# A morphological atlas of the avian uropygial gland

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*Dedicated to PIERCE BRODKORB, whose encouragement, friendship, and scholarship influenced the preparation of this monograph*

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## Introduction

The uropygial gland (also known as the uropygium, preen-, oil-, rump-, tail-, and coccygeal gland; glandula uropygii; the 'eloeodochon' of Coues 1890) is the only compact gland in the avian integument. Lying medially and dorsal to the levator muscles of the tail, this gland is usually bilobed and partly covered by skin and body feathers. It secretes a chemically complex oil through ducts in a papilla which often bears a feather tuft (*circulus uropygialis* of Baumel *et al.* 1979). Most reports and investigations on the gland for at least 150 years have concentrated on specific topics such as histology, morphology, function, chemical nature of secretions, and development.

The earliest published references to the uropygial gland focused almost entirely on function. Emperor Frederick II of Hohenstaufen about 1260 (Wood & Fyfe 1943) in his treatise on falconry gave the view that birds of prey transfer oil from the gland to their talons via the mandibles, the oil presumably being noxious and capable of killing the prey more quickly. Willughby (1678) noted that the 'oyly pap . . . recomposes and places them [feathers] in due order.' The French anatomist Cuvier (1799–1805) provided the first description of the gland's internal anatomy. Burton (1822) considered size as well as function of the gland in *Fregata aquila*. Audubon (1829) discussed the use of the glandular secretion in lubricating the plumage of 'The Bird of Washington' (the Bald Eagle, *Haliaeetus leucocephalus*). From 1832–1836, F.O. Morris and Charles Waterton exchanged acrimonious and unscientific letters in which they debated the functions ('office') of the gland

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mostly in domestic birds, and they even questioned the ability of birds to preen with oil. Macgillivray's (1837) interest in the gland was also largely functional, although he reported an increase in gland size at the time of moulting. Crisp (1860) questioned this report, and found no experimental evidence for such seasonal size change. Hussey (1860), Waterton (1860), and Matthews (1861) continued to be concerned with preening and the use of oil in 'barn-door' fowls.

Although these earlier authors were pre-occupied with the gland's functional attributes, some of their reports contained passing references to gland morphology in various birds (e.g., duck, fowl, dipper, robin). Nitzsch (1840) published the first account to include morphological information for glands in many taxa. He discussed for many groups of birds the gland's presence or absence, tufted vs. naked condition, relative sizes, and shapes. This hallmark publication by Nitzsch was followed by subsequent authors who either copied Nitzsch or provided information on gland morphology in additional species: Crisp (1860, 1862), Owen (1866), Kossmann (1871), Garrod (1874*a, b*), Coues (1890), and Newton (1893–1896). Beddard (1898) then published his renowned classification of birds in which he included some morphological notes on glands in many major taxa. Papers and books by Pycraft (1900, 1910), Lunghetti (e.g., 1906), Granvik (1913), and Paris (e.g., 1913) reported much new information about gland morphology in selected species. Thus, information about gland morphology in different groups and species was scattered among these and other publications through the first part of the 20th century. More recently, Elder (1954), Lucas & Stettenheim (1972), and Jacob & Ziswiler (1982) have provided information on gland morphology in additional taxa. These three publications and Stettenheim (1972) contain a wealth of references to various biological attributes of uropygial glands (histology, functions, and chemistry).

The degree to which any gland attribute can be used in avian taxonomy remains controversial. Early classifications of birds (Nitzsch 1840, Beddard 1898, Paris 1913, Verheyen 1955–1960) often employed gland morphology as diagnostic properties of given taxa, but many more modern schemes (e.g., Hancock & Kushlan 1984) have not. Jacob (e.g., 1978), Jacob & Ziswiler (e.g., 1982), and von Jacob & Hoerschelmann (1985) provide a chemotaxonomic approach in which they relate the qualitative chemical composition of gland secretions to the systematic positions of avian taxa. Their results seem to show qualitative differences at some ordinal, family, and subfamily levels. Perhaps it is too soon to evaluate this approach, i.e. whether it is any more fundamental in avian taxonomy than a scheme employing only gland morphology, as a taxonomic characteristic.

Despite a plethora of publications, to date no one has compiled a single, complete, comprehensive monograph on the gland's morphological variations in all major avian taxa. The present monograph covers, both generally and specifically, the morphology of the gland in all families and subfamilies, a review of the pertinent morphological literature, and corrections of erroneous and incomplete information about glands, much of this perpetuated from author to author over the years without questioning and adequate documentation. This comprehensive survey is deemed necessary prior to an accurate assessment of the function(s) of the gland's secretion and to the possible use of gland morphology as a character in avian systematics.

## Materials and methods

Most birds examined in this study were preserved in alcohol or other fluids in museum collections. For a few species, where such specimens were unavailable, I examined museum study skins but only for rare species that were believed to have tufted glands. Supplementing the museum studies were (1) birds caught in mist-nets, or collected with a shotgun in Florida, (2) road kills in Virginia, England, Ireland, Belize, and Malawi and (3) some freshly-dead birds from zoos (e.g., parrots, toucans, and hornbills). I dissected a gland from one or more species in each family intact from the alcoholic specimen, and freed it from connective and other non-glandular tissues. That gland was then used for the artist's illustrations and studies of feathers. These gland examples currently remain in my collection.

Anatomical nomenclature for the gland's major parts follows that of Baumel *et al.* (1979) as illustrated in Figure 1.

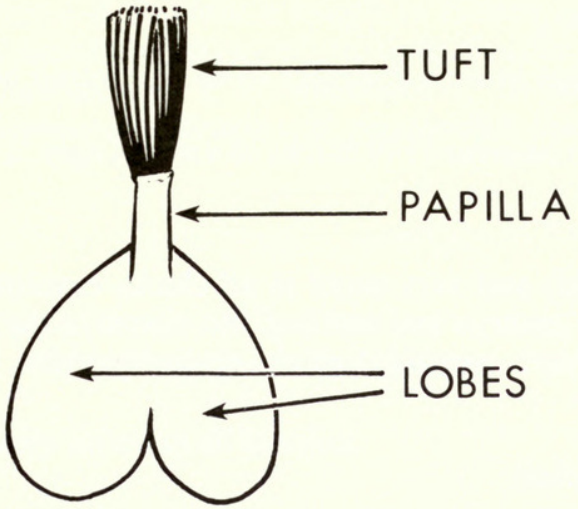



**Fig. 1** External morphological nomenclature of the uropygial gland.

Body and gland weights were taken, for the most part, from freshly killed birds, but some frozen birds (e.g., penguins, ducks, hawks) were thawed, weighed, and their glands dissected free for weighing. Linear dimensions of glands were usually not made. In only a few cases were zoo birds used for weights because I did not know whether the bird might have been emaciated at the time of its death. Glands from fresh birds were never compressed before weighing in order to preserve the gland's oil content at the time of death. The gland tuft, if present, was included in the gland weight, as was any oil in the tuft.

For the microscopic study of gland feathers, two or three feathers were dissected from a gland, cleared in xylene, and mounted in Canada balsam on a microscope slide. Each feather preparation could then be studied under the microscope at magnifications up to 50X. I did not consider gland histology or development (see reviews in Lucas & Stettenheim 1972 and Jacob & Ziswiler 1982) or the number of orifices in the papilla's tip (see Jacob & Ziswiler 1982).

This study resulted in the examination of representative glands from every family and all subfamilies (except one) as identified in Peters (1931–1986). In all, I examined 3011 individuals from 1433 species and 883 genera. The objectives of this examination were to determine for each individual the presence or absence of the gland, its shape, relative size, weight, presence or absence of the papilla and feather tuft. Any individual variations in these characteristics are noted in the systematic accounts to follow.

## Systematic accounts of gland morphology

Classification here follows that of Peters (1931–1986). The terminology for gland morphology (see Fig. 1) has been adapted from Baumel *et al.* (1979). At the end of the Morphology section for each family is the gland feather type (see section on Feathers on glands for definitions). Unless otherwise indicated, all specimens were considered to be adults. Format for the Material examined: for each species, the number of individuals examined; in parentheses, when available, sex, body weight in grams followed by gland weight as a percent of body weight. Z = zoo bird; SK = study skin. Accompanying gland illustrations contain a linear scale that equals 1 cm.

## Order Struthioniformes

**General characteristics.** Absent in adult Ostrich, Rhea, Cassowary, and Emu, but present (naked) in Rhea and Emu chicks. Present (naked or with minute feathers) in Apterygidae.

**Family Struthionidae** (Ostriches)

MORPHOLOGY. Absent in all age groups. Pycraft (1900) also found no glands in any age group of this species.
MATERIAL EXAMINED. *Struthio camelus* 11 (9 chicks of various ages, 2 ad.).

**Family Rheidae** (Rheas)

MORPHOLOGY. Present (naked) and very small in all chicks examined; absent in adult. Pycraft (1900) found the gland in the 'embryo and nestling' but absent in the adult of *Rhea americana*.
MATERIAL EXAMINED. *Rhea americana* 14 (11 chicks up to 4 months, 3 ad.). *Pterocnemia pennata,* 1 ad.

**Family Casuariidae** (Cassowaries)

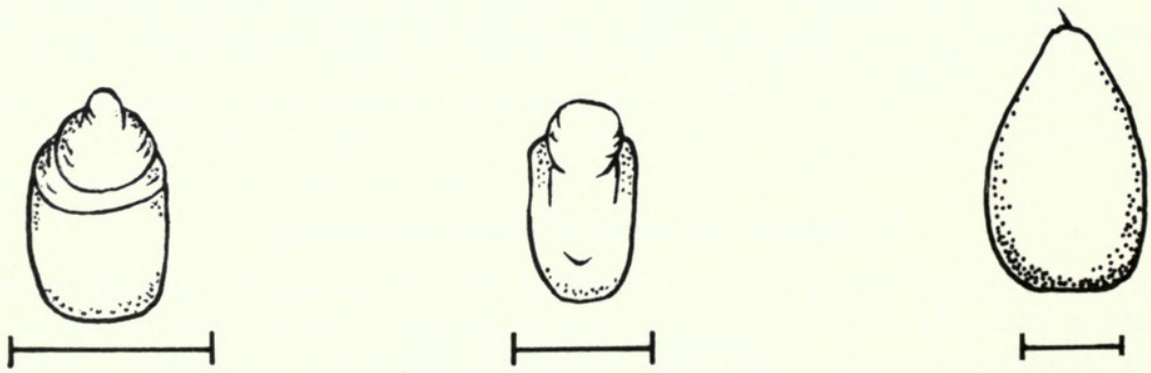
MORPHOLOGY. Absent in all age groups (absent in adult *fide* Pycraft 1900).
MATERIAL EXAMINED. *Casuarius casuarius* 4 (1 chick, 1 immature, 2 ad.).

**Family Dromaiidae** (Emus)

MORPHOLOGY. Present (naked) in all chicks examined; probably absent in adults (first reported by Pycraft 1900).
MATERIAL EXAMINED. *Dromaius novaehollandiae* 13 (chicks up to 2 weeks).

**Family Apterygidae** (Kiwis)

MORPHOLOGY. More terminally located than in any other family, apparently single-lobed, papilla conical, naked (or 1–2 minute 'bristle-like feathers' in *A. australis mantelli fide* Beddard 1898, 1899).
NOTE. Beddard (1898, 1899) was apparently the first to report a gland not only in *Apteryx* but also in any ratite bird. The kiwi gland is clearly different from every nonratite gland examined because of its single-lobed appearance and terminal location. Its presence only in adults distinguishes kiwis from other ratites. The presence of the gland in kiwis supports a suggested affinity between Apterygidae and Tinamidae (see Cracraft 1981).
MATERIAL EXAMINED. *Apteryx australis* 5 (1 chick, 4 ad.); *A. owenii* 1.



*Rhea americana* (chick)

*Dromaius novaehollandiae* (chick)

*Apteryx australis*

## Order Tinamiformes

**General characteristics.** Tufted with long feathers.

**Family Tinamidae** (Tinamous)
MORPHOLOGY. Indistinctly bilobed, papilla small or lacking, tufted. Verheyen (1960*a*) regarded the gland as always present in the family although 'sometimes vestigial.' In *Crypturellus* spp. the four

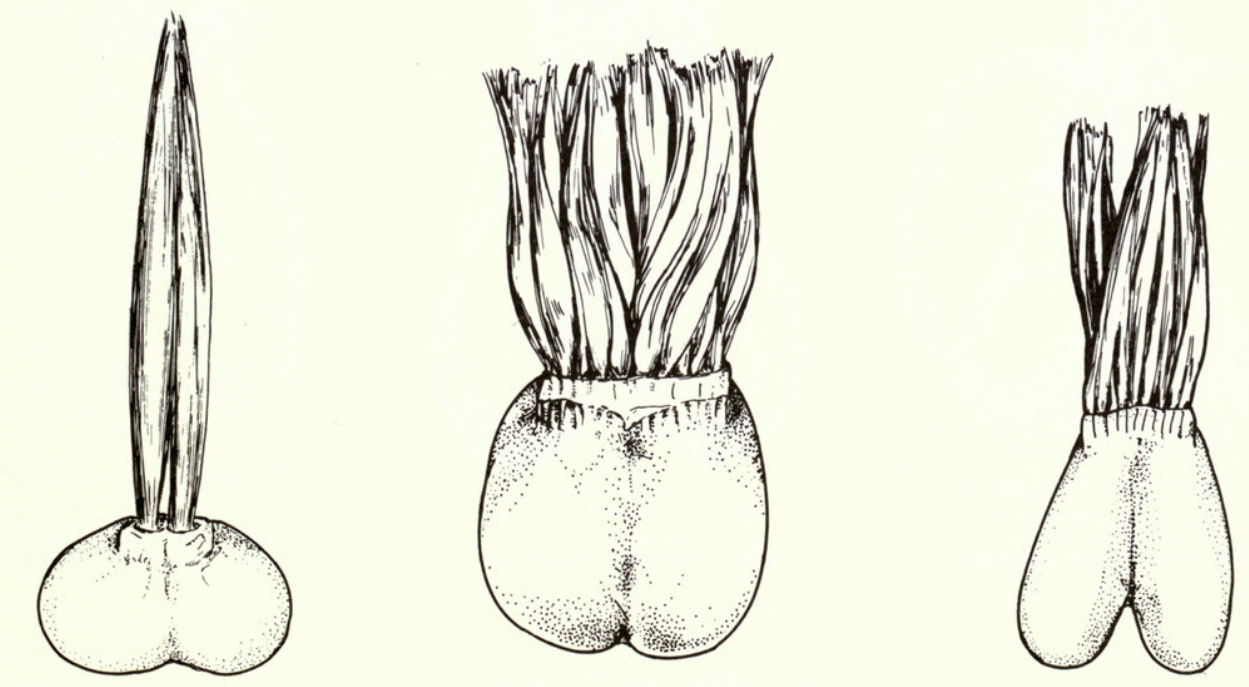
feathers, 2 long and 2 short, are 4–5, 3–4 mm in length; in *Eudromia* spp. the four feathers are 13, 12 mm; shorter (1·5 mm) in *Rhynchotus rufescens* (Jacob & Ziswiler 1982). Type II.
MATERIAL EXAMINED. *Crypturellus soui* 1; *C. undulatus* 1; *C. cinnamomeus* 2; *C. tataupa* 1; *Rhynchotus rufescens* 1; *Nothoprocta perdicaria* 1; *N. pentlandii* 1; *Eudromia elegans* 3; *E. formosa* 1; *Tinamotis pentlandii* 1.

## Order Procellariiformes

**General characteristics.** Densely tufted in all families.

**Family Diomedeidae** (Albatrosses)
MORPHOLOGY. Distinctly bilobed, papilla rounded and slightly raised, tufted (32 feathers in *Diomedea exulans*, Jacob & Ziswiler 1982). Type I.
MATERIAL EXAMINED. *Diomedea exulans* 1; *D. nigripes* 2; *D. immutabilis* 1; *D. melanophrys* 1; *Phoebetria palpebrata* 1.

**Family Procellariidae** (Fulmars, Petrels, Shearwaters)
MORPHOLOGY. Distinctly bilobed, papilla small or lacking, tufted (24–36 feathers, Paris 1913; 36–42 feathers in 2 species, Jacob & Ziswiler 1982). Type I.
MATERIAL EXAMINED. *Macronectes giganteus* 1; *Fulmarus glacialoides* 1; *F. glacialis* 2 (F im.: 642·4, 0·67); *Thalassoica antarctica* 2; *Daption capense* 1; *Pagodroma nivea* 1 (M: 245·0, 0·25); *Pterodroma hasitata* 5 (M: 481·3, 0·36; 364.9, 0·34. F: 459·0, 0·35); *P. hypoleuca* 1; *Halobaena caerulea* 1; *Pachyptila desolata* 1; *Bulweria bulwerii* 1; *Calonectris diomedea* 1 (F:410·0, 0·40); *Puffinus gravis* 7(M: 636·6, 0·44. F: 654·5, 0·39); *P. griseus* 3; *P. puffinus* 1(unsexed: 450·0, 0·53); *P. lherminieri* 2.



