorsal tract both erectors and depressors are band-shaped in the posterodorsal and longitudinal rows. Erectors are band-shaped and the depressors are cord-shaped in the anterodorsal rows. Tangential attachment of all muscles is frequent. A depressor-retractor type of muscle is not present. Delicate retractors at the bulb end of the follicle are usually present only in the anterodorsal rows.

Musculature is heaviest just anterior to the oil gland where all muscles have a cord-shaped configuration.

Comparison.--The following comments refer to *Phasianus*, *Chrysolophus* and *Gallus*. Muscle pattern and development are strikingly different in *Pavo* and will be discussed last.

The elongated shield-like shape of the dorsopelvic tract is similar in *Phasianus* and *Chrysolophus*. In *Gallus* several additional rows of follicles extend anteriorly and laterally as "wings" into the scapular apterium. The tract is widest anteriorly (7-8 cm in *Gallus*, 5-6 cm in *Phasianus* and 4-5 cm in *Chrysolophus*).

Musculature appears about equally developed in *Phasianus*, *Chrysolophus* and *Gallus*, but the pattern of muscle rows shows some differences. Neither *Chrysolophus* nor *Gallus* show a gradual change of dominance, laterally, from posterodorsal to longitudinal directed rows as did *Phasianus*. *Chrysolophus* is characterized by having longitudinal muscle rows present throughout the entire tract. In *Phasianus* longitudinal muscles are not present medially. Posterodorsal muscle rows in *Chrysolophus* are restricted to the medial 3 follicles of a chevron arm; in *Phasianus* they are restricted to the medial 4-5 follicles (Figure 22). Thus in the dorsal tract of *Chrysolophus*, anterodorsal and longitudinal muscle rows are the most dominant and frequent rows.

The pattern of posterodorsal and longitudinal muscle rows is highly variable in the dorsal tract of Gallus. In one preparation intercalary follicles (4-5 per row) were frequently present between chevron arms along the lateral border. As a result, longitudinal and posterodorsal muscle rows which connect thses follicles to adjacent chevrons displayed a zig-zag pattern while anterodorsal rows tended to take a transverse course. In another preparation in which the interscapular apterium was absent, well-developed longitudinal muscles extended from the interscapular tract into the dorsal tract. Several other conditions were also found. In one specimen both posterodorsal and longitudinal rows persisted laterally, but only posterodorsal rows medially. In another, only longitudinal rows were present laterally and only posterodorsal rows medially, a pattern similar to that of Phasianus. I did not find any specimens of Gallus in which apical feathers were connected by longitudinal muscles and in which longitudinal muscle rows were prominent throughout the tract. However, such a condition was found in a specimen examined by Lucas and Stettenheim (unpublished).

The pattern of muscle rows is most uniform and similar in the pelvic tract of Phasianus, Chrysolophus and Gallus. In general, anterodorsal muscle rows become more acute posteriorly. Anterior to the oil gland, anterodorsal, posterodorsal and longitudinal muscle rows are strong and equally developed. Posterodorsal rows tend to take a longitudinal course. In fact, the tendency in the pelvic region in these 3 genera is for the musculature to exhibit a longitudinal course.

In summary, no significant intersexual differences were noted in the arrangement and development of the feather muscles in the dorsopelvic tract among Phasianus, Chrysolophus and Gallus. Most interspecific differences seemed to be related to slight differences in the pattern of pterylosis. Some insignificant differences were found among individuals of Single Comb White Leghorn chickens.

Pavo.--Although the dorsopelvic tract is fairly uniform in width throughout its length (10 to 12 centimeters in hens, 14 to 16 centimeters in cocks), the pelvic tract can be distinguished from the dorsal tract by the pattern of pterylosis (Figure 31). However, the separation between the two is not distinct. In the pelvic tract the chevron-shaped rows of follicles and follicles within a row are spaced closer together than in the dorsal tract. Follicles of the pelvic tract are also larger than those of the dorsal tract and are arranged in closely aligned rows. Enlargement of follicles of the pelvic tract is more noticeable in cocks than in hens and is related to the fact that the large display feathers of the train are implanted in this region in males.

One characteristic feature of the pelvic tract is the presence of numerous small (2 millimeters long) intercalary down follicles which are located between the contour follicles in the pelvic tract of cocks and hens. Intercalary downs have been previously described for the pelvic tract of Pavo (Sager, 1955). I previously reported finding intercalary downs among the crown feathers of Pavo. Apparently, intercalary downs are unusual among galliforms (Lucas and Stettenheim, pers. comm.; Sager, 1955: 116). The anterior limit of intercalary downs may be used to determine the separation of the dorsal and pelvic tracts (Figure 31).

Since the follicles of the pelvic tract are large (about 2 centimeters long), the skin is also thick in this region (1.5 to 2 centimeters in cocks, about 0.5 centimeters in hens). In cocks, the skin of the pelvic tract is 15 to 20 times thicker than feathered skin elsewhere.

Like the cape feathers of Chrysolophus, feathers of the pelvic tract increase in length, posteriorly, in a chevron arm (Tables 2 and 10).

Feather musculature is extremely well developed in both hens and cocks (Figures 32, 33, 34 and 35). The dorsal tract is characterized by dominant anterodorsal muscle rows and the muscle pattern corresponds fairly closely to the pattern of pterylosis.

In the pelvic tract of cocks, dominant muscle rows course transversely across the tract in a rippled pattern and the chevron pattern of follicle arrangement is totally obscured. Distinct anterodorsal and posterodorsal rows are not apparent at the gross level. The rippled pattern of the transverse muscle rows corresponds to the location of the bulb ends of follicles which are covered by muscle. This feature was not present in any of the other species previously examined. The transverse pattern of muscle ridges diminishes at the lateral border where muscles do not completely cover the bulb ends of the follicles. Transverse muscles are most developed in the mid-region of the tract.

If the change in dominance from anterodorsal muscle rows to transverse muscle rows is used as the boundary between the dorsal and pelvic tracts, then the boundary line would be placed anterior to the level set by intercalary downs (compare Figures 32 and 33 with Figure 31).

A unique feature in the pelvic tract of _Pavo_, is the pelvic ridge (Figures 32 and 33), a group of about 5 large contour feather follicles arranged into 3 rows which are located at the anterolateral border of the pelvic tract. The bulb ends of these follicles extend deeper into the dermis than do follicles anterior to them, thus forming the ridge. Strong transverse muscles located medially, combined with strong posterodorsal muscle rows, laterally, connect these follicles and help to account for the distinctness and shape of the ridge (Figures 32, 33, 34 and 35). If the anteriormost boundary of the pelvic ridge is used to separate the dorsal tract from the pelvic tract, the level would be similar to that set by the anterior limit of intercalary downs (compare Figures 32 and 33 with Figure 31).

I have shown that musculature is heavy in the pelvic tract of _Pavo_. The degree of muscle development may also be used to separate the dorsal tract from the pelvic tract. This is best illustrated in Figures 34 and 35 where transmitted and reflected light were used in taking the photographs. These figures show an abrupt change in the degree of muscle development between the two tracts. A line formed by this transition may also represent a level of separation. It corresponds more to the boundary of the pelvic ridge and is at a level similar to the anterior limit placed on the intercalary downs. I believe that the pelvic ridge and the degree of muscle development are the best criteria for delimiting the two tracts in _Pavo_.

I have previously shown that the weight of feathers per unit length (i.e., feather ratio) of the cape feathers in _Chrysolophus_ is about twice that of the hackles of _Gallus_ (Table 8; 0.49 mg/mm for _Chrysolophus_, 0.25 mg/mm for _Gallus_) and that a greater mass of muscle appears to be associated with cape feathers than with hackle feathers (Table 9; 8.1 mg/6 cape feathers in _Chrysolophus_ _vs_ 5.5 mg/6 hackle feathers in _Gallus_).

A comparison of weights and lengths of feathers from the pelvic tract of the peacock with hackles of _Gallus_ and cape feathers of _Chrysolophus_ show that the weight of feathers per unit length of feathers of the train in _Pavo_ is about 5 times that of hackles and about 3 times that of cape feathers (compare Tables 8, 10 and 11).

TABLE 10

Lengths and weights of 16 consecutive feathers from a right chevron arm of the pelvic tract of a male Indian Peacock (Pavo cristatus). Refer to Figure 29 for technique in numbering the feathers.

Feather	Length (mm)	Weight (mg)	Feather ratio (mg/mm)
0	117	108.0	0.9231
1	184	184.6	1.0030
2	276	297.8	1.0790
3	364	414.9	1.1398
4	446	535.3	1.2002
5	559	678.4	1.2135
6	642	825.6	1.2860
7	732	1036.2	1.4155
8	793	1209.2	1.5248
9	870	1471.5	1.6914
10	953	1680.2	1.7631
11	1054	1919.0	1.8207
12	1132	2116.4	1.8696
13	1185	2214.4	1.8687
14	1265	2225.4	1.7590
15	1339	2006.9	1.4988

TABLE 11

Relationship of muscle weight to feather length and weight of 2 feathers (A and B) from the pelvic tract of a male Indian Peacock (Pavo cristatus). Refer to Figure 32 for the location of the feathers.

Feather	Length (mm)	Weight (mg)	Feather ratio (mg/mm)	Muscle weight (mg)
A	182	184.7	1.0148	16.5
B	803	1213.5	1.5112	30.1

Feathers of the train should also have a correspondingly greater mass of muscle per feather in order to support or to move this greater load. That this appears to be true is shown by comparing the data in Tables 9 and 11. The mass of muscle for 2 train feathers is 16.5 mg and 30.1 mg, respectively, and 5.5 mg and 8.1 mg for 6 hackles and 6 cape feathers, respectively. Thus, it appears that the musculature of feathers of the peacock train is relatively larger than that of the other birds I examined.

I have attempted to demonstrate again that the total mass of muscle appears to vary directly with the load of the feather it is required to move or support. The reader is reminded that values for _Pavo_ are for only 2 feathers and that a statistical analysis of more values from more feathers in all representatives is required to substantiate these proposed relationships.

On a functional basis, the course and attachment of a muscle are just as important as the mass of a muscle. Dissections of the muscles of two feathers, one from the anterior mid-region of the pelvic tract (Figure 36) and the other from the mid-central region of the tract (Figure 37) show that feather B has a greater muscle mass than feather A. The significance of this is apparently related to the longer display feathers found posteriorly within the tract (Table 10). Further comparison shows that erector-retractor muscles in the anterodorsal and posterodorsal rows are strongly pinnate posteriorly in the tract (Figure 37). Anteriorly, pinnate muscles are thin and individual retractors and erectors may be present (Figure 36). Also, transverse retractors attach to more of the follicle wall posteriorly than they do anteriorly. Mid-centrally, the transverse muscles cover the bulb end of the follicle. Laterally within the tract transverse retractors are slightly thinner and the posterodorsal erector-retractor muscles are slightly larger. It appears that contraction of both of these muscles would draw the bulb end of the follicle posteriorly and medially toward the mid-region of the tract thus spreading and elevating the feathers.

Musculature associated with the follicles of the pelvic ridge is also of significance in analyzing muscle action. It was previously pointed out that heavy transverse and posterodorsal retractor muscles attach to the follicles of this region. The contraction of these muscles would probably pull the bulb end of these follicles posteromedially toward the mid-dorsal line. This action may spread the feathers.

In courtship display the train of cocks is elevated to about 90 degrees and spread more than 180 degrees (Figure 5). It appears that the feathers which are lowermost in the display are those which arise from the pelvic ridge. At least the arrangement of the musculature in this region strongly suggests that those feathers which arise from the pelvic ridge could be placed in this position.

The heavy transverse retractors in cocks apparently allows the spreading of the train to occur in progressive rows. Assuming that the erector muscles elevate the feathers and the retractors in the anterodorsal and posterodorsal rows keep the follicles close together anteroposteriorly, the resultant shape of the train during display would be a uniform fan. Progressively longer feathers in the chevron arms (Table 10) also probably account for the symmetrical shape of the fan.

Intercalary down follicles each have a set of muscles attached tangentially to the lateral surfaces (Figure 37). Although these slips originate from the erector-retractor muscle of contour feathers, their mode of attachment suggests that they may act to retract and rotate the down feathers. A similar type of muscle, attached between remiges and under major coverts in the hand of the Bronze Turkey, was apparently first described and named _M_. _rotoretractor_ by Lucas and Stettenheim (unpublished).

It was previously shown that dermal muscles are absent from the pelvic tract of all forms I examined. The pelvic tract of _Pavo_ differs from the pelvic tract of _Phasianus_, _Gallus_ and _Chrysolophus_ in having a well developed, thick, loosely arranged sheet of muscle which extends from the pelvic tract to the caudal tract (Figures 32, 33, 34 and 35). The muscle is attached at all levels to the caudal-most follicles of the train and courses dorsally and laterally superficial to the bilobed oil gland. The muscle is attached to the connective tissue wall of the oil gland but it is not attached to down follicles which are superficial to the gland. The gross relationship of the muscle to the feathers and to the oil gland is best seen under reflected light rather than under reflected and transmitted light (compare Figures 32 and 33 with Figures 34 and 35). I did not examine the muscle microscopically. Since it is attached to the feather follicles, I assumed it to be composed of smooth muscle.

The action of this muscle in positioning the train was not determined experimentally. It is possible that portions of the muscle may contract independently. Muscle bundles attached to the outer end of the follicles might act as depressors, those attached to the inner end may serve as erectors. Another possibility is that the entire muscle serves to tense the skin of the pelvic tract. Until further experiments prove differently I take the latter view and call the muscle _M_. _tensor_ _pterylae_ _pelvicus_. The presence of this muscle only in _Pavo_ suggests that it may be related to positioning of the train.

Musculature of the pelvic tract in the peahen is similar to that in the cock but reduced (Figures 33 and 35). At the gross level muscle rows course transversely, anterodorsally and posterodorsally. The transverse rows, which consist of retractor muscles, are dominant but seldom cover the bulb end of the follicles as in males. A subpattern of diamonds

Figure 31.--Dorsal view of the skin covering the pelvis of an adult peacock showing pterylosis of the pelvic and part of the dorsal tract. All feathers have been clipped. Feathers of one follicle row (dark row marked with India ink) were selected for the determinations of weight and length listed in Table 10. R---L, the anterior limit of intercalary downs. Photograph of a whole mount under reflected light. Bouin fixation, unstained and partially cleared.

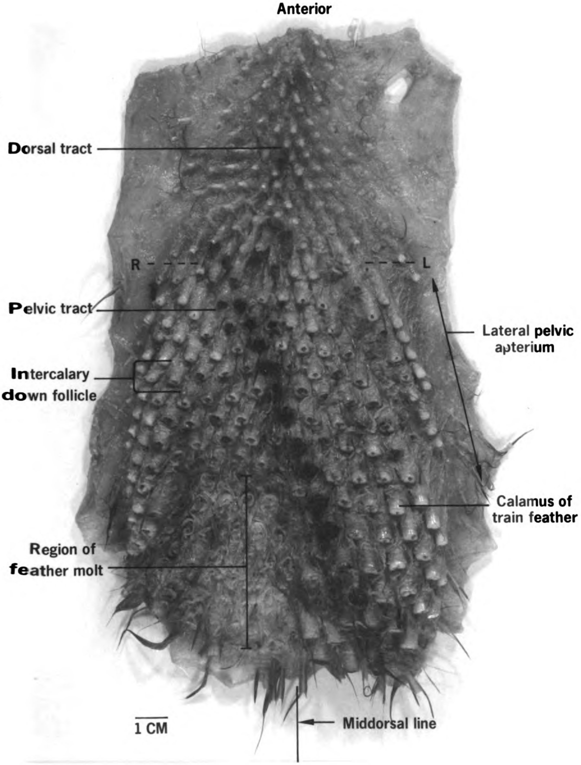
Anterior
Dorsal tract
R
L
Pelvic tract
Lateral pelvic apterium
Intercalary down follicle
Calamus of train feather
Region of feather molt
1 CM
Middorsal line

Figure 31

Figure 32.--Internal view of the skin covering the pelvis of an adult peacock showing feather muscles of the pelvic and part of the dorsal tract. (A) location at which Figure 36 was made; (B) location at which Figure 37 was made; R---L, anterior limit of transverse muscle rows; R'---L', anterior limit of the pelvic ridge. Photograph of a whole mount under reflected light. Bouin fixation, unstained and partially cleared.

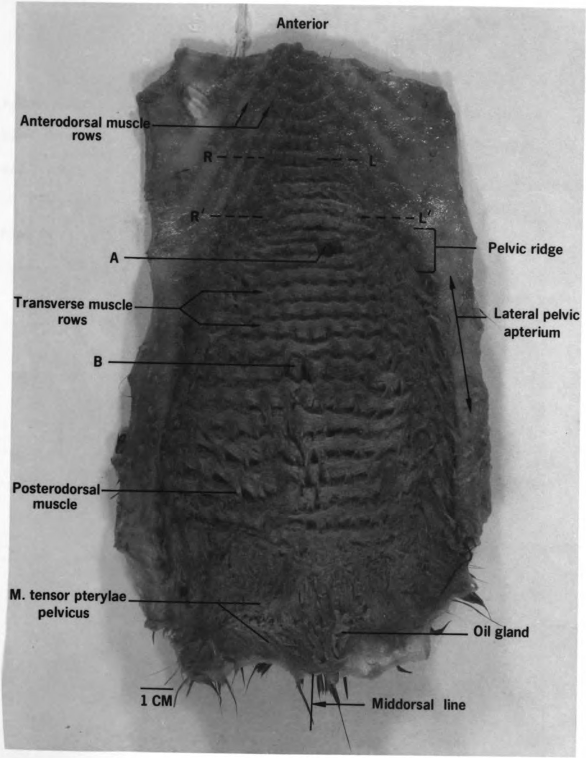
Anterior
Anterodorsal muscle rows
R
L
R′
L′
A
Pelvic ridge
Transverse muscle rows
Lateral pelvic apterium
B
Posterodorsal muscle
M. tensor pterylae pelvicus
Oil gland
1 CM
Middorsal line

Figure 32

Figure 33.--Internal view of the skin covering the pelvis of an adult peahen showing feather muscles of the pelvic tract and part of the dorsal tract. R---L, anterior limit of transverse muscle rows; R'---L'; anterior limit of pelvic ridge. Photograph of a whole mount under reflected light. Bouin fixation, unstained and partially cleared.