*Eudromia elegans* *Diomedea immutabilis* *Puffinus lherminieri*

**Family Hydrobatidae** (Storm Petrels)
MORPHOLOGY. Indistinctly (*Oceanites*) or distinctly (*Oceanodroma*) bilobed, papilla small, tufted (20 feathers in *O. melania*). Type I.

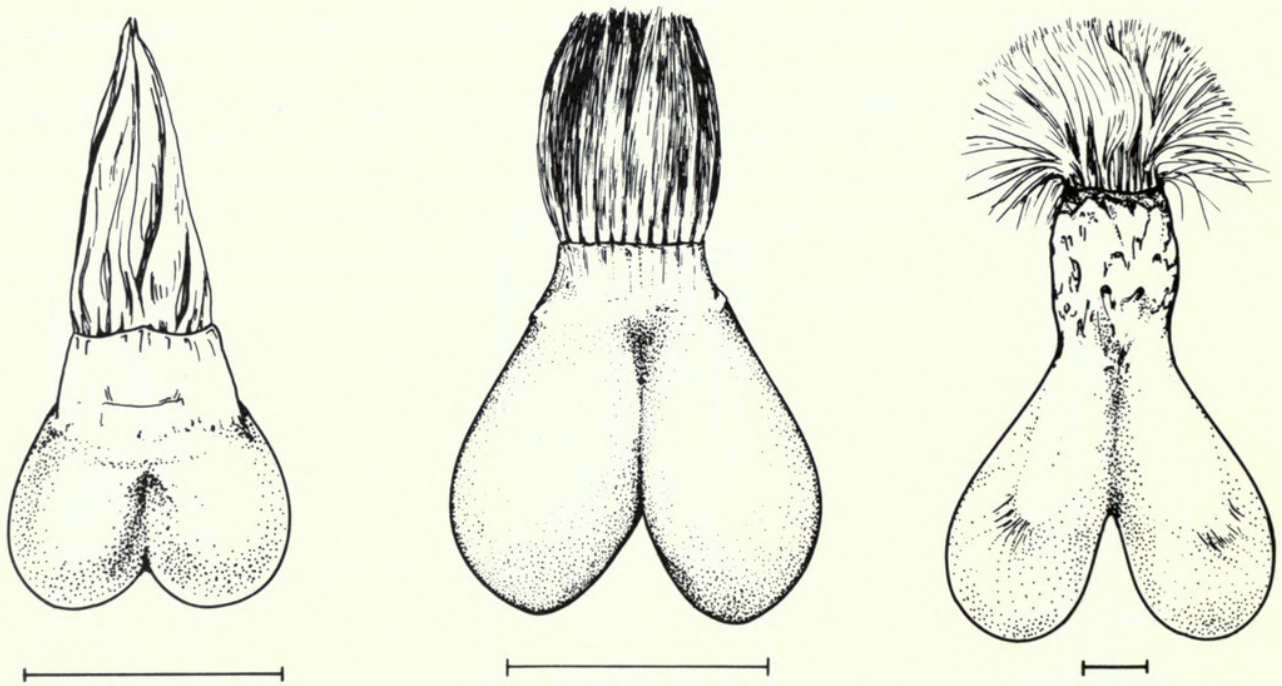
MATERIAL EXAMINED. *Oceanites oceanicus* 5 (M: 35·6, 0·40; 31·1, 0·46. F: 35·0, 0·40; 33·6, 0·38); *Oceanodroma leucorha* 1 (M: 29·5, 0·23); *O. melania* 1 (unsexed: 53·8, 0·69); *O. homochroa* 1 (M: 34·0, 0·31); *O. furcata* 1 (unsexed: 54·4; 0·39).

**Family Pelecanoididae** (Diving Petrels)
MORPHOLOGY. Distinctly bilobed, papilla small, tufted (20 feathers). Type I.
MATERIAL EXAMINED. *Pelecanoides magellani* 1; *P. georgicus* 1; *P. urinator* 1.

## Order Sphenisciformes

**General characteristics.** Densely tufted.

**Family Spheniscidae** (Penguins)
MORPHOLOGY. Distinctly bilobed, flattened and raised papilla, tufted. ('about 50' feathers, Paris 1913; 44–48 feathers in 2 species, Jacob & Ziswiler 1982). Illustrations in Grassé (1950: 286) and Jacob & Ziswiler (1982, Fig. 4a, p. 216) of *Spheniscus demersus,* lacking a feather tuft, are inaccurate, copied from Paris (1913) who illustrated one gland from which the tuft had undoubtedly been removed. Type IIa.
MATERIALS EXAMINED. *Aptenodytes patagonica* 1; *A. forsteri* 1; *Pygoscelis papua* 1; *P. adeliae* 2 (M: 4990, 0·06; 5348, 0·12); *P. antarctica* 1; *Eudyptes crestatus* 1; *E. chrysolophus* 1; *Eudyptula minor* 1; *Spheniscus humboldti* 1.



*Oceanodroma melania* *Pelecanoides magellani* *Aptenodytes forsteri*

## Order Gaviiformes

**General characteristics.** Deeply bilobed, densely tufted.

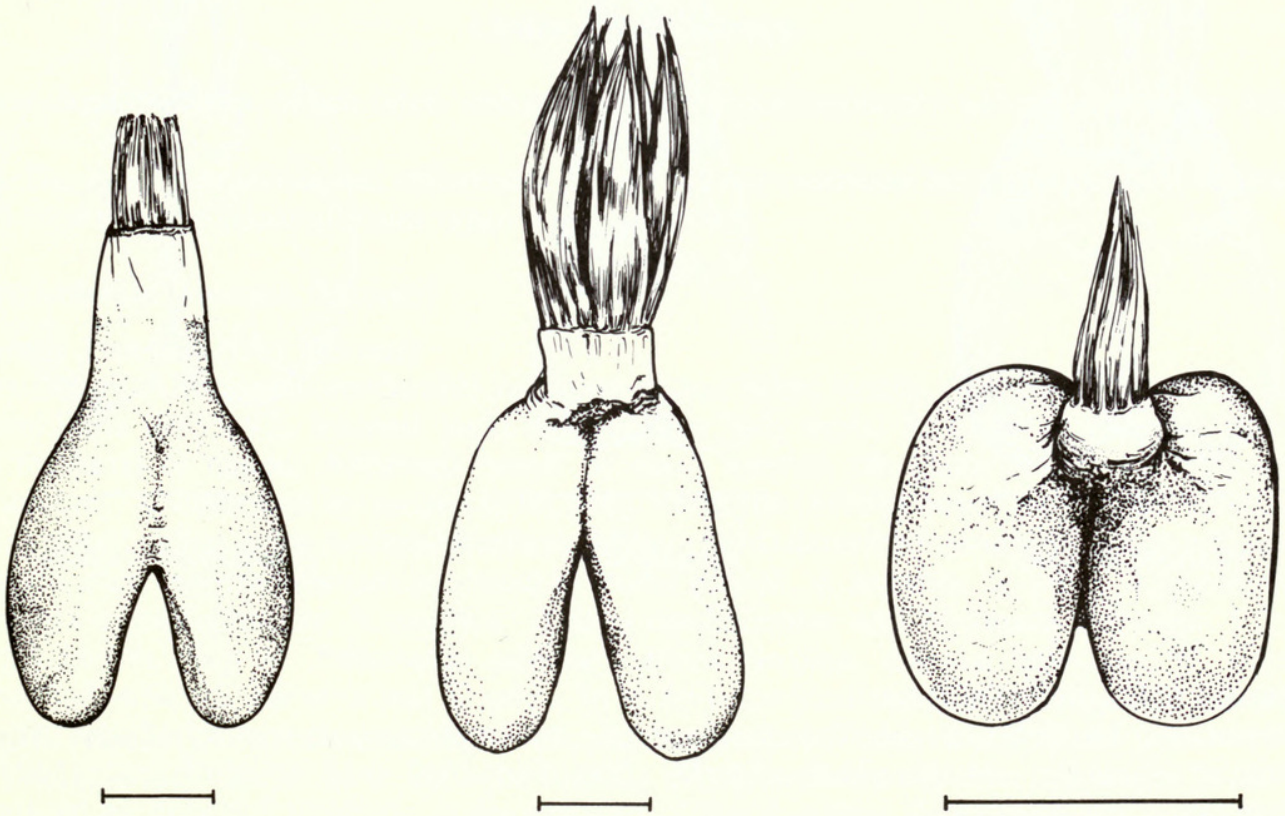
**Family Gaviidae** (Loons)
MORPHOLOGY. Distinctly bilobed and elongated, small papilla, tufted (30–40 feathers, Paris 1913; 26–28 feathers in 2 species, Jacob & Ziswiler 1982). Type I.

MATERIAL EXAMINED. *Gavia stellata* 5 (M: 1597, 0·19; 1638, 0·17. F: 1351, 0·21); *G. arctica* 2 (M: 1598, 0·30. 1 unsexed: 2082, 0·23); *G. immer* 15 (M: 2780, 0.09; 3180, 0·11; 3490, 0·11); *G. adamsii* 1 (unsexed: 4115, 0·19).

## Order Podicipediformes

**General characteristics.** Deeply bilobed, densely tufted.

**Family Podicipedidae** (Grebes)
MORPHOLOGY. Distinctly bilobed and somewhat flattened papilla raised nearly perpendicular to the two lobes, tufted (14–18 subterminal feathers in 2 species, Jacob & Ziswiler 1982). Verheyen (1959*d*) reported the gland as 'voluminous and crowned with long plumes.' Type I.
MATERIAL EXAMINED. *Rollandia rolland* 3; *R. microptera* 1; *Tachybaptus ruficollis* 1; *T. rufolavatus* 1; *T. dominicus* 1; *Podilymbus podiceps* 8 (M: 358·0, 0·42; 380·2, 0·19. F: 312·0, 0·22; 301·2, 0·26); *P. gigas* 1; *Podiceps major* 1; *P. auritus* 3 (M: 410·0, 0·23; 342·7, 0·22); *P. grisegena* 1; *P. nigricollis* 2; *P. occipitalis* 2; *P. taczanowskii* 1; *Aechmophorus occidentalis* 1.



*Spheniscus humboldti* *Gavia immer* *Podiceps auritus*

## Order Pelecaniformes

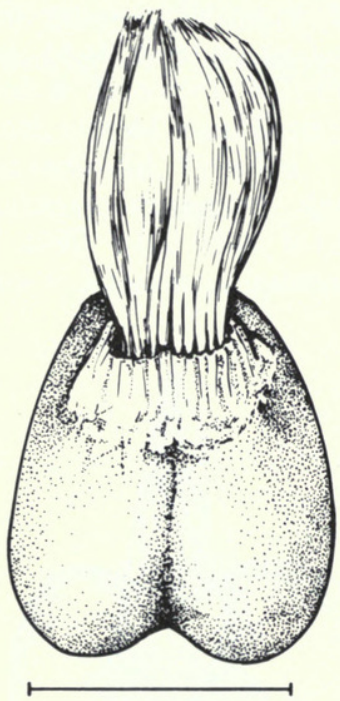
**General characteristics.** Densely tufted.

**Family Phaethontidae** (Tropicbirds)
MORPHOLOGY. Distinctly bilobed, papilla tufted (40 feathers in *P. lepturus*). Verheyen (1960*b*) stated (p. 12) that the gland 'lacks a nipple except in Phaethon.' Type I.
MATERIAL EXAMINED. *Phaethon aethereus* 1 (F: 496·0, 0·43); *P. rubricauda* 1; *P. lepturus* 3.

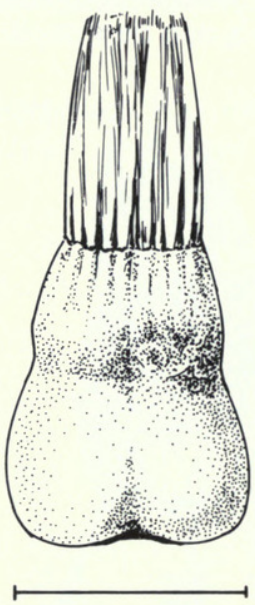
**Family Fregatidae** (Frigatebirds)
MORPHOLOGY. Indistinctly bilobed, papilla broad and flattened, tufted (ca 30 feathers in *F. magnificens*). Type I.
MATERIAL EXAMINED. *Fregata magnificens* 4 (M: 1365·5, 0·07; 1336, 0·07. F: 1512, 0·06); *F. aquila* 1; *F. minor* 1; *F. ariel* 1.

**Family Phalacrocoracidae**

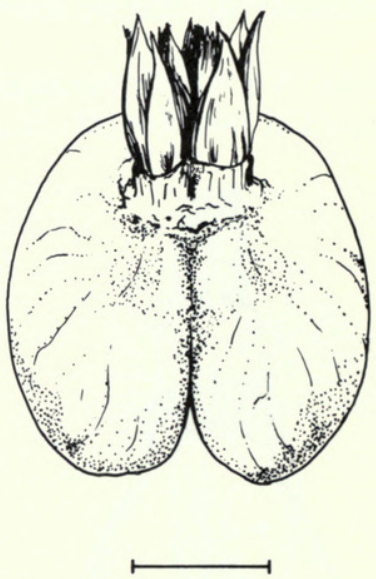
**Subfamily Phalacrocoracinae** (Cormorants)
MORPHOLOGY. Distinctly bilobed, papilla moderately developed, tufted (36–52 feathers in 2 species, Jacob & Ziswiler 1982). Papilla and feather tuft subterminal. Type I.
MATERIAL EXAMINED. *Phalacrocorax harrisi* 1; *P. auritus* 24 (M: 1660, 0·25; 1710, 0·25. $\bar{x}$ of 8F: 1048, 0·25); *P. aristotelis* 1; *P. magellanicus* 1; *P. bougainvillii* 1; *P. albiventer* 1.



*Phaethon lepturus*



*Fregata ariel*

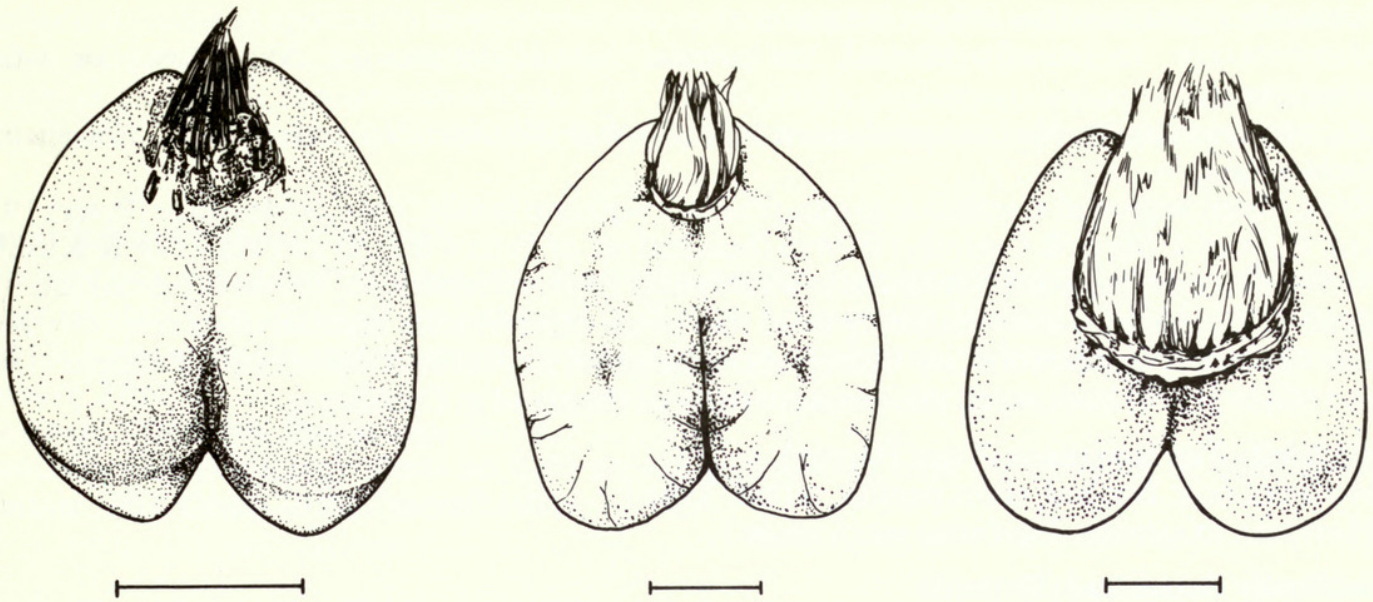


*Phalacrocorax auritus*

**Subfamily Anhinginae** (Darters)
MORPHOLOGY. Bilobed and somewhat flattened, papilla absent, short tuft of 14 feathers. Type I.
MATERIAL EXAMINED. *Anhinga anhinga* 11 (M: 1230, 0·16; 1352, 0·12; 1230, 0·16. F: 1307, 0·15; 1178, 0·17); *A. melanogaster* 2.

**Family Sulidae** (Boobies, Gannets)
MORPHOLOGY. Distinctly flattened and bilobed, papilla absent, tufted with 70 short feathers in *S. bassana* (Jacob & Ziswiler 1982). Type I.
MATERIAL EXAMINED. *Sula bassana* 3 (M subad.: 2200, 0·38; *S. dactylatra* 2; *S. sula* 1.

**Family Pelecanidae** (Pelicans)
MORPHOLOGY. Large and bilobed, papilla very short and broad, tufted (70 feathers, Paris 1913; 66 feathers in *P. onocrotalus*, Jacob & Ziswiler 1982). Tuft and openings obviously subterminal, Type I.
MATERIAL EXAMINED. *Pelecanus onocrotalus* 1; *P. philippensis* 1; *P. erythrorhynchos* 2 (M: 4700, 0·30; *P. occidentalis* 9 (M im.: 2730, 0·43; 3060, 0·32; unsexed ad.: 3320, 0·37).



*Anhinga anhinga* *Sula bassana* *Pelecanus onocrotalus*

## Order Ciconiiformes

**General characteristics.** Much inter- and some intrafamilial variation: naked, sparsely or densely tufted.

NOTE. The large morphological differences among glands examined here lend support to Olson's (1979) view that the Ciconiiformes is not a natural order.

**Family Ardeidae** (Herons, Bitterns)

**Subfamily Ardeinae** (Day Herons)

MORPHOLOGY. Although considerable variation occurs in the family, the gland is generally small (see also Paris 1913: 192), bilobed, lacks a papilla (or 'very short,' Paris 1913: 192), and is tufted (4–18 feathers) or naked. Although 'small' in many species, the gland cannot be regarded as 'rudimentary' as described by Jacob (1978: 168). Verheyen (1959*b*) noted that in the Ardeae, the gland is naked or has a few vestigial feathers. Miller (1924) described variations in the tuft among 13 species, then reported the tuft as absent in *Ardea goliath, A. herodias, A. cocoi, A. occidentalis, Notophoyx novaehollandiae, N. pacifica, Egretta candidissima,* and *Hydranassa tricolor.* I found the tuft absent only in *Pilherodias pileatus, Ardea pacifica, Egretta rufescens, E. tricolor, E. novaehollandiae, E. garzetta* and *E. sacra.* In *A. herodias* (contra Miller 1924), all 10 specimens examined here had extremely small feathers, often as few as 4. Beddard (1898) and Gadow (1893) reported that all Ardeidae have feathered glands. Thus in the family, the tuft might be absent, represented by only 4–8 feathers (*Ardea herodias, Agamia agami*), or tufted with 16–18 feathers (*Ixobrychus minutus fide* Jacob & Ziswiler 1982). Type I.

MATERIAL EXAMINED. *Pilherodias pileatus* 1*; *Ardea cinerea* 1; *A. herodias* 10 (M: 2695·0, 0·21; 1281·0, 0·05; 1790, 0·14. F: 1250·0, 0.17; 1507, 0·10); *A. pacifica* 1*; *A. melanocephala* 1; *A. purpurea* 1; *A. alba* 8 (M: 478·5, 0·15; 579·0, 0·12); *Egretta rufescens* 1*; *E. tricolor* *; *E. ibis* 11 (M: 342·6, 0·03. $\bar{x}$ of 5F: 286·8, 0·04); *E. novaehollandiae* 1*; *E. caerulea* 3 (F: 372·0, 0·07); *E. garzetta* 1*; *E. sacra* 1*; *Ardeola speciosa* 1; *A. striata* 7 (M: 220·3, 0·07; 220·1, 0·07; 195·4, 0·06); *Agamia agami* 2.

NOTE. Ligon (1967: 1) believed 'that the storks and herons are dissimilar' in many features (osteology, myology, pterylography and others); the dissimilar uropygial glands of the two groups add another difference.

*naked gland, present study.

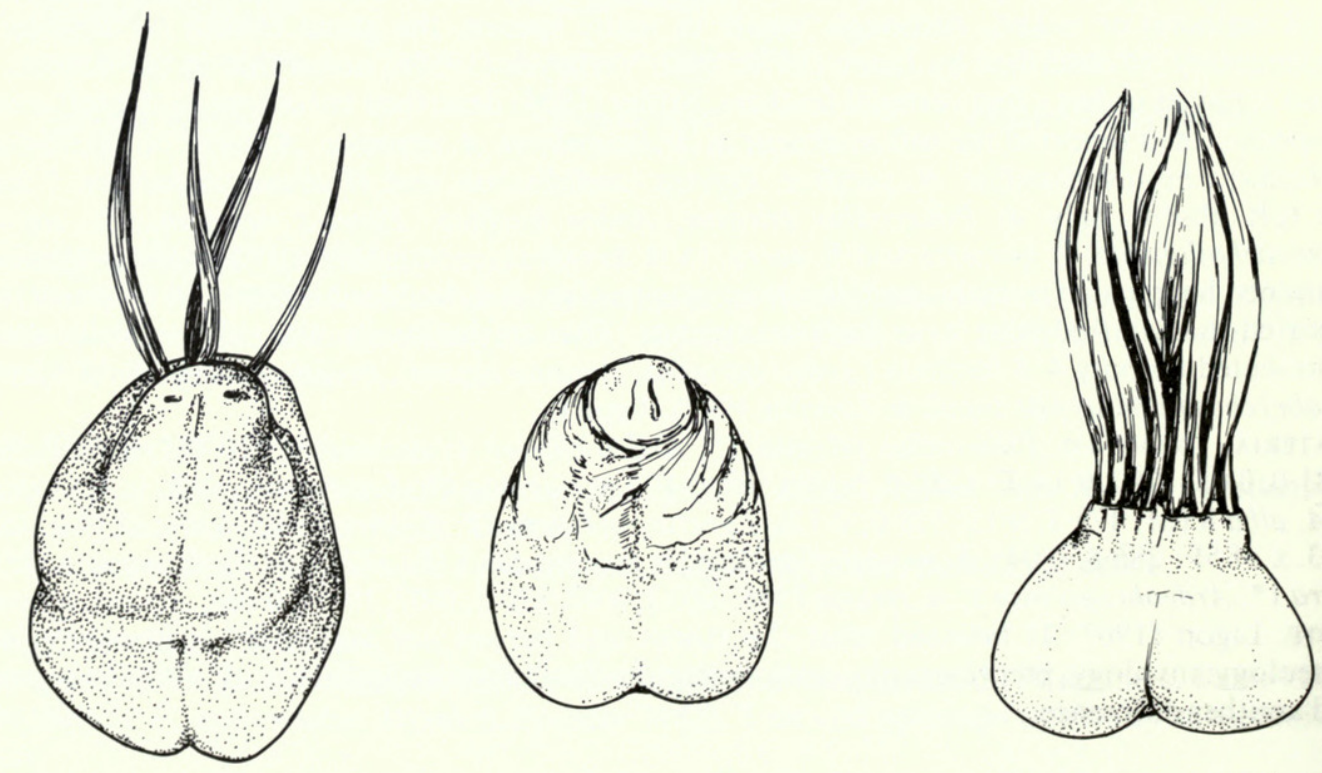
**Subfamily Nycticoracinae** (Night Herons)
MORPHOLOGY. Indistinctly bilobed, no papilla, tufted (*Nycticorax, Nyctanassa*) or naked (*Cochlearis*).
MATERIAL EXAMINED. *Nyctanassa violacea* 5 (M: 546·0, 0·04); *Nycticorax nycticorax* 2; *Cochlearius cochlearius* 2.
NOTE. Peters regarded *Cochlearis* as comprising a separate family, the Cochlearidae (Peters 1931, Vol. I, 1st ed.). Mayr & Cottrell, (1974 in their 2nd ed. of Peters' Vol. I) and Hancock & Kushlan (1984), however, included *Cochlearis* in a subfamily (Nycticoracinae) of the family Ardeidae. The gland of *Cochlearis* differs markedly from that of all other ardeids because of its relatively large size, distinctive appearance (see figure), and absence of papilla and feather tuft. Beddard (1898) and Miller (1924) both noted this distinctiveness of the gland in *Cochlearis*.

**Subfamily Tigrisomatinae** (Tiger Herons)
MORPHOLOGY. Bilobed, short papilla, tufted. Type I.
MATERIAL EXAMINED. *Tigrisoma mexicanum* 1.

**Subfamily Botaurinae** (Bitterns)
MORPHOLOGY. Indistinctly bilobed, no papilla, small tuft. Type I.
MATERIAL EXAMINED. *Ixobrychus exilis* 2 (M: 68·0, 0·05. F: 38·6, 0·03); *Botaurus lentiginosus* 5 (M: 564·0, 0·31; 789·0, 0·42; 720·0, 0·38. F: 599·3, 0·38).

**Family Scopidae** (Hammerhead)
MORPHOLOGY. Indistinctly bilobed, papilla short and somewhat flattened, and tufted (18 long feathers). The gland of this species is distinct from those of ardeids, more closely resembling that of *Balaeniceps* and the Ciconiidae (see figures). Type I.
MATERIAL EXAMINED. *Scopus umbretta* 2.

**Family Ciconiidae** (Storks)
MORPHOLOGY. Distinctly bilobed and large, papilla small, tufted (36 feathers in *C. ciconia*, Jacob & Ziswiler 1982). Unlike the illustration of *Mycteria* here, in *Anastomas, Ciconia nigra*, and



*Ardea herodias* *Cochlearius cochlearius* *Scopus umbretta*

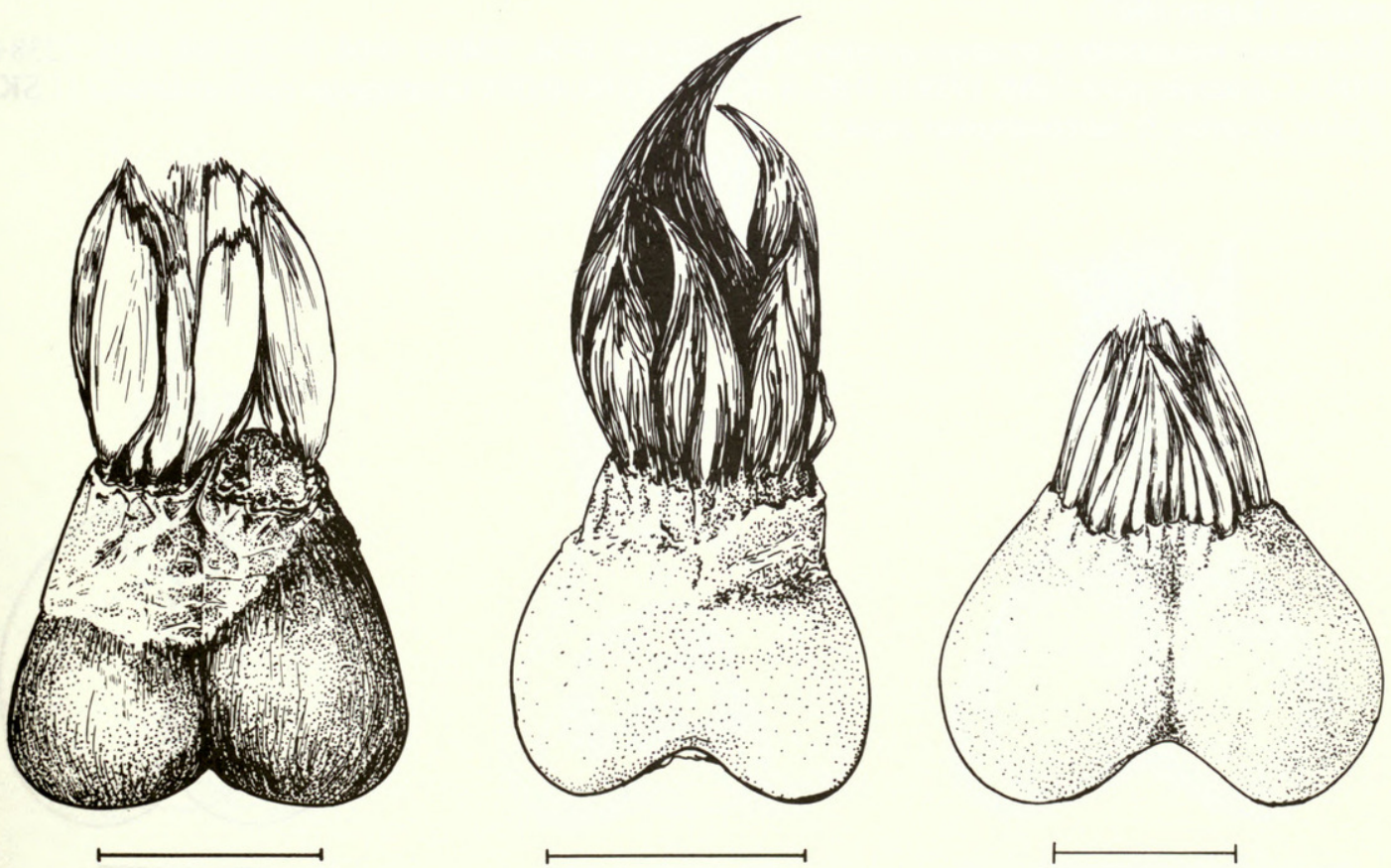
*Leptoptilos* the gland appears to be separated into right and left portions, each with a separate lobe, feather tufts and orifices, features implied by Nitzsch (1867: 131). Type I.
MATERIAL EXAMINED. *Mycteria americana* 3 (F: 2490·0, 0·05); *Anastomus oscitans* 1; *Ciconia nigra* 1; *C. abdimii* 1; *C. episcopus* 1; *C. ciconia* 1; *Ephippiorhynchus asiaticus* 1; *Leptoptilos crumeniferus* 1.

**Family Balaenicipitidae** (Shoebill)
MORPHOLOGY. Indistinctly bilobed and relatively small (see figure and Bartlett 1861), papilla small, tufted. With the exception of the large tuft in *Scopus*, I agree with Miller's (1924: 322) comment that 'in *Balaeniceps* the tuft is very much larger than in any heron,' although I did not count the feathers. Type II.
MATERIAL EXAMINED. *Balaeniceps rex* 1Z.
NOTE. Gland morphology sheds no light on the controversy over the affinities of *Balaeniceps* (Cottam 1957, Olson 1979, Cracraft 1981).

**Family Threskiornithidae** (Ibises, Spoonbills)

**Subfamily Threskiornithinae** (Ibises)
MORPHOLOGY (family). Distinctly bilobed, papilla absent, tufted (26–28 feathers, Paris 1913; 30 feathers in *E. ruber*, Jacob & Ziswiler 1982). Nitzsch (1867) implied that ibises have glands 'divided in half.' In the present study one specimen each of *Eudocimus albus* and *Platalea leucorodia* had glands with nearly separate lobes, separate orifices, and separate feather tufts. Type I.
MATERIAL EXAMINED. *Eudocimus albus 2 (M, Z: 999, 0·12); E. ruber* 2; *Plegadis falcinellus* 3 (M: 530·0, 0·18; F: 420.0, 0·19); *Threskiornis aethiopicus* 2.