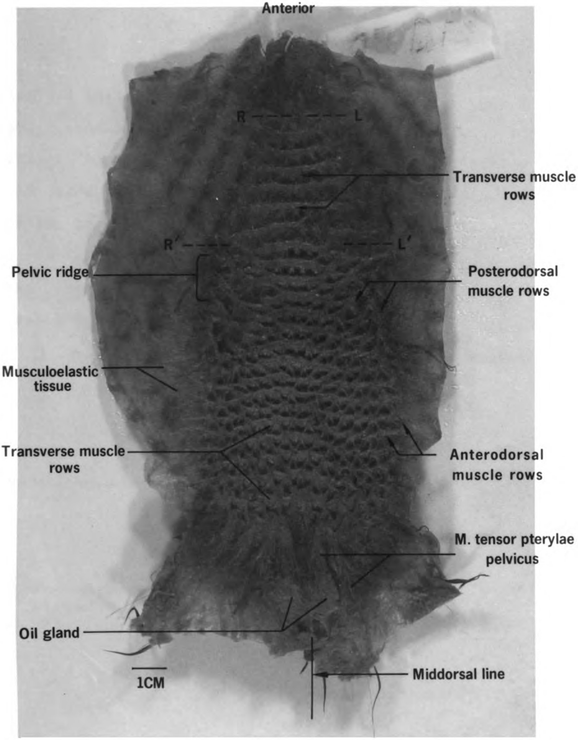
Anterior
R
L
Transverse muscle rows
R′
L′
Pelvic ridge
Posterodorsal muscle rows
Musculoelastic tissue
Transverse muscle rows
Anterodorsal muscle rows
M. tensor pterylae pelvicus
Oil gland
1CM
Middorsal line

Figure 33

Figure 34.--Internal view of the skin covering the pelvis of an adult peacock showing the feather muscles of the pelvic tract and part of the dorsal tract. (A) location at which Figure 36 was made; (B) location at which Figure 37 was made. Photograph, under transmitted and reflected light, of the same specimen shown in Figure 32. R---L anterior limit of transverse muscle rows; R'---L', anterior limit of the pelvic ridge. Bouin fixation, unstained and partially cleared.

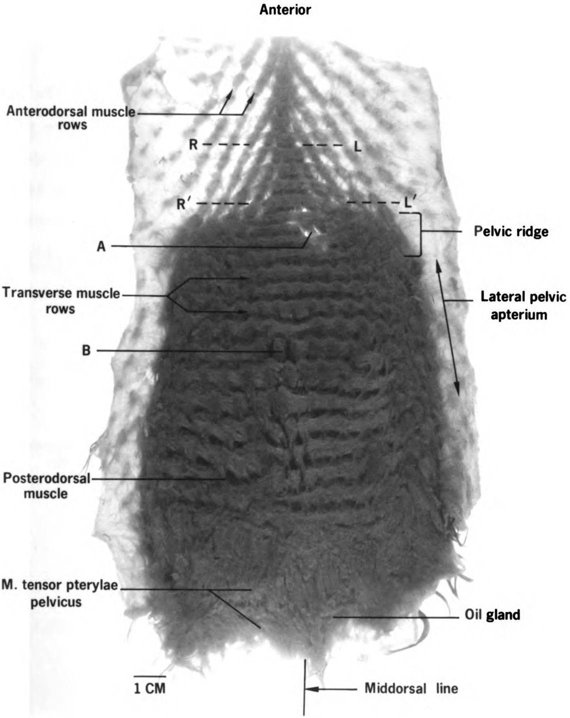
Anterior
Anterodorsal muscle rows
R
L
R′
L′
Pelvic ridge
A
Transverse muscle rows
Lateral pelvic apterium
B
Posterodorsal muscle
M. tensor pterylae pelvicus
Oil gland
1 CM
Middorsal line

Figure 34

Figure 35.--Internal view of the skin covering the pelvis of an adult peahen showing feather muscles of the pelvic tract and part of the dorsal tract. Photograph, under transmitted and reflected light, of the same specimen shown in Figure 33. R---L, anterior limit of transverse muscle rows; R'---L', anterior limit of pelvic ridge. Bouin fixation, unstained and partially cleared.

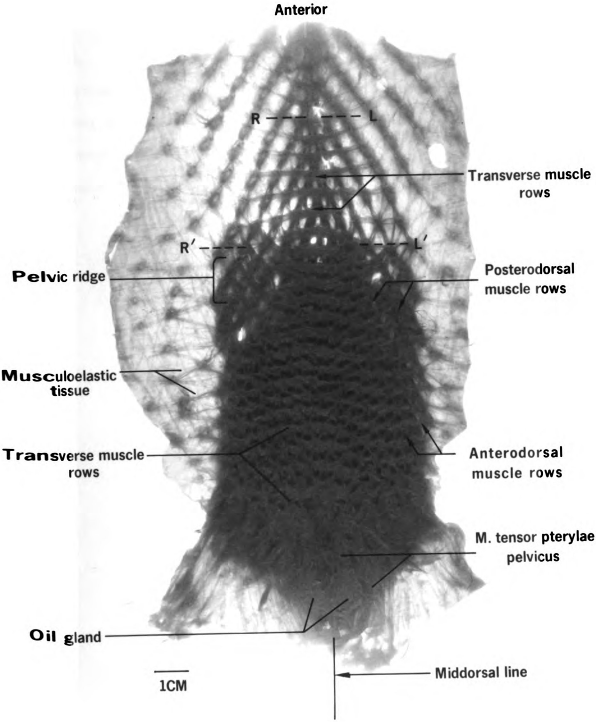
Anterior
R
L
Transverse muscle rows
R′
L′
Pelvic ridge
Posterodorsal muscle rows
Musculoelastic tissue
Transverse muscle rows
Anterodorsal muscle rows
M. tensor pterylae pelvicus
Oil gland
1CM
Middorsal line

Figure 35

Figure 36.--Dissection of feather muscles associated with 4 follicles of the anterior mid-region of the pelvic tract of the peacock. Refer to Figure 32 for the location from which the drawing was made. Intercalary follicles are present but are not shown in the figure.

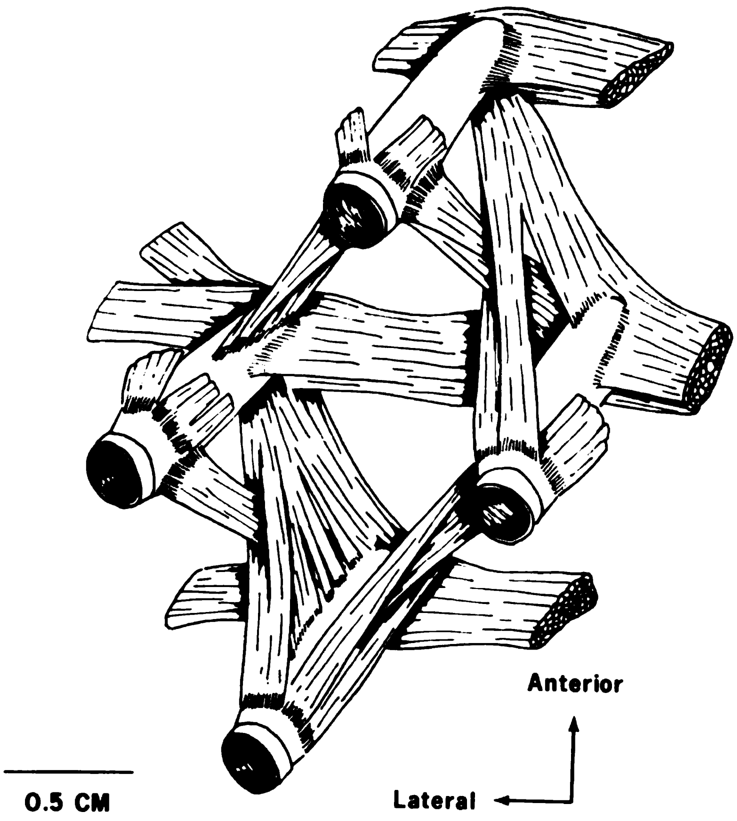

Figure 36

Figure 37.--Dissection of feather muscles associated with 4 follicles in the mid-central region of the pelvic tract of the peacock. Refer to Figure 32 for the location from which the drawing was made. Note the apparent increase in the size of muscles and more extensive attachment to the follicles of this area as compared to muscles of follicles located more anteriorly (compare with Figure 36).