**Subfamily Plataleinae** (Spoonbills)
MATERIAL EXAMINED. *Platalea leucorodia* 1; *P. ajaja* 1 (M: 985·0, 0·11).



*Mycteria americana* *Balaeniceps rex* *Threskiornis aethiopicus*

## Order Phoenicopteriformes

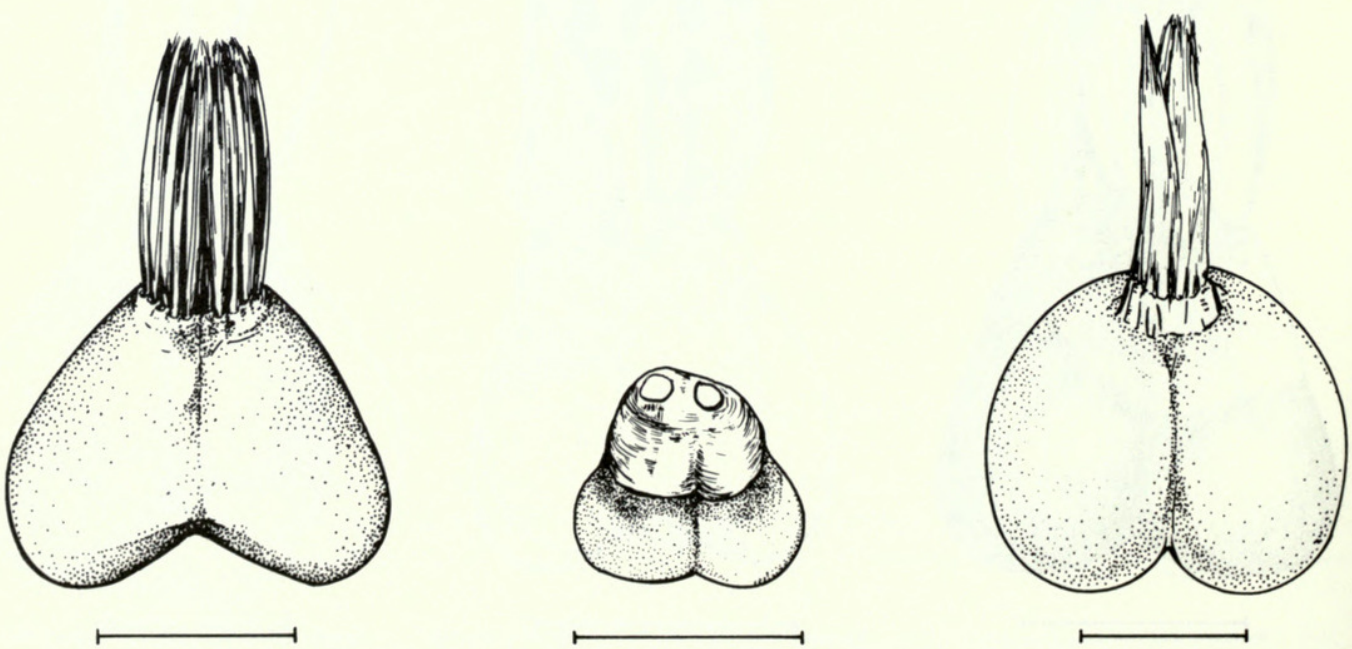
**General characteristics.** Densely tufted.

**Family Phoenicopteridae** (Flamingos)
MORPHOLOGY. Bilobed, papilla absent, tufted (30 feathers, Paris 1913). Type IIa.
NOTE. Paris (1913: 190) believed that the gland of *Phoenicopterus roseus* closely resembles that of the Anseriformes. In contrast, I found marked differences in the gland of *Phoenicoparrus* from both the Anseriformes and Ciconiiformes (see figures), relationships suggested by Sibley (1967), and Sibley *et al.* (1969). The gland resembles that of the Recurvirostridae, suggesting a charadriiform relationship as proposed by Olson & Feduccia (1980*b*).
MATERIAL EXAMINED. *Phoenicopterus ruber* 1; *Phoeniconaias minor* 2; *Phoenicoparrus andinus* 1; *P. jamesi* 1.

## Order Falconiformes

**General characteristics.** Inter- and some intrafamilial variation: naked or sparsely to densely tufted.

**Family Cathartidae** (American Vultures)
MORPHOLOGY. Indistinctly bilobed, round papilla, naked; two separate, distinct orifices. Nitzsch's (1867) report that 'vultures of the New World' have a short circlet of feathers at the gland apex appears to be in error. I did not confirm Fisher's (1943) statement that down is often present on the oil gland in *Coragyps atratus*.
NOTE. My findings support Ligon's (1967: 1) view 'that the Cathartidae are not at all closely related to the remainder of the Falconiformes.' The naked glands of the Cathartidae, however, differ markedly from the heavily tufted glands of the Ciconiidae, to which cathartids might otherwise be related (Ligon 1967).
MATERIAL EXAMINED. *Coragyps atratus* 5 (M: 2221·0, 0·04; 2245·0, 0·04. F: 2135·0, 0·05; 2238·0, 0·04); *Cathartes aura* 7 (M: 1939·0, 0·02. $\bar{x}$ of 5F: 2019·0, 0·02); *Gymnogyps californianus* 2 (1 SK); *Vultur gryphus* 2; *Sarcoramphus papa* 2.



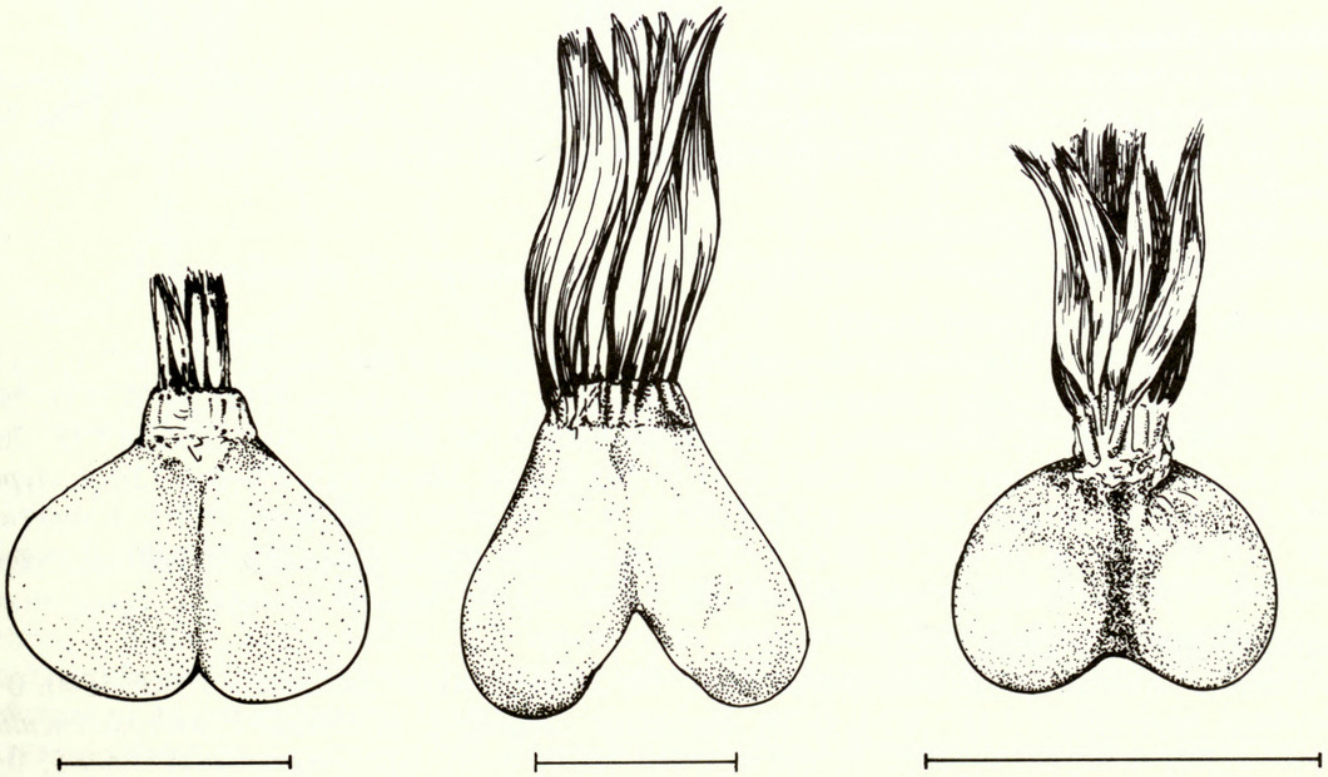
*Phoenicoparrus jamesi* *Cathartes aura* *Pandion haliaetus*

**Family Accipitridae**

**Subfamily Pandioninae** (Osprey)
MORPHOLOGY. Large and distinctly bilobed, indistinct papilla, tufted (18 feathers, Jacob & Ziswiler 1982). Type I.
NOTE. Sometimes included in a separate family, Pandionidae (Cracraft 1981), the Osprey's gland differs from those of the Accipitrinae by being much heavier and having a longer, usually denser feather tuft.
MATERIAL EXAMINED. *Pandion haliaetus* 5 (M: 1433·0, 0·28; 1363·0, 0·31. F: 1500·0, 0·32).

**Subfamily Accipitrinae** (Hawks, Eagles)
MORPHOLOGY. Bilobed, papilla moderately developed, sparsely (*Ictinia*) to densely (*Haliaeetus*) tufted (12–20 feathers in 7 species, Jacob & Ziswiler 1982). Type 1.
MATERIAL EXAMINED. *Aviceda leuphotes* 1; *Elanoides forficatus* 2 (M: 492·0, 0·13); *Harpagus bidentatus* 1; *Ictinia plumbea* 1; *I. mississippiensis* 1; *Haliaeetus leucocephalus* 3 (ad. sex?: 3625, 0·07); *Neophron percnopterus* 2; *Gyps fulvus* 1; *Circus hudsonius* 2 (F: 324·6, 0·03); *Melierax canorus* 1; *Accipiter nisus* 1; *A. striatus* 10 (subad. M: 84·2, 0·05; 98·0, 0·04; 88·9, 0·06. $\bar{x}$ of 4 ad. F: 157·3, 0·06); *A. cooperii* 4 (ad. F: 411·7, 0·07; 390·0, 0·07); *A. gentilis* 4 (subad. M: 816·0, 0·06; 775·0, 0·05; 918·0, 0·07. Ad. F: 930·0, 0·03); *Geranospiza caerulescens* 1; *Buteo lineatus* 9 (ad. M: 612·3, 0·05; 595·7, 0·06. Ad. F: 601·0, 0·05; 566·7, 0·07); *B. platypterus* 2 (subad. M: 489·4, 0·04; 309·0, 0·05); *B. swainsoni* 1 (ad. M: 874·0, 0·04); *B. jamaicensis* 14 (ad. M: 1307·3, 0·04. Subad. M: 856·3, 0·06. Subad. F: 1210·0, 0·04; 1272·0, 0·08); *B. lagopus* 3 (ad. M: 860·0, 0·04); *Pithecophaga jefferyi* 1; *Aquila chrysaetos* 1.

**Family Sagittariidae** (Secretarybird)
MORPHOLOGY. Distinctly bilobed, papilla moderately developed, tufted (20 feathers). In most specimens the gland appears to be nearly separated into two distinct lobes, with separate papillae and feather tufts. Although writing about 'Les Cariamiformes,' Verheyen (1957*c*) stated erroneously that the gland is absent in *Sagittarius*. Type I.
MATERIAL EXAMINED. *Sagittarius serpentarius* 6.



*Buteo jamaicensis* *Sagittarius serpentarius* *Falco columbarius*

**Family Falconidae**

**Subfamily Polyborinae** (Caracaras)
MORPHOLOGY. Distinctly bilobed, papilla moderately developed, densely tufted.
MATERIAL EXAMINED. *Daptrius ater* 1; *Polyborus plancus* 2 (unsexed im.: 900·5, 0·07).

**Subfamily Falconinae** (Falcons)
MORPHOLOGY. Distinctly bilobed, papilla moderately to well developed, tufted (17 feathers in *Falco tinnunculus,* Jacob & Ziswiler 1982), or rarely, naked. Both Miller (1924) and Verheyen (1959*c*) reported naked glands in *Microhierax fringillarius* and Nitzsch (1867) noted naked glands in two specimens of *M. caerulescens*. In my study all glands of 11 individuals of four species of *Microhierax* were naked, but all other genera and species in this subfamily had tufted glands. Type I.
MATERIAL EXAMINED. *Micrastur ruficollis* 1: *Spiziapteryx circumcinctus* 1; *Polihierax semitorquatus* 1; *P. insignis* 4; *Microhierax* (mostly SK) *caerulescens* 7; *M. fringillarius* 2; *M. erythrogenys* 1; *M. melanoleucus* 1; *Falco sparverius* 16 ($\bar{x}$ of 6 M: 100·3, 0·05. $\bar{x}$ of 6 F: 119·2, 0·08); *F. tinnunculus* 1; *F. columbarius* 2 (F: 191.0, 0·09); *F. mexicanus* 1; *F. rufigularis* 1; *F. rusticolus* 1; *F. peregrinus* 3 (M: 617·0, 0·08).

## Order Anseriformes

**Gland characteristics.** Densely tufted.
MORPHOLOGY (order). Large and distinctly bilobed, papilla moderately developed, tufted (22–90 feathers in 15 species, Jacob & Ziswiler 1982). The Anhimidae differ from the Anatidae only by having a gland that is less distinctly bilobed. Type I.

**Family Anatidae**

**Subfamily Anseranatinae** (Pied Geese)
MATERIAL EXAMINED. *Anseranas semipalmata,* 1.

**Subfamily Dendrocygninae** (Whistling Ducks)
MATERIAL EXAMINED. *Dendrocygna bicolor* 1.

**Subfamily Anserinae** (Swans, Geese)
MATERIAL EXAMINED. *Cygnus olor* 1 (im. M: 10435, 0·16); *C. columbianus* 1; *Coscoroba coscoroba* 1; *Anser albifrons* 1 (F: 2556, 0·11); *A. caerulescens* 2 (M: 2330, 0·13; 2154, 0·12); *A. rossii* 1 (M: 1616, 0·15); *A. canagicus* 1 (M: 1855, 0·10); *Branta canadensis* 2 (M: 2435, 0·11. F: 3929, 0·15); *Cereopsis novaehollandiae* 1.
**Subfamily Tadorninae** (Shelducks)
MATERIAL EXAMINED. *Alopochen aegyptica* 1; *Tachyeres pteneres* 1; *T. patachonicus* 1.

**Subfamily Anatinae** (Typical Ducks)
MATERIAL EXAMINED. *Rhodonessa caryophyllacea* 1; *Aix sponsa* 3 (M: 642·0, 0·26; 573·1, 0·32. F: 595·2, 0·32); *A. galericulata* 1; *Anas strepera* 1 (M: 849·5, 0·20); *A. crecca* 3 (M: 251·0, 0·31; 295·5, 0·27. F: 262·0, 0·29); *A. aucklandica* 1; *A. platyrhynchos* 2 (M: 880·0, 0·23); *A. acuta* 1 (F: 708·5, 0·26); *A. discors* 8 (M: 341·5, 0·40; 368·2, 0·33. F: 365·5, 0·36; 384·0, 0·35; 430·0, 0·32); *A. clypeata* 2 (M: 672·0, 0·27); *Aythya valisineria* 3 (M: 893·3, 0·27. F: 792·0, 0·30; 884·2, 0·24); *A. americana* 2 (F: 1172·0, 0·28); *A. collaris* 11 ($\bar{x}$ of 8 M: 749·6, 0·32. F: 697·5, 0·31; 745·0, 0·30); *A. marila* 2 (F: 843·0, 0·22; 991·6, 0·20); *A. affinis* 2 (M: 882·8, 0.22. F: 783·4, 0·22).

**Subfamily Merginae** (Sea Ducks)
MATERIAL EXAMINED. *Somateria mollissima* 1 (M: 2255, 0·18); *S. spectabilis* 1 (M: 1540, 0·26); *Melanitta perspicillata* 1 (F: 703·1, 0·20); *Bucephala clangula* 1; *B. albeola* 1; *Mergus cucullatus* 5 (M: 571·0, 0·34; 671·0, 0·37. F: 671·3, 0·30; 526·0, 0·28); *M. serrator* 1 (F: 599·5, 0·36); *M. merganser* 2 (M: 1577, 0·21. F: 1027, 0·29); *M. australis* 1.

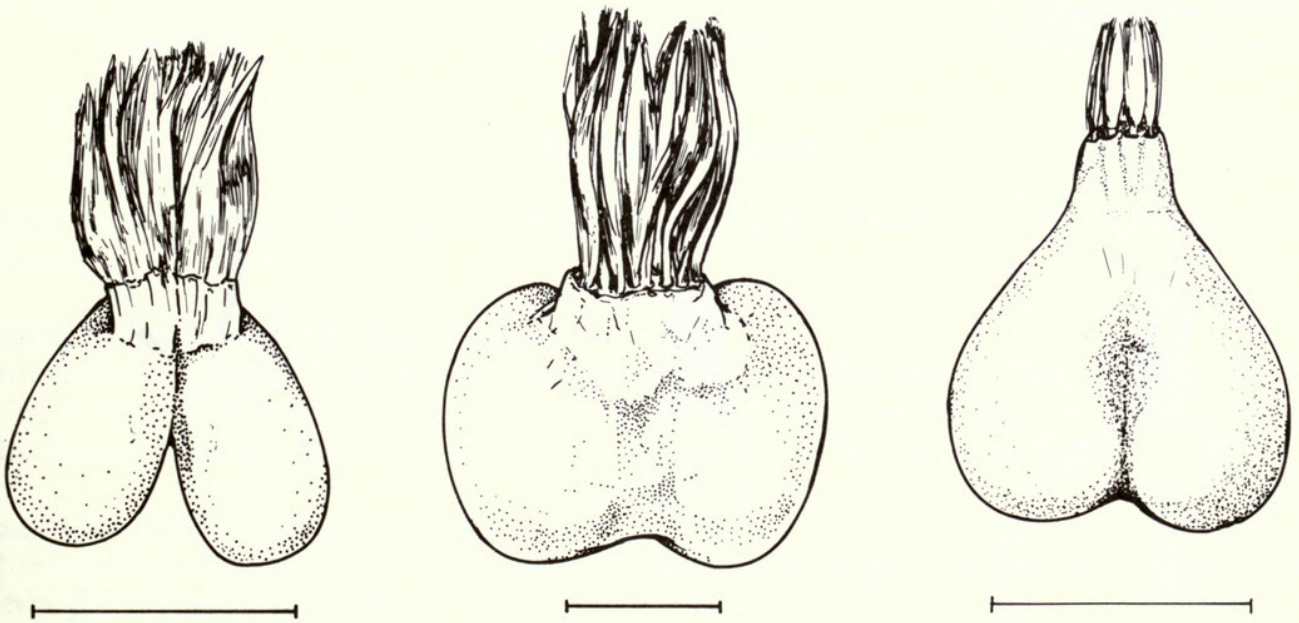
**Subfamily Oxyurinae** (Stifftailed Ducks)
MATERIAL EXAMINED. *Oxyura jamaicensis* 2 (M: 596·7, 0·27).

**Family Anhimidae** (Screamers)
MATERIAL EXAMINED. *Anhima cornuta* 1 (M, Z: 2600, 0·13); *Chauna chavaria* 1.

## Order Galliformes

**Gland characteristics.** Inter- and intrafamilial variation: sparsely to densely tufted, or, rarely, naked.
NOTE. Glands of most galliform families do not resemble those of the Anseriformes. These differences do not support an anseriform-galliform relationship (see also Olson & Feduccia 1980*a*). I did not confirm Pettingill's (1985) statement that 'certain species' of Galliformes lack a gland.

**Family Megapodiidae** (Megapodes)
MORPHOLOGY. Bilobed, papilla large, naked or tufted (6 feathers). The present study and the reports of Miller (1924) and Clark (1964) demonstrate naked glands in *Leipoa, Alectura, Tallegalla jobiensis,* and *Aepypodius arfakianus,* whereas tufted glands are known from five species of *Megapodius* and *Macrocephalon maleo.* Beddard (1898: 302) reported that megapodes have 'oil gland nude,' and both Sharpe and Ogilvie-Grant regarded the glands of these birds as nude (*fide* Miller 1924). Type I.
MATERIAL EXAMINED. *Megapodius nicobariensis* 2; *M. freycinet* 3; *M. pritchardii* 6; *Alectura lathami* 1; *Aepypodius arfakianus* 1.



*Anas discors* *Anhima cornuta* *Megapodius pritchardii*

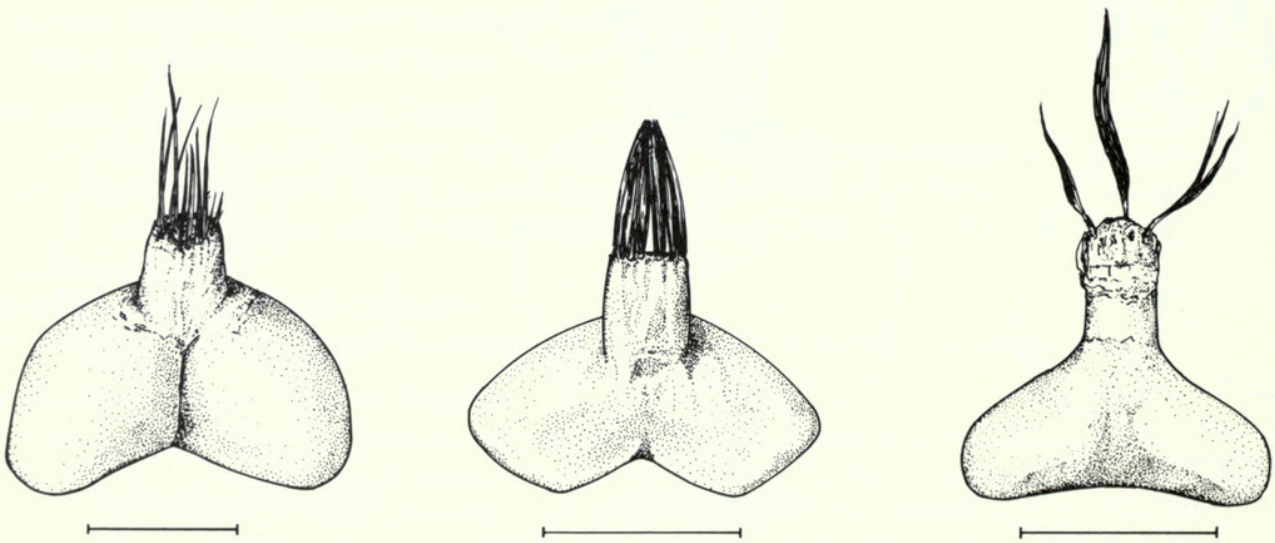
**Family Cracidae** (Curassows, Guans, Chachalacas)
MORPHOLOGY. Distinctly bilobed, papilla large, tuft usually short and sparsely feathered (6–12 feathers, 2–4 mm). Miller (1924: 322) reported an 'apparently bare' gland in one specimen of *Ortalis vetula,* and noted a 'virtually vestigial' tuft in all the Cracidae, this last conclusive statement confirmed in the present study. Type I.
MATERIAL EXAMINED. *Crax nigra* 1; *C. alberti* 1; *C. globulosa* 1; *Penelope jacu-caca* 1; *Ortalis guttata* 2; *O. vetula* 1; *Pipile pipile* 1.

**Family Tetraonidae** (Grouse, Ptarmigans)
MORPHOLOGY. Distinctly bilobed, papilla large, tufted (10–12 feathers, Jacob & Ziswiler 1982). Type I.
MATERIAL EXAMINED. *Tetrao urogallus* 2; *Lyrurus tetrix* 1; *Lagopus lagopus* 1 (M: 576·0, 0·18); *Canachites canadensis* 1 (M: 552·4, 0·02); *Bonasa umbellus* 3 (M: 552·2, 0·03. F: 591·5, 0·03); *Pedioecetes phasianellus* 1 (F: 664·0, 0·03); *Tympanuchus cupido* 1 (M: 863·5, 0·02); *Centrocercus urophasianus* 1 (M: 2221·7, 0·04).

**Family Phasianidae** (Quails, Pheasants, Peacocks)
MORPHOLOGY (family). Usually distinctly bilobed, papilla large, tuft variable (6–12 feathers, Paris 1913; 5–10 feathers in 6 species, Jacob & Ziswiler 1982; only 2 in *Rollulus*) or, rarely, absent (one specimen of *Crossoptilon mantchuricum* was naked as were five specimens of *Argusianus*). Earlier, Nitzsch (1840), Newton (1893–1896), Beddard (1898), Grassé (1950), and Verheyen (1956*d*) had reported the absence of a gland in *Argusianus* (= *Argus*). Beddard (1898) found a tuft in one specimen of *Callipepla squamata* but a naked gland in another specimen. Type I.

**Subfamily Odontophorinae** (American quail)
MATERIAL EXAMINED. *Callipepla squamata* 2 (F: 209·4, 0·06); *Lophortyx californica* 3 (M: 133·2, 0·09. F: 169·4, 0·08); *Colinus virginianus* 9 ($\bar{x}$ of 4 M: 151·8, 0·15. $\bar{x}$ of 4 F: 156·5, 0·16); *Cyrtonyx montezumae* 1.

**Subfamily Phasianinae** (Partridges, Quails, Pheasants)
MATERIAL EXAMINED. *Francolinus adspersus* 1; *F. ahantensis* 1; *Perdix perdix* 1 (F: 360·0, 0·09); *Coturnix coturnix* 1; *Excalfactoria chinensis* 3; *Arborophila torqueola* 1; *A. brunneopectus* 1; *Rollulus roulroul* 1; *Tragopan temmincki* 1; *Lophophorus impejanus* 1; *Crossoptilon auritum* 1; *C. mantchuricum* 1; *Lobiophasis bulweri* 1; *Gallus gallus* 5 (M: 2270, 0·02); *Gallus gallus* × *Meleagris gallopavo* 1; *Catreus wallichii* 1 (M, Z: 1340, 0·05); *Phasianus colchicus* 2 (M: 1374.7, 0·03; 1292, 0·02); *Syrmaticus reevesii* 1; *Chrysolophus pictus* 1; *Argusianus argus* 5; *Pavo cristatus* 3 (M, Z: 3350, 0·02); *Afropavus congensis* 3.

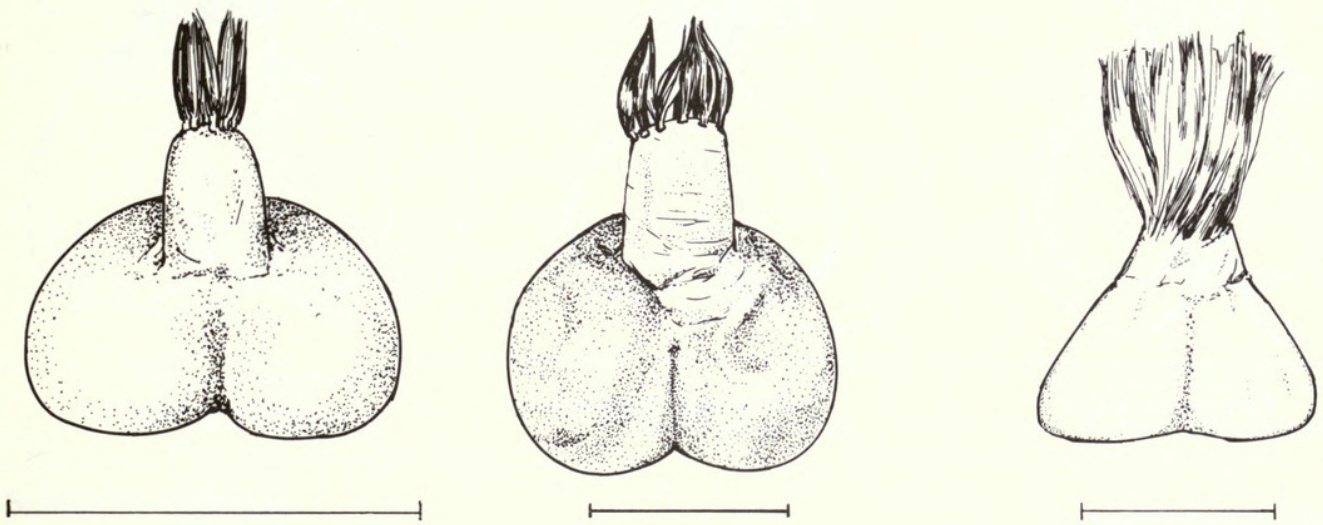


*Crax alberti* *Lyrurus tetrix* *Phasianus colchicus*

**Family Numididae** (Guinea fowl)
MORPHOLOGY. Distinctly bilobed, papilla large, tufted (8 feathers in *N. meleagris*, Jacob & Ziswiler 1982; only 2 in *Phasidus*). Type I.
MATERIAL EXAMINED. *Phasidus niger* 1; *Numida* sp. 1; *N. meleagris* 1; *Guttera pucherani* 1; *Acryllium vulturinum* 1.

**Family Meleagrididae** (Turkeys)
MORPHOLOGY. Distinctly bilobed, papilla large, tufted (7, 9 feathers, Jacob & Ziswiler 1982). Type I.
MATERIAL EXAMINED. *Meleagris gallopavo* 5 (ad. M: 7400, 0.02. Subad. M: 3740, 0·02. Subad. F: 1870, 0·04).

**Family Opisthocomidae** (Hoatzin)
MORPHOLOGY. Bilobed, papilla small, tuft (up to 12 feathers) variable in size, or gland naked. Beddard (1898), Gadow (1893), and Verheyen (1956*c*) described the gland as feathered. I found that 9 nestlings, 'young,' or 'juveniles' had minute tufts, 2 'subadults' were naked, and 3 'adults' had tufted glands. Type I.
MATERIAL EXAMINED. *Opisthocomus hoazin* 14.



*Numida* sp. *Meleagris gallopavo* *Opisthocomus hoazin*

## Order Gruiformes

**Gland characteristics.** Inter- and intrafamilial variation: gland absent, naked, or sparsely to densely tufted.

**Family Mesoenatidae** (Mesites, Monias)
MORPHOLOGY. Absent (also reported as such by Gadow 1893, Miller 1924, Verheyen 1958*a*, Van Tyne & Berger 1976). Beddard (1898: 381) erroneously reported the gland as present and nude.
MATERIAL EXAMINED. *Mesoenas variegata* 1; *M. unicolor* 1; *Monias benschi* 2.

**Family Turnicidae** (Bustard-Quails)
MORPHOLOGY. Distinctly bilobed, papilla moderately developed, tufted (also reported by Verheyen 1958*a*; ca 10 feathers). Type I.
MATERIAL EXAMINED. *Turnix sylvatica* 2; *T. tanki* 1; *T. suscitator* 1; *Ortyxelos meiffrenii* 1.

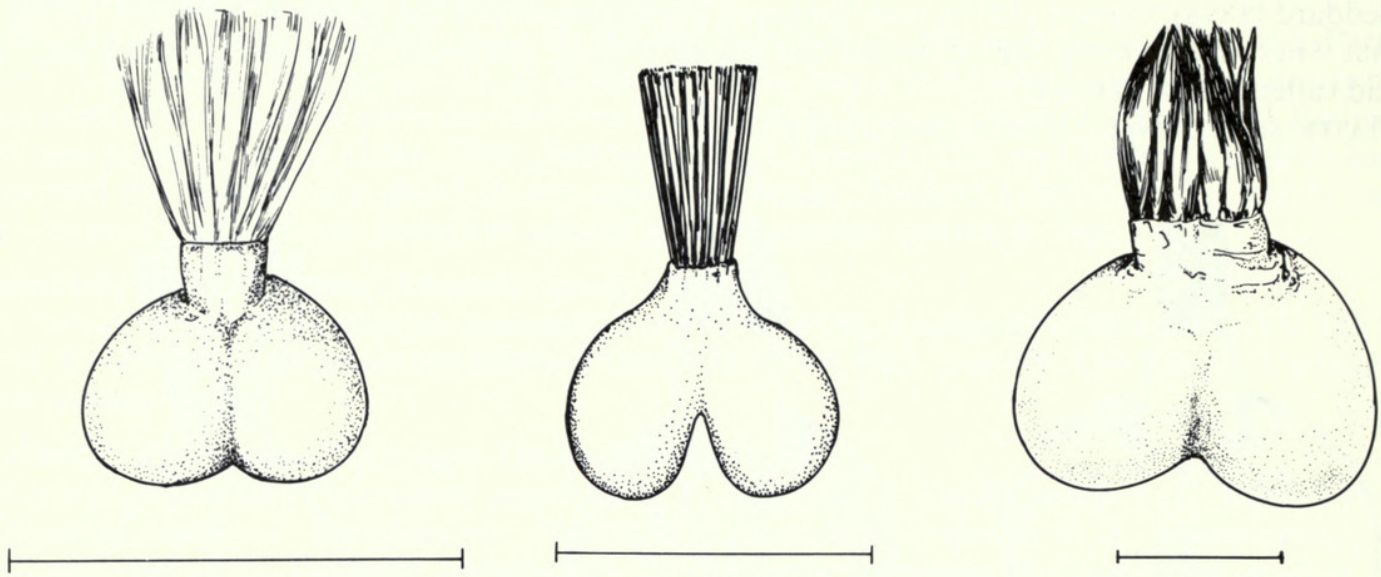
**Family Pedionomidae** (Collared Hemipodes)
MORPHOLOGY. Distinctly bilobed, papilla moderately developed, tufted (12 feathers). Type I.
NOTE. Gadow (1891) and Beddard (1898) reported a tufted gland in this family. Olson & Steadman (1981) believe that *Pedionomus* is a charadriiform, but the tufted gland supports no specific relationship for this family.
MATERIAL EXAMINED. *Pedionomus torquatus* 2.