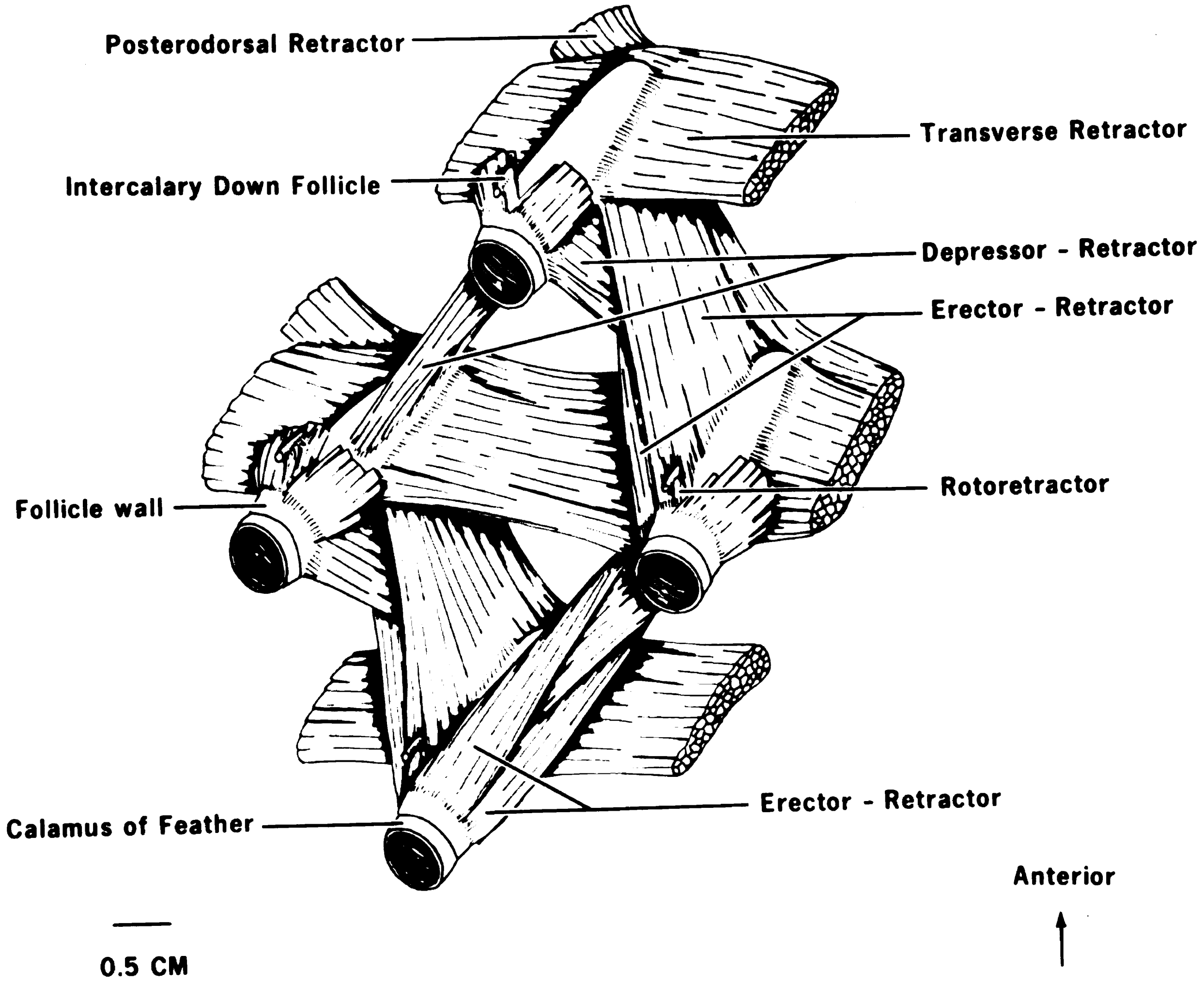
Posterodorsal Retractor
Transverse Retractor
Intercalary Down Follicle
Depressor - Retractor
Erector - Retractor
Rotoretractor
Follicle wall
Calamus of Feather
Erector - Retractor
Anterior
0.5 CM

Figure 37

is formed by intersecting muscle rows, a pattern characteristic of hens but not of cocks. These sexual differences in muscle morphology appear to be related to differences in feather displays which are discussed later. Rotoretractor muscles of intercalary downs and *M. tensor pterylae pelvicus* are also present in hens but show little differences when compared with cocks, except that the tensor muscle appears less developed in hens.

Musculoelastic tissue

Musculoelastic tissue is absent from the interscapular apterium in *Phasianus*, *Gallus* and *Chrysolophus*.

It is present in the lateral pelvic apteria in all species I examined. The alternating set of smooth muscle bundles and elastic tendons is directed transversely, is narrow and is spaced further apart in the anterior region than in the posterior region. Caudally, muscle bundles are wider, stouter and lie close together giving it a sheet-like appearance. Musculoelastic tissue in the lateral pelvic apteria is thinnest in *Pavo*, heaviest in *Chrysolophus*. In *Pavo* musculoelastic tissue in the caudal region of the lateral pelvic apterium is not formed into a close-knit sheet, and the pattern is similar to that lateral to the dorsal tract. Musculoelastic tissue is absent superficial to *M. tensor pterylae pelvicus*.

Summary of the Descriptive Morphology of the Smooth Muscles

Three kinds of smooth muscles are found within the dermis of the skin: (1) Muscoloelastic tissue, (2) feather muscles and (3) tensor muscles associated with certain tracts. These muscles differ in their location on the bird, in the form, arrangement and course of muscle fibers and in their relationship to the feather follicles. Specific similarities and differences within pterylae, among pterylae and among *Phasianus colchicus*, *Gallus gallus*, *Chrysolophus pictus* and *Pavo cristatus* are summarized following general statements on each kind of muscle.

Musculoelastic tissue

Musculoelastic tissue is characterized by an alternating series of anastomosing bundles of smooth muscles and elastic tendons which are arranged together in a sheet. Typically it crosses most apteria and lies deep to isolated follicles when the latter are present in apteria and may pass beneath the outermost follicles of some pterylae.

Of the 3 kinds of smooth muscle, muscoloelastic tissue shows the least variability between sexes and among congeneric species examined. Slight differences in the thickness of the sheet and the size of the smooth muscles and the tendons are found in different regions of the bird. The following features are similar in all species I examined.

Musculoelastic tissue in the crural apteria is delicate but thicker anteroventrally than posteroventrally.

Musculoelastic tissue is absent in the lateral body apteria (except at the narrow apex of the lateral body tract where a few scattered fibers unite with the radial muscles of follicles of the lateral border of the pectoral tract).

Musculoelastic tissue is absent in the scapular apteria except at the caudal end of the humeral tract. It is absent in the humeral apteria except at the anterior end.

Musculoelastic tissue is well developed in the ventral cervical apterium and lateral sternal apteria and weakly developed in the pectoral apteria and the anterior half of the sternal apterium.

Musculoelastic tissue is absent in the median abdominal apterium and in the interscapular apterium in *Phasianus*, *Gallus* and *Chrysolophus*. The apterium is absent in *Pavo*.

Musculoelastic tissue is present in the pelvic apteria in all species examined, but it is noticeably thinnest in *Pavo* and heaviest in *Chrysolophus*.

Feather muscles

Isolated feathers may be present in some apteria (e.g., ventral cervical apterium). Feather muscles of isolated follicles within apteria are arranged into bundles which attach at many levels to the follicle and radiate out to the dermis and to the deeper muscloelastic tissue when the latter is present. Lucas and Stettenheim (unpublished) characterized these muscles as feather muscles of the radial type. Radial muscles are also present at the apterial borders of all pterylae.

Feather muscles are variably developed within pterylae. Typically, fibers are arranged into bundles which attach at different elevations between adjacent follicles. Depending upon their attachments and presupposed actions, previous investigators have named some of the feather muscles erectors, depressors and retractors. These individual muscles vary in shape and size.

Generally a single depressor muscle passes through a double erector. Retractor muscles which course between 2 follicles at the same elevation are generally thinnest except in particular instances which will be reviewed shortly.

Together, bundles of erectors, depressors and retractors are organized into rows. Muscle rows may or may not correspond to the pattern of follicle rows, the latter of which was determined in the section on pterylosis by examination of the external surface. Certain muscle rows may be dominant over others depending upon the thickness of muscles within a row.

Muscle rows course in a particular direction. The intersection of muscle rows between contiguous follicles form subpatterns of quadrilaterals or triangles depending upon the number of muscle rows, their direction and their dominance.

Similarities and differences in muscle shape, size, type, arrangement into rows and rows into patterns are compared in pterylae of *Phasianus colchicus*, *Gallus gallus*, *Chrysolophus pictus* and *Pavo cristatus* and are summarized below.

In general, muscles of all follicles bordering pterylae are of the radial type. I found feather muscles associated with follicles of all contour feathers, semiplumes, downs and bristles, but not associated with follicles of filoplumes. This agrees with the findings of Lucas and Stettenheim (unpublished). Muscles of intercalary follicles found at the borders of most tracts form a pattern of muscle rows which is usually ruptive to the clear pattern found elsewhere in the tract.