**Family Gruidae** (Cranes)
MORPHOLOGY (family). Large and bilobed, papilla small with the end large and tufted (14–16

feathers, Paris 1913; 32 feathers in *G. grus*, Jacob & Ziswiler 1982; 20 feathers in *Grus*, Nitzsch 1867). Gadow (1893) described the gland of *Grus grus* as naked, but that report was probably erroneous because of the tufted glands now known from all other species examined. Type I.

**Subfamily Gruinae**

MATERIAL EXAMINED. *Grus canadensis* 9 (ad. M: 3520, 0·05. Subad. M: 2360, 0·03. Ad. F: 3880, 0·05; 3560, 0·05); *G. antigone* 1; *Anthropoides paradisea* 2.



*Turnix suscitator* *Pedionomus torquatus* *Grus canadensis*

**Subfamily Balearicinae**

MATERIAL EXAMINED. *Balearica pavonina* 2.

**Family Aramidae** (Limpkin)

MORPHOLOGY. Distinctly bilobed, papilla moderately developed, tufted (14 feathers). Type I.
MATERIAL EXAMINED. *Aramus scolopaceus* 9 ($\bar{x}$ of 6 M: 1128·6, 0·28. F: 1300, 0·29).

**Family Psophiidae** (Trumpeters)

MORPHOLOGY. Indistinctly bilobed, papilla absent, sparse and short tuft (20 feathers). Nitzsch (1867) made the contradictory statement (p. 123), '. . . of the naked oil-gland, which is furnished with a circlet of feathers at the tip.' Type I.
MATERIAL EXAMINED. *Psophia crepitans* 1; *P. leucoptera* 3.

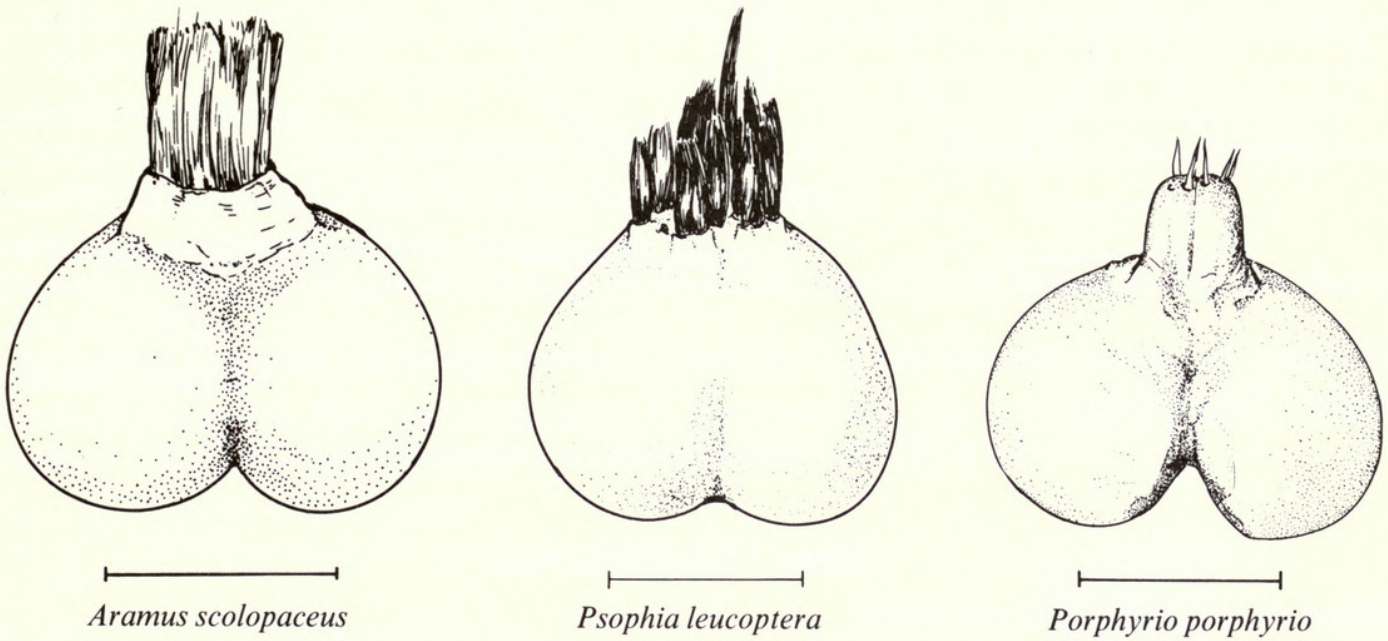
**Family Rallidae** (Rails, Coots, Gallinules)

MORPHOLOGY (family). Distinctly bilobed, papilla usually large, tuft variable (Verheyen 1957*b*) (11–17 feathers in 5 species, Jacob & Ziswiler 1982; 6 in *Porphyrio*) or gland naked. Miller (1924), Verheyen (1957*b*), and Ripley (1976) stated that *Himantornis* has a naked gland, a condition that I confirmed. Beddard (1898: 321) stated that Ralli 'have as a rule a tufted oil gland but *Porzana carolina* is an exception.' Miller (1924) and I each found that 5 different specimens of this species all had tufted glands. In *Atlantisia rogersi* 2 specimens at the British Museum had naked glands, but 2 specimens at the American Museum of Natural History and Museum of Comparative Zoology each had tufted glands. Type I.

**Subfamily Rallinae**

MATERIAL EXAMINED. *Rallus longirostris* 3 (F: 186·3, 0·23); *R. elegans* 3 (F: 298·0, 0·16; 372·7, 0·29); *R. limicola* 6 (M: 66·3, 0·34. F: 65·3, 0·09), *R. owstoni* 1; *R. wakensis* 1; *Atlantisia rogersi* 5; *Tricholimnas sylvestris* 1; *Dryolimnas cuvieri* 1; *Rallina eurizonoides* 1; *Cyanolimnas cerverai* 1; *Gallirallus australis* 2; *Himantornis haematopus* 1; *Crecopsis egregia* 1; *Crex crex* 1; *Anurolimnas*

*castaneiceps* 2; *Limmocorax flavirostra* 2; *Porzana carolina* 5 (M: 66·9, 0·15. F: 65·9, 0·22); *P. albicollis* 1; *Porzanula palmeri* 2; *Laterallus albigularis* 1; *Micropygia schomburgkii* 1; *Coturnicops noveboracensis* 1; *Sarothrura rufa* 1; *Poliolimnas cinerus* 1; *Tribonyx mortierii* 1; *Amaurornis phoenicurus* 1; *Gallicrex cinerea* 1; *Gallinula chloropus* 8 (M: 364·2, 0·11; 211·5, 0·23. $\bar{x}$ of 4 F: 274·3, 0·18; *Porphyriornis nesiotis* 1; *P. comeri* 1; *Porphyrula alleni* 1; *P. martinica* 4 (F: 203·6, 0·16); *Porphyrio porphyrio* 1, *P. poliocephalus* 1; *Notornis mantelli* 1.



*Aramus scolopaceus* *Psophia leucoptera* *Porphyrio porphyrio*

**Subfamily Fulicinae**
MATERIAL EXAMINED. *Fulica americana* 8 (M: 625·0, 0·11. F: 395·4, 0·16; 386·5, 0·17).

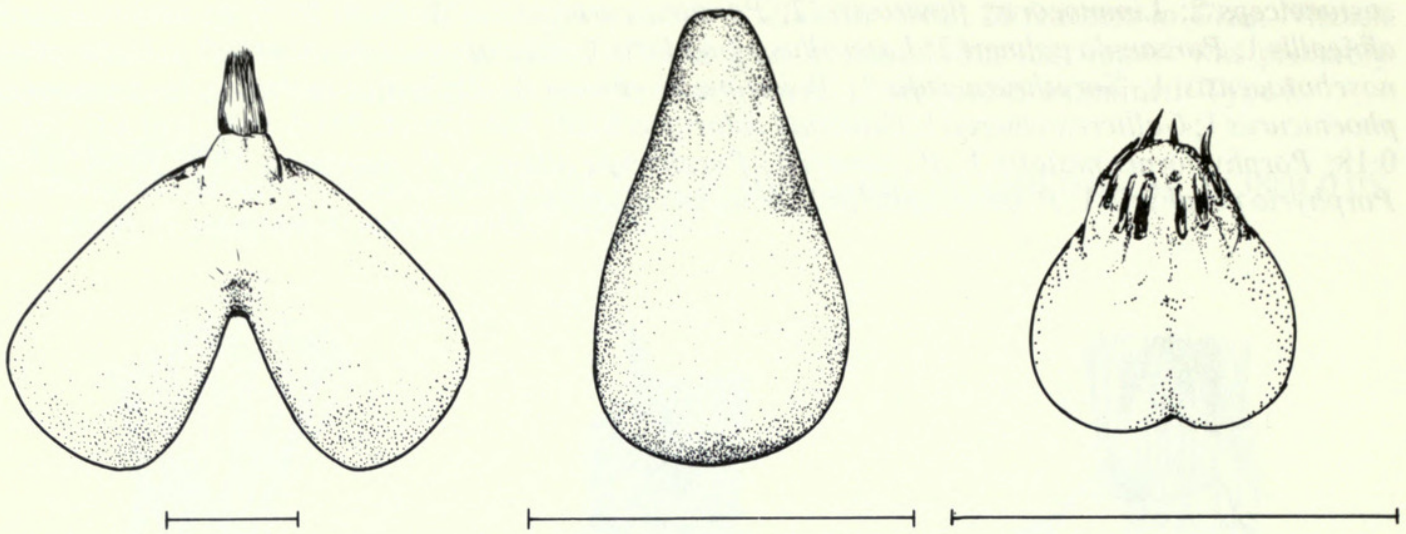
**Family Heliornithidae** (Sun-Grebes)
MORPHOLOGY. Broad and bilobed, papilla moderately developed, tufted (16 feathers). Type I.
MATERIAL EXAMINED. *Podica senegalensis* 1; *Heliopais personata* 1; *Heliornis fulica* 1.

**Family Rhynochetidae** (Kagu)
MORPHOLOGY. Apparently single-lobed, indistinct papilla, naked. The gland is not 'rudimentary' as stated by Jacob (1978: 168).
MATERIAL EXAMINED. *Rhynochetos jubatus* 1.

**Family Eurypygidae** (Sun-Bittern)
MORPHOLOGY. Indistinctly bilobed, papilla moderately developed, tufted (10 1–2 mm feathers). Miller (1924: 322) concluded: 'Gadow gives the oil-gland of *Eurypyga* as bare; Beddard states that it is generally nude but occasionally tufted. In each of my two fresh examples, . . . there was a small tuft present.' Type I.
MATERIAL EXAMINED. *Eurypyga helias* 3.

**Family Cariamidae** (Cariamas)
MORPHOLOGY. Apparently single-lobed, papilla large, naked. The unusual shape is described by Nitzsch (1867) as distinctly 'of a conical pyriform shape.'
MATERIAL EXAMINED. *Cariama cristata* 1.

**Family Otidae** (Bustards)
MORPHOLOGY. Gland absent in all species examined, a condition previously noted by Nitzsch (1840), Gadow (1893), Beddard (1898), Paris (1913), Grassé (1950), Verheyen (1957*b*) and Van Tyne & Berger (1976). Paris (1913) reported 'well marked outlines of the gland' in embryos.



*Heliopais personata* *Rhinochetos jubatus* *Eurypyga helias*

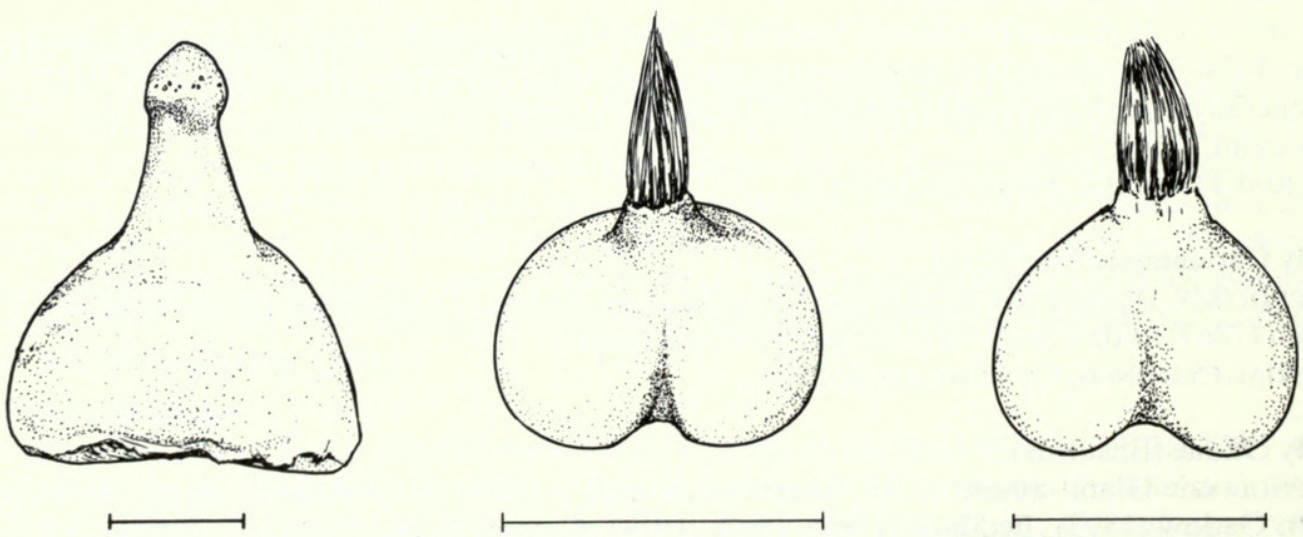
MATERIAL EXAMINED. *Choriotis kori* 2; *C. australis* 1; *Lophotis ruficrista* 1; *Eupodotis senegalensis* 2; *Lissotis melanogaster* 1.

## Order Charadriiformes

**Gland characteristics.** Heavily tufted.
NOTE. 10 families were described by Verheyen (1958*b*) as being tufted. All individuals of 16 families in the present study had tufted glands. Type I.

**Family Jacanidae** (Jacanas)
MORPHOLOGY. Bilobed, papilla moderately developed (*contra* 'without a well-developed nipple' Verheyen 1957*d*), tufted (12 feathers).
MATERIAL EXAMINED. *Jacana spinosa* 2.

**Family Rostratulidae** (Painted Snipe)
MORPHOLOGY. Bilobed, papilla indistinct, tufted (12 feathers).
MATERIAL EXAMINED. *Rostratula benghalensis* 1.



*Cariama cristata* *Jacana spinosa* *Rostratula benghalensis*

**Family Haematopodidae** (Oyster-catchers)
MORPHOLOGY. Bilobed, papilla small, tufted (28 feathers, Jacob & Ziswiler 1982).
MATERIAL EXAMINED. *Haematopus ostralegus* 2.

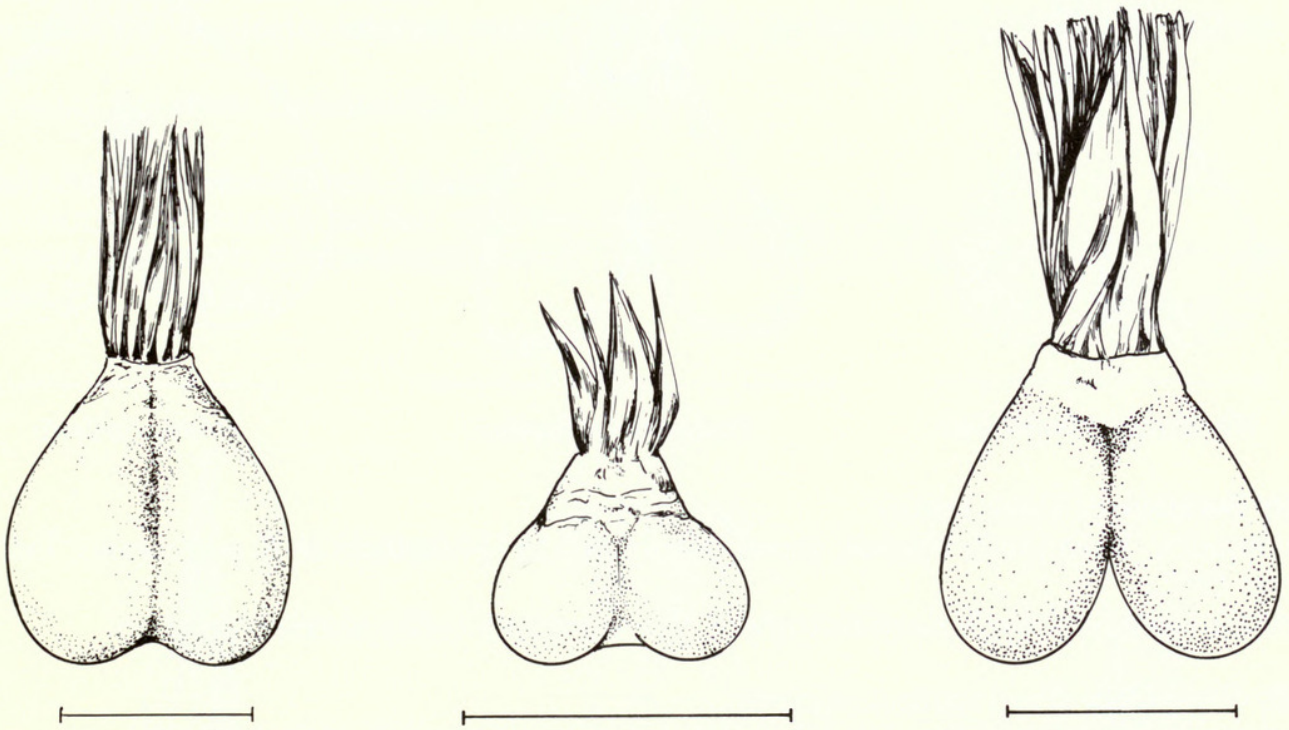
**Family Charadriidae** (Lapwings, Plovers)
MORPHOLOGY (family). Distinctly bilobed, papilla moderately developed, tufted (12–24 feathers, Paris 1913; 12–14 feathers, Jacob & Ziswiler 1982).

**Subfamily Vanellinae**
MATERIAL EXAMINED. *Vanellus vanellus* 2; *Hoplopterus spinosus* 2; *Hoploxypterus cayanus* 1; *Zonifer tricolor* 1.

**Subfamily Charadriinae**
MATERIAL EXAMINED. *Squatarola squatarola* 2 (M: 205·3, 0·22. F: 216·2, 0·14); *Charadrius hiaticula* 1; *C. vociferus* 4 (F: 92·0, 0·08; 94·1, 0·07); *Eupoda montana* 1.

**Family Scolopacidae** (Woodcock, Sandpipers)
MORPHOLOGY (family). Distinctly bilobed, papilla small, tufted (12–24 feathers in 4 species, Jacob & Ziswiler 1982).

**Subfamily Tringinae**
MATERIAL EXAMINED. *Bartramia longicauda* 1; *Numenius minutus* 1; *Tringa totanus* 1; *Actitis macularia* 2 (F: 28·5, 0·12); *Catoptrophorus semipalmatus* 5 (M:297·8, 0·19).



*Haematopus ostralegus* *Charadrius vociferus* *Catoptrophorus semipalmatus*

**Subfamily Arenariinae**
MATERIAL EXAMINED. *Arenaria interpres* 5.

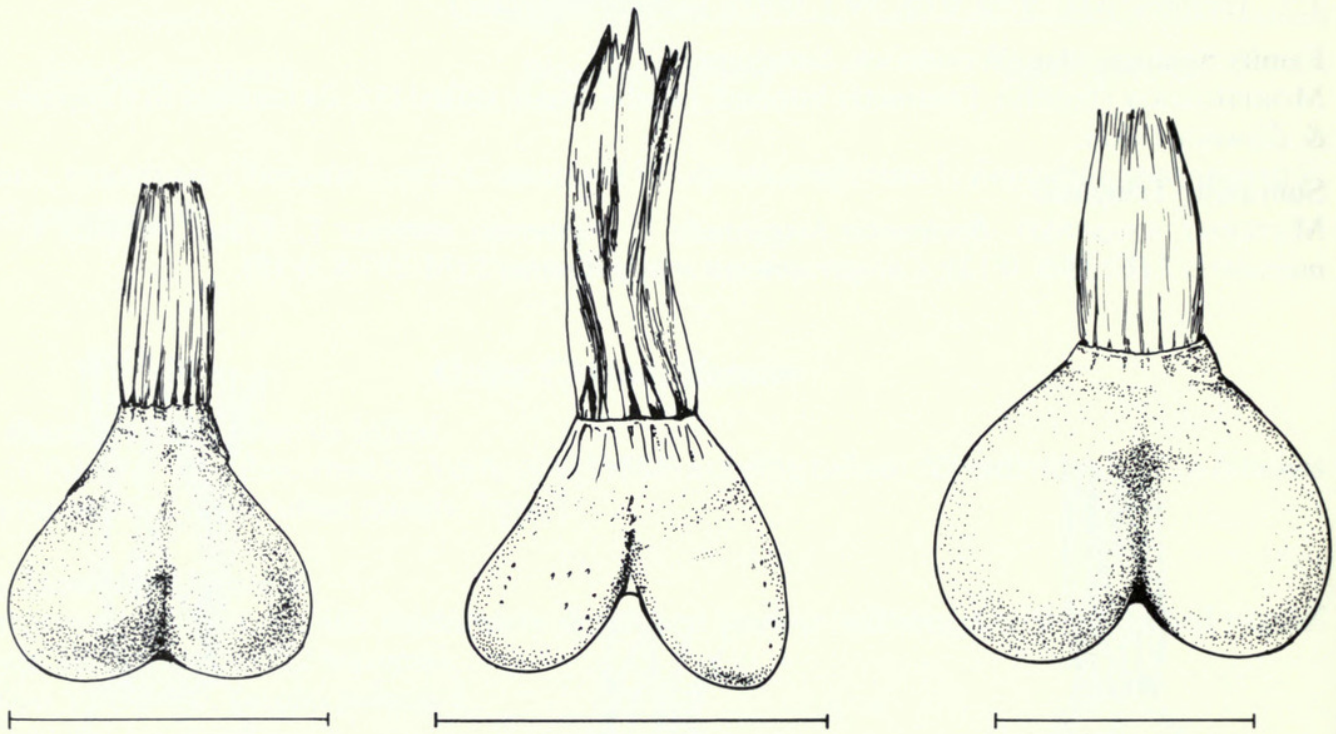
**Subfamily Scolopacinae**
MATERIAL EXAMINED. *Limnodromus scolopaceus* 8 ($\bar{x}$ of 4M: 104·2, 0·18. F: 121·1, 0·20); *L. griseus* 6 (F: 101·9, 0·12; 85·2, 0·12); *Capella gallinago* 3 (F: 101·5, 0·09); *Philohela minor* 5 (M: 106·0, 0·09. $\bar{x}$ of 4F: 179·2, 0·09).

**Subfamily Eroliinae**
MATERIAL EXAMINED. *Calidris canutus* 2 (M: 94·5, 0·08); *Crocethia alba* 2 (F; 49·9, 0·07); *Ereunetes pusillus* 2; *Erolia minutilla* 1; *E. fuscicollis* 1; *E. alpina* 2.

**Family Recurvirostridae** (Avocets, Stilts)
MORPHOLOGY. Bilobed, papilla small, tufted (ca 20 feathers).
MATERIAL EXAMINED. *Himantopus himantopus* 3; *Recurvirostra americana* 1 (F: 289·4, 0·20).

**Family Phalaropodidae** (Phalaropes)
MORPHOLOGY. Distinctly bilobed, papilla small, tufted.
MATERIAL EXAMINED. *Phalaropus fulicarius* 4 (unsexed: 40·5, 0·62; 40·4, 0·53. F: 42·0, 0·79); *Lobipes lobatus* 3 (F: 27·7, 0·42).

**Family Dromadidae** (Crab-plovers)
MORPHOLOGY. Distinctly bilobed, papilla apparently absent, tufted (16 feathers).
MATERIAL EXAMINED. *Dromas ardeola* 1.



*Himantopus himantopus* *Phalaropus fulicarius* *Dromas ardeola*

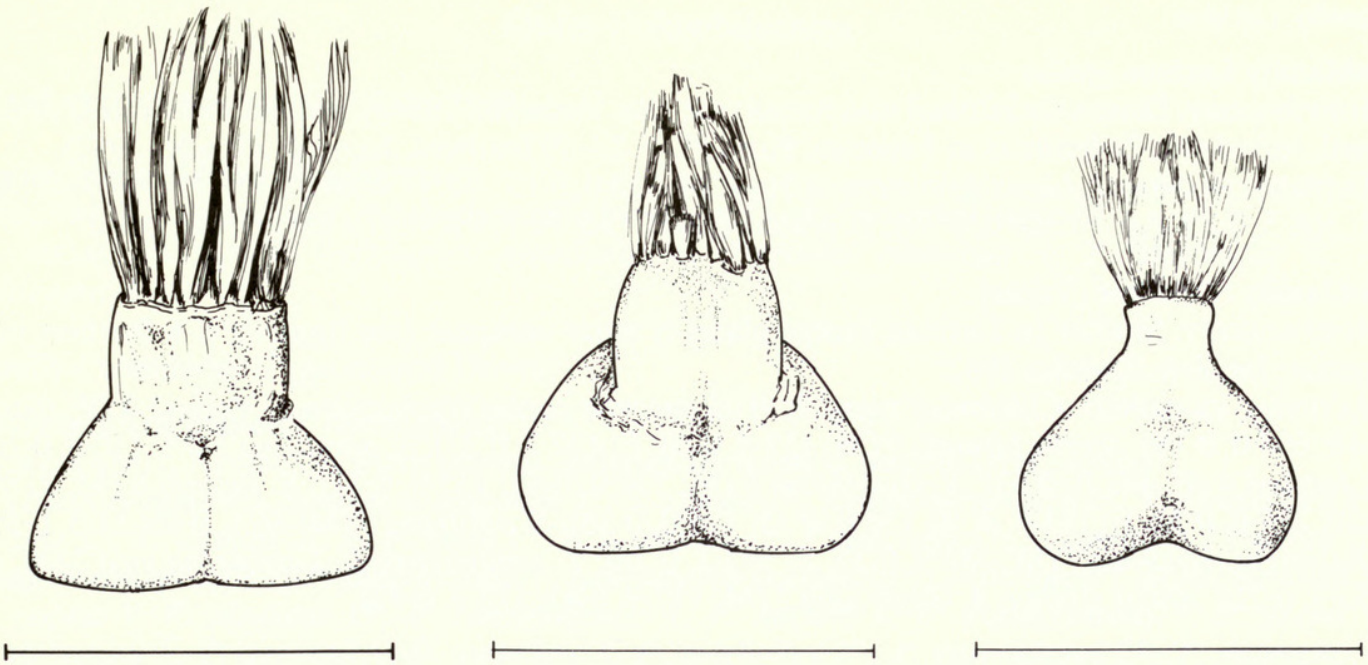
**Family Burhinidae** (Thick-knees)
MORPHOLOGY. Indistinctly bilobed, broad papilla, tufted (14 feathers in *B. oedicnemus,* Jacob & Ziswiler 1982).
MATERIAL EXAMINED. *Burhinus oedicnemus* 1; *B. senegalensis* 1; *Esacus recurvirostris* 1.

**Family Glareolidae** (Pratincoles, Coursers)
MORPHOLOGY (family). Indistinctly bilobed, large and round papilla, tufted (14 feathers).

**Subfamily Cursoriinae**
MATERIAL EXAMINED. *Cursorius cursor* 1.

**Subfamily Glareolinae**
MATERIAL EXAMINED. *Stiltia isabella* 1; *Glareola pratincola* 1.

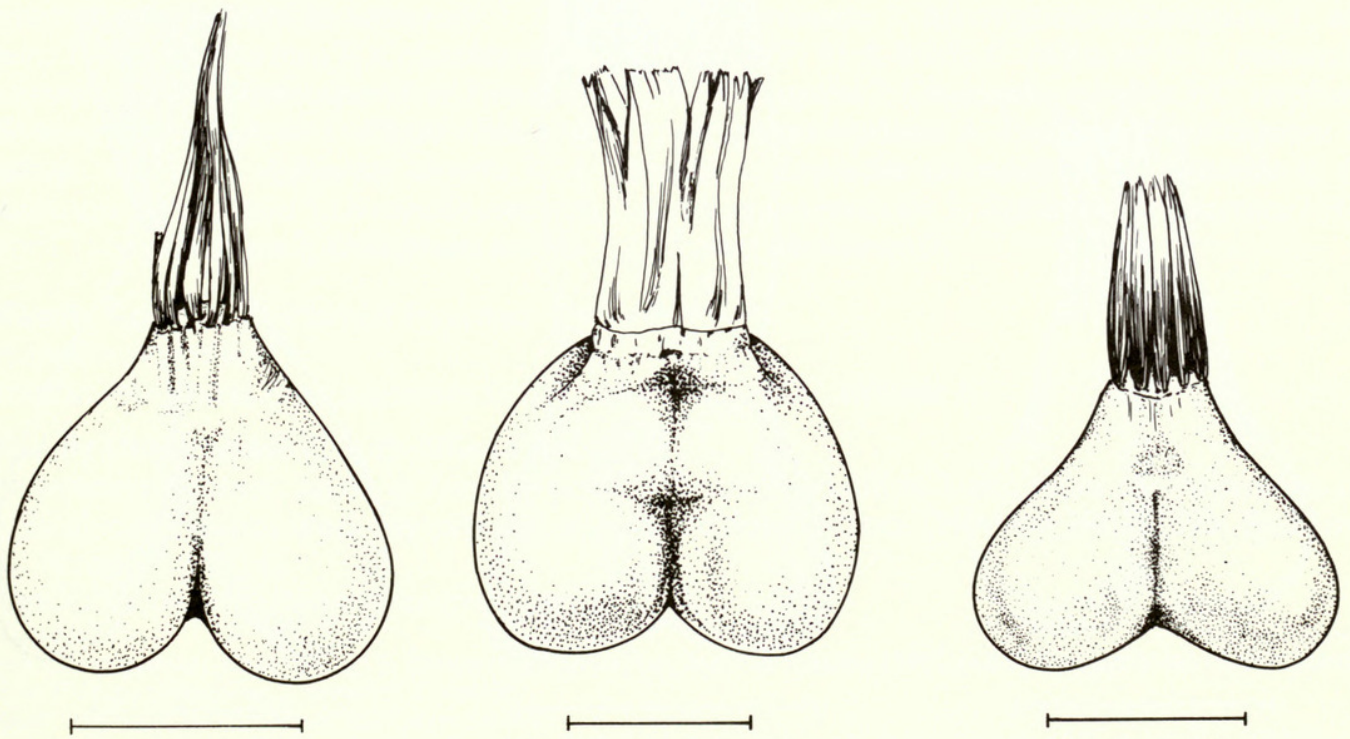
**Family Thinocoridae** (Seed-snipe)
MORPHOLOGY. Indistinctly bilobed, papilla moderately developed, tufted (16 feathers).
NOTE. Based upon comparisons of gland morphologies, the present study confirms the belief of Sibley *et al.* (1968: 243) that seed-snipe 'are more like ... the Charadriiforms than any other group.'
MATERIAL EXAMINED. *Thinocorus orbignyianus* 1; *T. rumicivorus* 1.



*Burhinus oedicnemus* *Cursorius cursor* *Thinocorus rumicivorus*

**Family Chionididae** (Sheath-bills)
MORPHOLOGY. Distinctly bilobed, papilla moderately developed, tufted (16–18 feathers, Paris 1913).
MATERIAL EXAMINED. *Chionis alba* 1.

**Family Stercorariidae** (Skuas, Jaegers)
MORPHOLOGY. Distinctly bilobed, papilla apparently absent, tufted.
MATERIAL EXAMINED. *Stercorarius pomarinus* 2 (F: 616·0, 0·37); *S. longicaudus* 4 (ad M: 333·9, 0·23. Subad. F: 271·5, 0·28).