Muscle size was determined by weighing or measuring the volume of individual muscles attached to feathers in homologous tracts. Although the data were not analyzed statistically, results show that the sizes of the feather muscles appear to vary directly with the size and to the load of the feather. Generally, feather musculature is heaviest posteriorly in a tract.

The general shape of the femoral tract and orientation of muscle rows are similar in both sexes in *Phasianus*, *Gallus*, *Chrysolophus* and *Pavo*. However, *Pavo* shows the greatest differences in the shape and form of feather muscles within rows. In *Pavo*, thin flat depressors interdigitate with each other and anterodorsal rows have tendons located mid-way between each follicle. These features are not characteristic of Phasianus, Gallus and Chrysolophus where band-like single depressors pass through flat double erectors, and mid-tendinous segments are absent in the belly of the muscle.

In comparison to the other representatives, feather musculature is least developed in the crural tract of Pavo where muscle rows are extremely thin on both the internal and the external surface of the leg. Distinction between individual erectors and depressors is difficult due to the presence of numerous tendons in the belly region of the muscle. Muscles of the radial type are extremely abundant on the medial surface.

Musculature of the lateral body tract is thin and similar in all representatives.

Feather musculature of the humeral tract is well-developed and similar in all species examined. Anteromedial and posteromedial muscle rows are dominant. Double erectors and single depressors are about equally developed.

Next I shall summarize the feather musculature of the ventral capital, ventral cervical, pectoral, sternal and abdominal tracts. In general the gross pattern of muscle rows within these tracts shows uniformity among all species examined. Slight differences are found in Pavo which is characterized by relatively thinner musculature in all ventral tracts.

In the interramal region, elongated diamond-shaped quadrilaterals are present in *Phasianus*, *Gallus* and *Chrysolophus*, but not in *Pavo*, which has muscles of the radial type.

Among representatives studied, musculature of the ventral neck is least developed in *Pavo* and strongest in *Chrysolophus*. In *Pavo* muscle bundles are thin flat bands. In *Chrysolophus* erectors are thick bands and the depressors are cord-shaped.

Musculature of the pectoral tract is weakest in *Pavo*. Retractors at the bulb are present in the anterior 1/3 of the tract in all representatives, but only along the lateral region in *Pavo*.

Slight differences are found in the musculature of the sternal and abdominal tracts among species. The medial longitudinal muscle row is absent in *Chrysolophus*, weakly developed in *Pavo*, moderately developed in *Phasianus* and well developed in *Gallus*. In the caudal region of the abdominal tract, erectors and depressors are cord-shaped in *Phasianus*, *Gallus* and *Chrysolophus*, band shaped in *Pavo*.

Feather musculature of the dorsally located pterylae shows great variability and differences in the size and shape of individual muscles, in their arrangement into rows, and in their gross pattern within pterylae between sexes and among species.

Greatest differences are found in association with feathers which apparently serve a display function.

The depressed crest feathers in male *Chrysolophus* and the erected crest in both sexes of *Pavo* have heavier feather muscles as compared to the other follicles of the dorsal capital tract.

The arrangement of the stout double cord-like depressors, the band-like retractors at the neck end of the follicle, and the thin band-like erectors suggest that feather erection would be less than normal and that movement, if any, of the crest feathers of *Chrysolophus* is probably stronger in the direction of depression than of erection.

The erected crest feathers of *Pavo* are characterized by the total absence of depressors and erectors. Two-thirds of the outer ends of the follicles are interconnected by retractor muscles which are arranged randomly rather than into rows.

Feather muscles of the "ear" tufts in *Phasianus* show little modification, if any, to explain the erection of the "ears" during courtship display. The presence of *M. tensor pterylae capitalis dorsalis* may explain the compression of the "ears". The mechanism for erection requires further investigation.

Feather musculature of the dorsal cervical tract is extremely well developed in *Chrysolophus*, heavy in *Gallus*, moderately developed in *Phasianus* and least developed in *Pavo*. Greatest differences in muscle pattern, arrangement and attachment occur among males and appear to be related

to their feather displays. Greatest similarities exist between females of _Phasianus_ and _Gallus_ and between males and females of _Pavo_. The pattern and arrangement of the feather muscles are similar in hens and cocks of the same species, but are much more developed in the latter.

The dorsal cervical tract of _Gallus_ differs from _Phasianus_ by having dominant muscle rows coursing posterodorsally and longitudinally, while in _Phasianus_ dominant muscle rows course posterodorsally and anterodorsally. Longitudinal diagonal muscle rows are more abundant in _Gallus_ than in _Phasianus_. A smaller depressor-erector ratio in _Gallus_ than in _Phasianus_ suggests that hackles have either a greater ability for erection, or a lower ability for depression than do homologous feathers of _Phasianus_. Retractor muscles at the neck end of the follicles are best developed in the posterodorsal and longitudinal rows of _Gallus_ and are more abundant than in _Phasianus_. The predominance of longitudinally directed rows in _Gallus_ suggests that movement of the hackles is possibly more antero-posteriorly than in _Phasianus_.

In the dorsal cervical tract of _Chrysolophus_, extremely dense musculature is associated with the follicles of the cape, while thin musculature is associated with the smaller contour follicles adjacent to the cape. Feathers of the cape have a greater mass of muscle than do homologous feathers of _Gallus_. Dominance of muscles rows varies within the tract.

Anterodorsal and posterodorsal rows are dominant in the mid-region. Longitudinal rows are absent. Posterodorsal and transverse rows are dominant caudally. The transverse rows consist only of heavy retractors at the neck end of the follicles. Longitudinal and posterodorsal rows are dominant laterally. Again, retractors are well represented at the neck end. The above features are absent in Phasianus, Gallus and Pavo.

Musculature of the dorsal cervical tract is least developed in Pavo and appears to be similar to that described by Lucas and Stettenheim (unpublished) for the turkey.

Greatest differences among species in the arrangement of muscles associated with the interscapular tract seem related to differences in the pattern of pterylosis of this region.

Feather musculature is extraordinarily developed in the pelvic tract of Pavo. A pattern of qudrilaterals is not evident at the gross level simply because of the large amount of muscle present between follicles. Anterodorsal and posterodorsal muscle rows are present but are obscured due to the dominance of very heavy transverse muscle rows. The transverse muscle rows cover most of the inner end of the follicle. The principal features of the musculature of the train feathers are the heavy transverse retractors at the bulb end and the pinnately arranged erector-retractor and depressor-retractor muscles in the posterodorsal rows.

Intercalary down follicles are abundant among the contour feathers of the pelvic tract in Pavo but are absent in the pelvic tract of the other species I examined. Small rotoretractor muscles connect these feathers with the erector-retractor muscles of the larger feathers of the train.

The arrangement and pattern of feather musculature of the dorsal and pelvic tracts of Phasianus, Gallus and Chrysolophus show only slight differences among individuals and species.

Tensor muscles

Smooth tensor muscles associated with the feathers are of limited distribution in the birds I examined. Bundles of muscle fibers are arranged into a sheet which generally courses between two feather tracts. Typically, they attach at least at one end to feather follicles and do not have the characteristic alternating bundles of muscle and elastic tendons as do musculoelastic tissue.

M. tensor pterylae femoralis courses from the femoral tract to the pelvic tract. It is present in both sexes of all representatives I examined, but it is thickest in male Chrysolophus.

M. tensor pterylae capitalis dorsalis is present only in male Phasianus, the only species which possess accessory integumentary "ears".

M. tensor pterylae pelvicus courses from the caudal tract to the pelvic tract. Its presence only in Pavo cristatus-suggests that it may play a role in the positioning of the feathers of the train during courtship display.

M. protractor pennati cervicalis dorsalis is present only in Chrysolophus. It differs from the foregoing muscles in its form and attachment. The muscle is a plexiform sheet which arises from a tendon at the angle of the jaw and crosses beneath the follicles of the ventrolateral capital tract to attach to the outer end of the lateral-most follicles of the cape. Experiments involving muscle extirpations show that the muscle is responsible for extending and elevating the cape during courtship display.

Action of the Smooth Muscles of the Skin

The gross morphology of feather muscles, musculoelastic tissue and tensor muscles of certain feather tracts has just been summarized. These muscles differ in form, in arrangement and course of muscle fibers, in their attachment to the feather follicles, and in their location on the bird. All are found within the dermis.

The proposed actions of the muscles are based primarily upon morphological evidence and evidence obtained from preliminary experiments involving muscle extirpations and muscle stimulation. Each kind of muscle will be treated separately.

Musculoelastic tissue

Musculoelastic tissue is composed of bundles of smooth muscle alternating with elastic tendons. I have shown that musculoelastic tissue is present only in certain regions in the birds I examined. It is notably absent from the lateral cervical apteria and the lateral body apteria. Similar conditions were reported by Lucas and Stettenheim (unpublished) for the chicken.

Considering the elastic and contractile elements of the musculoelastic tissue, it appears that musculoelastic tissue functions to tighten the skin between certain feathered areas of the body. This may be important in aerodynamics as suggested by Petry (1951) and also in stabilizing the contours of adjacent tracts so that controlled shifts in the position of the skin can be accomplished (Lucas and Stettenheim, unpublished). It follows that skin, where musculoelastic tissue is present, is possibly under a greater tension and probably offers a greater resistance to deforming forces than skin where musculoelastic tissue is absent.

Lucas and Stettenheim (unpublished) were unable to explain the absence of musculoelastic tissue in the lateral cervical apteria of the chicken, a region where the skin is particularly loose, and the lateral body apteria, where the skin is not exceptionally loose.

With respect to the lateral cervical apteria, the only explanation I can offer concerns the presence, course and possible action of the <u>cervical component</u> of <u>M</u>. <u>cucullaris pars cervicalis</u>, which passes from the neck to the lateral border of the interscapular tract. It may be that the ability of this muscle to anchor the lateral borders of the interscapular tract is greater than that possible by musculoelastic tissue.

A similar hypothesis is offered to explain the absence of musculoelastic tissue in the lateral body apteria where portions of the dermal muscles *M*. *pectoralis thoracica pars subcutaneus thoracics* and *M*. *serratus superficialis pars metapatagialis* course beneath it.

However, some apteria may have both striated dermal muscles and musculoelastic tissue associated with them. It may be that the action of the two systems, in these instances, is synergistic and augmentative. Whether or not this is true requires further testing.

Petry (1951) demonstrated that striated muscle fibers unite by elastic tendons to musculoelastic tissue in the lateral cervical apterium of the pigeon. But, he did not identify the source of the striated muscle. Dissections of skins of pigeons by Lucas and Stettenhaim (unpublished) verify the presence of musculoelastic tissue in the lateral cervical apteria. Petry's finding of striated muscle united with musculoelastic tissue provides a morphological basis for considering augmentation and synergism between these two systems.

I have previously mentioned that during the lateral display of male *Chrysolophus*, the plumage of the rump appeared to shift downward on one side. This pronounced movement appeared to occur without elevation of the feathers at right angles to the body axis and was assumed to result from movement of the skin. I also showed that striated dermal muscles are absent from this region and that the apparent shifting of the plumage of this region must be controlled by some other mechanism.

I have also shown that the musculoelastic tissue and _M_. _tensor_ _pterylae_ _femoralis_ is more developed in the lateral pelvic apteria of _Chrysolophus_ than in the pelvic apteria of the other species examined. The similarity in the pattern, arrangement and attachment of the feather muscles of the pelvic tract of _Chrysolophus_, _Gallus_ and _Phasianus_ cannot explain shifting of the plumage. Some shifting of the plumage also seemed to occur in the lateral display of _Phasianus_ and _Gallus_, but the movement was less pronounced and less extensive than in _Chrysolophus_. This might be related to the fact that the musculoelastic tissue and _M_. _tensor_ _pterylae_ _femoralis_ is thinner in _Phasianus_ and _Gallus_ than in _Chrysolophus_. However, more evidence and further experimentation are needed to draw conclusions as to the role of these two muscles in shifting of the plumage.

Feather muscles

Similarities and differences in the gross morphology of the feather muscles in _Phasianus_, _Gallus_, _Chrysolophus_ and _Pavo_ have been described, compared and reviewed.

The terminology of the feather muscles, given by previous investigators, has been based largely upon the supposed action of the muscle(s) in question. I have retained the terminology of erector, depressor, retractor, erector-retractor, depressor-retractor and rotoretractor throughout this study and have assumed that these muscles act in the ways they have been named.

In general, the action of a muscle may depend upon the position, size and orientation of the feather follicle and upon the course, shape, size and attachment of the muscle to the follicle. There are several factors which may influence the force exerted by a muscle on the follicle. Of significance is the size of the muscle, the angle at which the muscle attaches to the follicle, the change in this angle during contraction, the length of the lever arms, the internal arrangement of the muscle fibers within the muscle and the interaction with other muscles. Factors concerning the internal architecture of muscles have been investigated extensively by van der Klaauw (1963). In my study only the size, shape, course, attachments and interaction with other muscles are stressed. However, the other factors must be included on any quantitative analysis of muscle action. Also, I have not examined the finer details of the kinetic relationships among the feather follicles and the underlying dermis and epidermis which might be of value in ascribing lever action.

With respect to the action of the feather muscles, the follicle apparently functions for the attachment of the muscles and serves as a lever for moving the feathers. It is assumed that the outer end of the follicle, at the surface of the skin, is the fulcrum. If this is true the skin is expected to move very little during erection or depression of a typical contour feather. A different lever system concerning cape feathers of Chrysolophus will be discussed later.

Feather muscles of isolated down feathers in apteria are arranged radially. Due to the small lever system present and the radial nature of the muscle fibers, less movement would be expected in comparison to the feathers in pterylae. Thus, radial muscles probably function to incline the feather in any direction, though not strongly.

Feather musculature of pterylae is "typically" arranged into bundles, the bundles into individual muscles, and the muscles into rows. The reader is reminded that in the bird there is a gradual transition from muscles of the radial type to muscles arranged into bundles and into rows. The best example is in the femoral tract.

Erector, depressor and retractor muscles within rows vary in shape and size from thin bands to thick cords. Usually a depressor muscle passes through a double erector. However, bundles of both muscles sometimes interdigitate with one another.

Generally, muscle fibers in the above types run parallel to one another and to the longitudinal axis of the muscle. Usually, erectors are thinner than the depressors. I have shown that the mass of the depressor muscles is about twice that of the erectors. Assuming muscle size is proportional to strength, depressors appear to be stronger than the erectors. One would think that the erectors would be the stronger, as it should require more force to elevate the feather than to depress it. However, the stretched conditions of the muscles must be considered. My measurements were taken in fixed skins with the muscles assumed to be in the relaxed state. It is generally known that the force of a muscle developed during contraction is greater if the muscle is under stretch. It may be that the stretch factor is more prominent in the erectors than in the depressors and that erectors are the stronger of the two. However, it is quite possible that selection is for depression. Strong depression of the feathers would appear to be very advantageous in streamlining the plumage during flight. A comparative study of the feather musculature of flying and flightless birds might show some interesting relationships.

Generally, fibers of the erectors are longer than the depressors. In general muscle length affects the range of movement but not the power. There is a greater range of movement in long muscles than in short muscles. This may explain differences in the extent of elevation of the feathers from a normal position to various levels of elevation.

Some feather muscles have their fibers pinnately arranged. Muscles with this form of fiber arrangement are either of the erector-retractor or the depressor-retractor type. In most well-developed pterylae depressor-retractor muscles are the more common of the two. Both are prominent in the anterodorsal and posterodorsal rows of the pelvic tract of _Pavo_.

The significance of pinnateness in muscle action has been discussed by Pfuhl (1936), Mollier (1937), Dullenmeijer (1951), Bock (1960) and Bourne (1960). In general, pinniform muscles are capable of exerting a greater force than are parallel-fibered muscles. Thus when power is the principal requirement muscle fibers may be arranged in a pinniform fashion.

Retractor muscles may be present in well developed pterylae. They course at the same elevation between two follicles. They are more often found at the bulb end of the follicle than at the neck end. Also, they are usually thinner than erectors or the depressors and they predominate in rows where follicles are close together (usually the anterodorsal directed rows).

It has been assumed that retractor muscles act to draw the feathers closer together without elevating or depressing them. However, depending upon their attachments they may supplement erection and depression.

The action resulting from the force of muscles is dependent upon the magnitude and direction of forces on the follicle and is based upon the angles of attachment, the length of the weight arms and the length of the power arms. It may be that retractors attached at a right angles to the follicles at the bulb ends have a greater ability, through a long power arm, to lift a greater load than do retractor muscles attached at right angles to the neck; the latter having a short power arm.

Very thick transverse rows of retractor muscles are attached to the bulb ends of the follicles in the pelvic tract of _Pavo_. Erector and depressors muscles are absent from these rows. Transverse rows consisting only of retractors are not present in the pelvic tract of any of the other species I examined. It appears that these muscles are responsible for producing the spread-shape form of the train during courtship display.

Retractor muscles which attach tangentially to a follicle probably act to rotate the feathers. _Rotoretractor_ muscles are found in association with intercalary down feathers in the pelvic tract of the peacock. Tangential attachments of erector and depressor muscles apparently account for the twisting of the feathers as they are being elevated or depressed.

The morphological aspects of the action of the feather muscles strongly suggest that this mechanism is developed in order to make movement of the feathers possible. The organization of muscles into opposing sets apparently allows for greater efficiency in the lever system. The longer the follicle, apparently the greater the extent of muscle attached to it. Differences in muscle size and attachments appear to account for variations in the degree, direction and extent of feather movement. Also, it appears that the organization of the muscles into rows insures a non-random direction to the movement. The strength and dominance of particular muscle rows and the reciprocal action of synergic and antagonistic muscles may be important in producing the smooth movement of the feathers one observes in displaying and preening birds.

Apparently feather muscles are innervated by sympathetic nerves (Langley, 1902a, 1902b, 1904). Langley (1904: 225) credits Jegorow (1890) for first demonstrating this in the turkey. Neural control is integrated through the central nervous system (Weber, 1906; Langworthy, 1925; Rogers, 1928). In general their investigations have demonstrated that stimulation of the sympathetic system, the thalamus or the cerebral cortex, or removal of the cerebral cortex affected the movement of the feathers. However, these investigators apparently assumed that feather movements were due to the contraction of the feather muscles, for they did not report observing the movements of the muscles themselves.

Thus, in order to gain further information as to the action of the feather muscles, I electrically stimulated erector and depressor muscles associated with the feathers of the mid-region of the dorsopelvic tract of the chicken. I selected this tract because feathers are elevated during preening and strongly depressed during agonistic display and because dermal muscles are absent from this region of the body. The specific location of the experiments was follicle L-1, 10 feather rows anterior to the oil gland.

Six Single Comb White Leghorn chickens were used and all birds were anesthetized with Equi-Thesin®. Feather shafts were clipped and muscles were exposed from the external surface by removing the epidermal layer of skin around the feather follicle. A Harvard model 935B stimulator was used to deliver 250 cycle multiple stimuli of 0.1 volt to individual muscles. The stimulus was applied for about 1 second. Observations of movements of the skin, feather shafts and feather muscles were made at 10X with a dissecting microscope.

All attempts to produce erection of the feathers failed. Stimulating individual erector or depressor muscles always produced marked depression of the feathers even when the frequency and strength of the stimulus were altered. These results would be expected in a situation where one muscle is larger than its antagonist. The muscle with the greater mass would probably dominate over the smaller muscle. This appears to have happened when I attempted to produce erection by stimulating the erector muscles. Determinations on muscle volume from 10 follicles in the immediate vicinity of the experimental site revealed that the mass of the depressor muscles is about twice that of the erectors (mean depressor-erector ratio = 2.03).

Even though these preliminary experiments were only partially successful, some information concerning the action of the depressor muscles was obtained. That the depressor muscles contracted when stimulated was evidenced by the shortening and thickening of the muscles and the movement of the feather shaft. Depression of feathers usually involved 2 or 3 rows of feathers anterior and posterior to the application of the stimulus. During depression some rotation of the feather shaft was observed. The skin appeared to remain stationary as the feathers were being depressed.

The most significant feature brought out in these experiments is that depression of feathers is brought about by the contraction of the depressor muscles and that this form of feather movement is independent of the movement of the skin. This supports conclusions of muscle action based on morphology and observations of feather movement during display. Although attempts to erect feathers were not successful with the present technique, morphological evidence strongly suggests that erector muscles elevate the feathers.

The action of the feather muscles is upon the feather by way of the feather follicle. In general, the plumage, depending upon the feather tract involved, is capable of being erected, rotated and depressed at various degrees.

These movements are independent to the movement of the skin. Erecting and depressing the plumage may serve several functions. Feather movements may aid in thermoregulation, sunbathing, preening and defecation or serve as a social signal in displays. Depressor muscles are generally stronger than erector muscles. This feature would be advantageous in streamlining the plumage for flight and in sleeking of the feathers as seen in certain displays.

Tensor muscles

These kinds of smooth muscles are of limited distribution in the birds I examined. Of significance is the fact that all tensor muscles are associated with feathers which are conspicuously positioned during display. Muscle fibers of the tensor muscles are longer than those of the feather muscles and they do not have the intermittent tendons characteristic of musculoelastic tissue. Thus they appear capable of contracting over a greater distance than are the other smooth muscles of the skin. In this respect they appear similar to the striated dermal muscles.

M. tensor pterylae femoralis courses between the femoral and pelvic tract in all species I examined. Its stronger development in *Chrysolophus* than in *Gallus*, *Phasianus* or *Pavo* appears to be related to the apparent shifting of the plumage of the pelvic tract during the lateral display of *Chrysolophus*.

M. tensor pterylae capitalis dorsalis is present only in male *Phasianus*, the only species which possesses integumentary "ears". The action of this muscle appears to be responsible for depression of the "ears".

M. tensor pterylae pelvicus is large and found only in *Pavo*. It is attached at all levels to the caudal-most follicles of the train feathers. The action of this muscle may aid in raising or lowering the feathers of the train or tensing of the skin between the pelvic and caudal tracts. Both the train and the tail are elevated during courtship display. It may be that *M. tensor pterylae pelvicus* aids in elevating the tail.

M. protractor pennati cervicalis dorsalis is present only in *Chrysolophus*. I have previously shown that partial destruction of this muscle affects the protraction and elevation of the cape feathers during courtship display.

In summary, except for *M. protractor pennati cervicalis dorsalis*, the actions and functions of the smooth tensor muscles of the skin are highly speculative. I have shown that their restricted distribution appears to be related to feather displays. However, their specific roles in positioning the skin and the feathers require further investigation.

SUMMARY AND CONCLUSIONS

This investigation was undertaken in an attempt to determine the relationship of the dermal and smooth muscles of the skin to feather display.

Feather displays and the gross anatomy of the smooth and striated muscles of the skin are described and compared among several representatives of 4 genera of the Subfamily Phasianinae.

Movements and postures of the feathers are described for the lateral courtship displays of cock *Phasianus colchicus*, *Gallus gallus*, *Chrysolophus pictus* and *Chrysolophus amherstiae*, and for the frontal courtship display of cock *Pavo cristatus* and for the frontal agonistic display of cock *Gallus gallus*.

Depending upon the display, body feathers are shifted, elevated, rotated and depressed at various degrees.

Most conspicuous feather displays are localized in different regions of the plumage and homologous regions of the plumage among representatives of different genera may move differently.

"Ear" tufts on the dorsolateral head of male *Phasianus* are elevated and inclined outward during most of the breeding season and during lateral courtship display. "Ear" tufts are absent in *Gallus*, *Chrysolophus* and *Pavo*.

In the lateral courtship display of Chrysolophus cape feathers of the anterior dorsal neck are extended and elevated upward to the eye. This results in a uniformly spread fan which is parallel to the long axis of the head. Either side of the cape may be fully positioned, but both sides are never fully extended and elevated at the same time. A cape, like that found in *Chrysolophus*, is absent in *Gallus*, *Phasianus* and *Pavo*.

In the courtship display of *Pavo*, train feathers of the rump are elevated and spread in a symmetrically shaped fan over the body. *Pavo* is the only representative in which the feathers are so strongly spread transversely with respect to the longitudinal axis of the body. Clipping of the tail feathers shows that elevation of the train is not dependent upon the elevation of the tail.

Feathers in different regions of the plumage on the same individual may assume different feather postures.

In the frontal agonistic display of *Gallus*, hackle feathers of the dorsal neck are strongly elevated at right angles to the body while the rest of the body plumage is strongly depressed.

Shifting of the plumage of the rump seems to move groups of feathers and occurs without erecting or depressing them. Shifting of the plumage is present in the lateral courtship display of *Gallus*, *Phasianus* and *Chrysolophus*, but is more pronounced in *Chrysolophus*.

Except for the "ear" tufts in *Phasianus*, fluffing of all body feathers occurs in the lateral courtship display of *Phasianus* and *Gallus*.

There are no apparent differences in the feather displays among Single Comb White Leghorn, Bantam Rhode Island Red and Araucana chickens or among *Chrysolophus pictus* and *C. amherstiae*. I found great differences in feather displays among male representatives of different genera. Females of the same species sometimes perform displays which are similar to but weaker than those of males.

Feathers of the neck in all birds studied, regardless of their degree of erection in display, appear to move closer together when the head is retracted and further apart when the head is extended. This form of movement of the feathers, as well as shifting of the plumage is assumed to be dependent upon the shifting of the skin. Erection, depression and rotation of the feathers at various degrees are assumed to move independent to the movement of the skin.

Crests of peafowl appear permanently erected while those of male *Chrysolophus* appear permanently depressed. Crests are absent in the different breeds of chickens I examined and in *Phasianus*.

Feather movements during display are compared with those observed during preening. Some regional differences and differences in the extent of erection of the feathers are found. Except for the cape feathers of Chrysolophus and the hackles of Gallus, body feathers are generally ruffled when they are preened. That cape feathers and hackles are not elevated during preening appears to be related to the method of preening these feathers. Display feathers of the train in Pavo are only slightly elevated and spread, and never attain full display posture when they are preened.

Observations on the movement of feather shafts during erection and depression of clipped feathers in Gallus support the hypothesis that feather raising and lowering are not dependent upon the shifting of the skin. Constriction of the skin in the anterior lateral neck causes the feather shafts to move closer together transversely, but without altering the degree of feather erection.

The pattern of pterylosis shows some significant features about the localization of the display feathers. Follicles of the hackles of Gallus, the cape feathers of Chrysolophus, the train feathers of Pavo and the crest feathers of Chrysolophus and Pavo are conspicuously enlarged. Also the skin where these feathers are implanted is conspicuously thickened. In general, the larger the follicle the thicker the skin.

Intercalary downs, present among the contour feathers of the crown and pelvic tract of Pavo, are absent in homologous regions in the other representatives studied.

The lengths and weights of feathers within most tracts show a gradual decrease posteriorly along the arms of chevron rows. Exceptions to this are found in the cape of *Chrysolophus* and the train of *Pavo* where feather length and feather weights increase posteriorly along the arm of a chevron row. The latter may be related to the fan-shaped form of the feather group in the display of these birds.

The gross morphology of 10 striated dermal muscles is described for *Phasianus*, *Gallus*, *Chrysolophus* and *Pavo*. As a group, dermal muscles lie deep to the dermis. They may be attached to the skeleton or to appendicular muscles and are always attached to the skin at one end. *Mm*. *constrictor colli*, *cucullaris pars dorsocutaneus* and *gastrolumbalis* have both their origins and insertions restricted to the skin.

Striated dermal muscles show little, if any, relationship to feather displays. They are arranged into sheets and are of limited distribution. No dermal muscles are found associated with the "ear" tufts of *Phasianus*, the crests of *Chrysolophus* and *Pavo* or the feathers of the train in *Pavo*.

Histological examination of teased dermal muscle at the insertion end shows that striated muscles are not attached to the follicle. Rather, they attach by fascia to the undersurface of the skin, generally beneath groups of feathers at the corders of feather tracts. They usually cross apteria.

Eight dermal muscles are found in all representatives. *M*. *cucullaris pars dorsocutaneus* is present only in

Chrysolophus and *Pavo* and *M. gastro-lumbalis* is present only in *Gallus*.

Six dermal muscles are associated with the loose skin of the neck. Of these the *cranial component* of *M. cucullaris pars cranialis* is relatively more developed beneath the hackles of *Gallus* and the cape of *Chrysolophus* than beneath feathers of homologous regions in *Phasianus* or *Pavo*. Results from experiments involving extirpations of the cranial attachment of the *cranial component* of *M. cucullaris pars cranialis* in *Gallus* demonstrate that partial destruction of this muscle does not affect erection of the hackles. During agonistic display experimental chickens appeared to raise their hackles just as high and quickly as did control birds.

Results from preliminary experiments involving muscle and nerve stimulation in chickens support the findings and conclusions of Langley (1904) that the striated dermal muscles tense the skin.

Tightening and relaxing of the skin of the neck may explain how feathers of the neck, regardless of their degree of erection, move closer together when the head is retracted and further apart when the head is extended.

Three functional types of smooth muscles, part of a complex associated with the feathers, are found within the dermis of the skin; (1) musculoelastic tissue, (2) feather muscles, (3) tensor muscles. Musculoelastic tissue shows little variability between sexes and among representatives of different genera. Musculoelastic tissue is noticeably heavy in the lateral pelvic apteria of male Chrysolophus.

Feather muscles and tensor muscles show great differences in pattern, arrangement and degree of development among birds.

Feather muscles are arranged into bundles which attach at different elevations between adjacent follicles. The follicle apparently functions for the attachments of muscles and serves as a lever for moving the feather. Variations in the relative development of muscles within rows, their attachments to the feather follicle and the direction and pattern of muscle rows apparently reflect variations in lever systems which appears to explain variations in the degree of erection, depression and rotation of the feathers observed during preening and in certain displays.

Electrical stimulation of depressor muscles causes depression of the feather.

Feather musculature is very similar among Single Comb White Leghorn, bantam Rhode Island Red and Araucana chickens, and among Chrysolophus pictus and C. amherstiae. This appears to be because feather displays are most similar among the breeds of chickens and among the congeneric species I studied.

The gross pattern of feather musculature is similar in both sexes of the same species, but feather musculature is less well developed in the hens. This appears to be because hens perform feather displays that are similar to but weaker than those of males.

No notable differences in the pattern and arrangement of the feather and tensor muscles are found in the crural, lateral and all ventrally located tracts among the birds I examined.

Tensor muscles are of limited distribution in the birds I examined. Bundles of muscle fibers are arranged into a sheet which generally courses between two feather tracts.

Slight differences in the development of *M. tensor pterylae femoralis* are found. The muscle courses from the pelvic tract to the femoral tract in all representatives but it is thickest in male *Chrysolophus*.

Greatest differences in the size, arrangement and pattern of the feather and tensor muscles are found in the dorsally located tracts in males among species of different genera.

M. tensor pterylae capitalis dorsalis is present only in male *Phasianus*, the only species which possesses accessory integumentary "ears". Feather musculature of the "ear" tufts is weak and does not differ appreciably from that of adjacent areas. *M. tensor pterylae capitalis dorsalis* may explain the compression of the "ears" but cannot explain their erection.

The skin is thick and feather musculature is well-developed beneath the crests of *Chrysolophus* and *Pavo*.

In *Chrysolophus* erectors are thin and have attachments to the bulb and mid-region of the follicles. Follicles are implanted at extreme acute angles to the surface of the skin so that the bulb end of one follicle is practically touching the neck end of the follicles anterior to it. This distance is spanned by a double cord-like depressor. Except for the crest of *Chrysolophus*, double cord-shaped depressors are infrequent in the birds I examined. From the attachments of the muscles, it appears that movement, if any, of the crest feathers in *Chrysolophus* is stronger in the direction of depression than of erection.

Crest feathers of *Pavo* are implanted perpendicular to the surface of the skin. Depressors and erector muscles are absent. Strong retractor muscles, not arranged into rows, are confined to the outer end of the follicles. This arrangement is not present in any of the other species I examined.

Musculature of the hackles in *Gallus* differs from that of homologous feathers in the dorsal part of the neck in the other representatives by having heavy longitudinal and posterodorsal muscle rows. Retractor muscles, at the neck end, are more developed in these rows than in the anterodorsal rows. They comprise about 24 per cent of the total muscle volume of a feather. A low depressor-erector ratio in *Gallus* suggests that hackles may have either a greater ability for erection or a lower ability for depression than do homologous feathers of *Phasianus*.

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Greatest differences in the feather musculature of the dorsal part of the neck are found in male *Chrysolophus*. *Chrysolophus* differs from the other representatives in having an abrupt transition from the well developed musculature of the cape to the less developed musculature of the rest of the dorsal cervical tract. Anterodorsal and posterodorsal rows are dominant in the mid-region. Posterodorsal muscle rows approach a transverse course medially and become much thicker caudally. Unlike *Gallus*, longitudinal muscle rows are absent except at the lateral borders of the cape. Here they are dominant with the posterodorsal rows. Heavy retractor muscles are found at the neck end of the follicles in the posterodorsal rows and occupy as much as 2/3 of the outer end of the follicle. *M. protractor pennati cervicalis dorsalis* is a smooth tensor muscle arranged in a well developed plexiform sheet. It extends from the outer ends of the lateral-most follicles of the cape to the external ear opening and attaches to a tendon at the angle of the jaw. *M. protractor pennati cervicalis dorsalis* is present only in male and female *Chrysolophus*.

Results from experiments involving transections of *M. protractor pennati cervicalis dorsalis* demonstrate that partial destruction of this muscle drastically affects extension and elevation of the cape during lateral courtship display.

No significant differences are noted in the arrangement and relative development of the feather muscles in the pelvic tract among Phasianus, Chrysolophus or Gallus. However, significant differences are found in Pavo.

The skin of the pelvic tract of Pavo is about 2 centimeters thick, the feathers are unusually large and the feather musculature is heavier than in any other homologous region among the birds I examined. Of significance is the fact that dominant muscle rows course transversely across the tract. Only in Pavo is this feature so distinct. Transverse rows are composed only of retractor muscles which attach to the bulb end of the follicles. It appears that contraction of these muscles may account for the pronounced transverse spreading of the train as seen in courtship display. Depressor-retractor and erector-retractor muscles have their fibers arranged in a pinniform fashion and comprise the anterodorsal and posterodorsal rows. The other gallinaceous birds I examined so not have homologous muscles so well developed. M. tensor pterylae pelvicus is attached to the caudal-most follicles of the train. The presence of this muscle only in Pavo suggests that it may be related to positioning of the train.

I conclude that the striated dermal muscles have little to do with feather displays. They appear to tense the skin in particular regions of the body. Tightening of the skin appears to be coordinated with other body functions. Probable functions of each dermal muscle are discussed; however, no definite conclusions are reached. In general, my conclusions on the actions of the dermal muscles agree with those of Langley (1904).

Whether striated muscle fibers in gallinaceous birds unite with musculoelastic tissue as they do in pigeons (Petry, 1951) requires further investigation.

Finally, this study strongly suggests that modifications of the feather muscles appear to be adaptations for displays in order to make movement of the feathers possible which in turn makes particular regions of the plumage more conspicuous.

Permanently positioned feathers can also be explained by modifications of the feather muscles. Whether or not they have a display function was beyond the scope of this study. However, their movements would seem to depend upon the positioning of the body.

Except for the action of *M. protractor pennati cervicalis dorsalis*, deductions of the functions of the smooth tensor muscles are inconclusive. Also the mechanism responsible for shifting of the plumage of the rump in the lateral courtship display of *Chrysolophus* is not clear. These features require further investigation.

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