*Chionis alba* *Stercorarius pomarinus* *Larus atricilla*

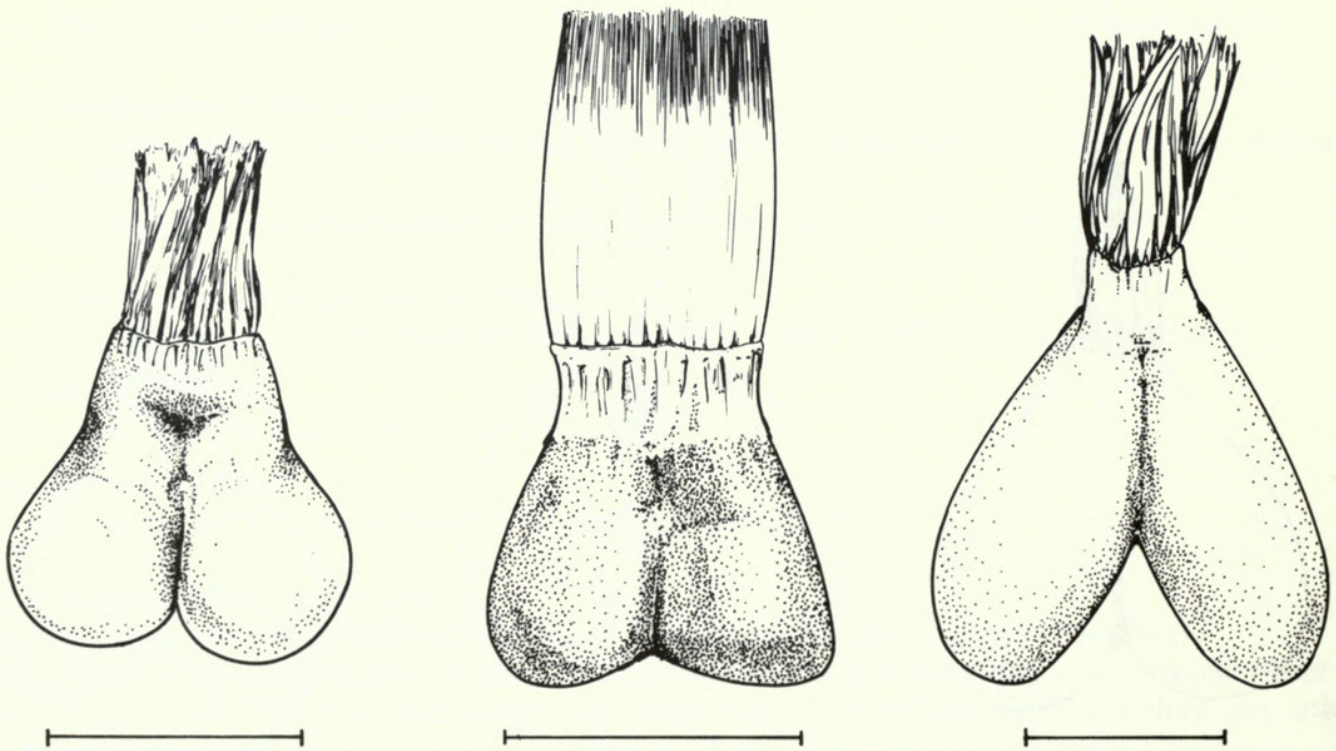
**Family Laridae**

**Subfamily Larinae** (gulls)
MORPHOLOGY. Distinctly bilobed and broad (see also Verheyen 1954*a*), papilla moderately developed, tufted (18–26 feathers in 4 species, Paris 1913; 22–29 feathers, Jacob & Ziswiler 1982).
MATERIAL EXAMINED. *Larus delawarensis* 5 (ad. M: 330·0, 0·15. Ad. F: 440·0, 0·13); *L. atricilla* 8 (ad. M: 368·5, 0·29. Ad. F: 320·0, 0·20); *L. philadelphia* 2 (ad. F: 179·8, 0·21); *Rissa tridactyla* 2.

**Subfamily Sterninae** (Terns)
MORPHOLOGY. Similar to Larinae except gland is more compact (see figures); 6–8 feathers in 4 species, Jacob & Ziswiler 1982.
MATERIAL EXAMINED. *Chlidonias nigra* 2; *Hydroprogne caspia* (*tschegrava* of Peters) 4 (F: 686·0, 0·18; 698·0, 0·18); *Sterna hirundo* 9 (M: 117·4, 0·26. F: 137·7, 0·33); *S. paradisea* 2 (M: 110·9, 0·16); *S. forsteri* 4 (F: 147·0, 0·33); *S. anaethetus* 6 (M: 130·0, 0·43; 135·0, 0·31); *S. fuscata* 8 (M: 218·0, 0·29; 218·6, 0·25. F: 141·0, 0·38; 156·0, 0·35; 174·0, 0·38); *S. albifrons* 5 (M: 46·1, 0·46; 51·3, 0·57); *Thalasseus maximus* 7 (M: 385·9, 0·35. F: 353·2, 0·26); *T. sandvicensis* 3; *Larosterna inca* 2 (M, Z: 153·3, 0·21); *Anous stolidus* 4; *Gygis alba* 2 (M: 117·9, 0·43; 113·3, 0·47).

**Family Rynchopidae** (Skimmers)
MORPHOLOGY. Bilobed, papilla broad and apparently double, densely tufted (24 feathers).
MATERIAL EXAMINED. *Rynchops niger* 6 (M: 211·4, 0·20).

**Family Alcidae** (Auks, Murres, Puffins)
MORPHOLOGY. Elongated and bilobed, papilla moderately developed, tufted (Verheyen 1958*d*; 30–50 feathers, Paris 1913; 2–8 (sic?) feathers, Jacob & Ziswiler 1982; 20–40, present study).
MATERIAL EXAMINED. *Plautus alle* 2; *Pinguinus impennis* (mounted bird) 1; *Uria lomvia* 1; *U. aalge* 1; *Cepphus grylle* 1 (F: 363·0, 0·22); *C. columba* 3 (M: 380·0, 0·18. F: 371·5, 0·19); *Synthliboramphus antiquus* 2 (M: 180·5, 0·25); *Ptychoramphus aleuticus* 2 (F: 207·9, 0·47); *Aethia cristatella* 1; *Cerorhinca monocerata* 2 (M: 631·5, 0·31); *Lunda cirrhata* 2 (F: 673·5, 0·30; 792·4, 0·20).



*Sterna fuscata* *Rynchops niger* *Lunda cirrhata*

## Order Columbiformes

**Gland characteristics.** Naked or absent.

**Family Pteroclididae** (Sand-grouse)
MORPHOLOGY. Indistinctly bilobed, papilla broad and well developed, naked.
MATERIAL EXAMINED. *Syrrhaptes paradoxus* 1; *Pterocles namaqua* 1; *P. decoratus* 1; *P. lichtensteinii* 1.

**Family Columbidae** (Pigeons and Doves)

**Subfamily Treroninae** (Fruit pigeons)
MORPHOLOGY. Absent or, when present, indistinctly bilobed, papilla large, naked.
MATERIAL EXAMINED. *Sphenurus apicauda* 1*; *S. oxyura* 1*; *Treron curvirostra* 2*; *T. pompadora* 2*; *T. olax* 1*; *T. vernans* 2*; *T. bicincta* 1*; *T. s. thomae* 1*; *T. australis* 1*; *T. calva* 1*; *T. waalia* 1*; *Phapitreron leucotis* 2; *P. amethystina* 1; *Leucotreron occipitalis* 1; *Ptilinopus*** *dupetithouarsii* 1; *P. regina* 1; *P. insularis* 1*; *P. raratongensis* 1; *P. huttoni* 1; *P. porphyraceus* 1; *P. greyii* 1; *P. richardsii* 1; *P. perousii* 1; *P. superbus* 3; *P. pulchellus* 2*; *P. coronulatus* 2*; *P. monacha* 1; *P. iozonus* 1*; *P. rivoli* 3*; *P. eugeniae* 1*; *P. hypogastra* 1*; *P. jambu* 1; *P. aurantiifrons* 1; *P. ornatus* 2; *P. tannensis* 1*; *Chrysoena victor* 1*; *Alectroenas pulcherrima* 1; *A. madagascariensis* 2; *Megaloprepia magnifica* 1*; *Ducula oceanica* 1; *D. pacifica* 1; *D. aenea* 1; *D. bicolor* 1; *D. spilorrhoa* 1; *D. badia* 1*; *D. rufigaster* 1; *D. zoeae* 1*.

**Subfamily Columbinae** (Pigeons, Doves)
MORPHOLOGY. Except for some individuals or varieties of *Columba livia,* the gland is present in all genera and species of Columbinae thus far examined. Indistinctly bilobed, papilla large, naked. Reported by Beddard (1898) as absent in *Ptilopas puella* (= *Columba puella* of Peters), *Starnoenas* (also absent *fide* Garrod 1874*a*), and *Turacoena,* all genera and species unavailable for the present study.
MATERIAL EXAMINED. *Columba livia*† 2 (M: 268·0, 0·05. F: 312·8, 0·08); *C. palumbus* 1; *C. leucocephala* 3 (F: 205·2, 0·10; 264·0, 0·05); *C. guinea* 1; *C. fasciata* 1; *Macropygia unchall* 1; *M. amboiensis* 2; *M. ruficeps* 1; *M. phasianella* 1; *M. nigrirostris* 2; *Ectopistes migratoria* 2; *Zenaidura macroura* 8 (M: 123·0, 0·01; 134·4, 0·03; 105·7, 0·02. F: 123·4, 0·01; 117·1, 0·03); *Z. auriculata* 1; *Zenaida asiatica* 1 (M: 173·2, 0·02); *Nesopelia galapagoensis* 1; *Streptopelia orientalis* 1; *S. capicola* 1; *S. senegalensis* 3; *Geopelia humeralis* 1; *G. striata* 2; *G. cuneata* 1; *Metriopelia melanoptera* 1; *M. aymara* 1; *Scardafella inca* 1; *Columbigallina passerina* 1 (F: 41·5, 0·02); *C. talpacoti* 1; *C. minuta* 1; *Claravis pretiosa* 3; *Oena capensis* 6; *Turtur afer* 1; *T. chalcospilos* 2; *Chalcophaps indica* 3; *C. stephani* 1; *Henicophaps albifrons* 1; *Phaps chalcoptera* 1; *Ocyphaps lophotes* 3; *Lophophaps ferruginea* 1; *Geophaps smithii* 2; *Aplopelia larvata* 1; *A. simplex* 1; *Leptotila verreauxi* 1; *L. rufaxilla* 1; *L. plumbeiceps* 3; *L. cassini* 5; *Oreopelia caniceps* 1; *Geotrygon versicolor* 1; *Gallicolumba luzonica* 1; *G. beccarii* 1; *G. rubescens* 2; *Otidiphaps nobilis* 1; *Caloenas nicobarica* 2.

**Subfamily Gourinae** (Crowned Pigeons)
MORPHOLOGY. Absent
MATERIAL EXAMINED. *Goura cristata* 1; *G. scheepmakeri* 1; *G. victoria* 1.

**Subfamily Didunculinae** (Tooth-billed Pigeons)
MORPHOLOGY. Absent. Jacob & Ziswiler (1982) reported a gland in 2 specimens of *Didunculus,* an inexplicable difference from the present and all previous reports (Newton 1893–1896, Beddard 1898, Verheyen 1957*a*).
MATERIAL EXAMINED. *Didunculus strigirostris* 3.

*gland absent, present study; absent in *Treron* (Garrod 1874*a*). Jacob & Ziswiler (1982 and V. Ziswiler in litt.) found glands in adult *Treron pompadora, T. vernans, T. waalia.*
**gland 'very small in *Ptilinopus' fide* Garrod 1874*a*.
†absent in some varieties such as Fantail, Oriental, Roller, Maltese, White Carneau (Darwin 1900, Johansson 1927, Levi 1941, Verheyen 1957*a*).

## Order Psittaciformes*

**Gland characteristics.** Tufted or absent.

**Family Psittacidae** (Lories, Parrots, Macaws)

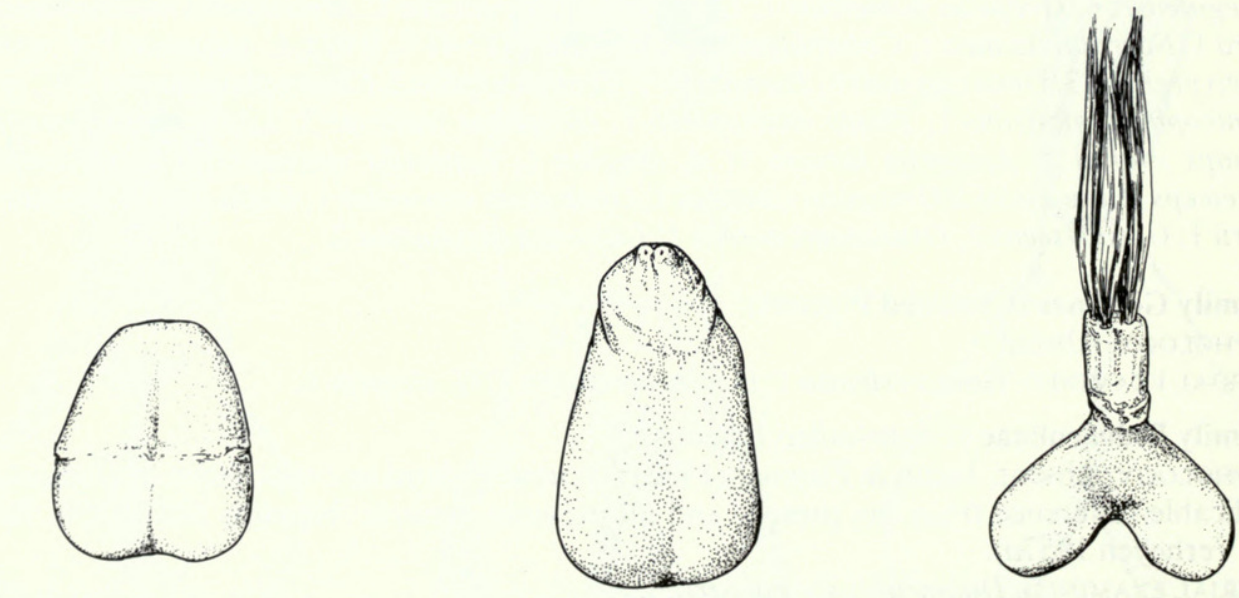
**Subfamily Strigopinae** (Owl Parrots)
MORPHOLOGY. Distinctly bilobed, papilla large, tufted.
MATERIAL EXAMINED. *Strigops habroptilus* 1.

**Subfamily Nestorinae** (Keas)
MORPHOLOGY. Distinctly bilobed, papilla well developed, tufted (13 feathers, Jacob & Ziswiler 1982).
MATERIAL EXAMINED. *Nestor notabilis* 3.

**Subfamily Loriinae** (Lories)
MORPHOLOGY. Distinctly bilobed, papilla large, tufted (5–8 feathers in 3 species, Jacob & Ziswiler 1982). Type I.
MATERIAL EXAMINED. *Chalcopsitta atra* 1; *Eos cyanogenia* 1; *E. squamata* 1; *E. bornea* 3; *Trichoglossus ornatus* 1; *T. haematod* 3; *T. chlorolepidotus* 1; *Psitteuteles johnstoniae* 1; *Domicella garrula* 3; *Vini stepheni* 1; *Glossopsitta porphyrocephala* 1; *Charmosyna josefinae* 1; *C. papou* 1; *Oreopsittacus arfaki* 1; *Neopsittacus musschenbroekii* 1.

**Subfamily Micropsittinae** (Pigmy Parrots)
MORPHOLOGY. Distinctly bilobed, papilla large, tufted (3–4 feathers, Jacob & Ziswiler 1982).
MATERIAL EXAMINED. *Micropsitta pusio* 1.

**Subfamily Kakatoeinae** (Cockatoos)
MORPHOLOGY. Absent or when present, distinctly bilobed, papilla large, tufted (4–8 feathers in 2 species, Jacob & Ziswiler 1982).
NOTE. Newton (1893–1896: 653) stated that the gland 'exists, though hardly in a functional condition, in ... *Cacatua cristata* (Cockatoo) ...' = *Kakatoe sulphurea citrino-cristata* of Peters. Nitzsch (1867), Garrod 1874*b*, Gadow (1893), and Grassé (1950), noted no gland in *Cacatua sulfurea* and its absence in *C. roseicapella* was reported by Paris (1913). I found that specimens of both of these species had tufted glands.



*Pterocles lichtensteinii* *Zenaidura macroura* *Ara chloroptera*

*many zoo and captive birds.

MATERIAL EXAMINED. *Probosciger aterrimus* 4†; *Calyptorhynchus baudinii* 1; *Callocephalon fimbriatum* 2; *Kakatoe galerita* 7; *K. sulphurea* 4; *K. alba* 3; *K. moluccensis* 1; *K. haematuropygia* 1; *K. leadbeateri* 1; *K. sanguinea* 1; *K. tenuirostris* 1; *K. roseicapella* 3; *Nymphicus hollandicus* 4.

**Subfamily Psittacinae** (Macaws, Parrots)
MORPHOLOGY. Distinctly bilobed, papilla large, tufted (12 feathers, Paris 1913; 3–11 feathers in 33 species, Jacob & Ziswiler 1982) or gland absent. Type I.
NOTE. Miller (1924: 324) reported no gland in *Orthopsittaca* and *Diopsittaca* (= *Ara* of Peters), but listed no species. Jacob (1978: 168) stated that the gland is absent in *Ara* but indicated on species.
MATERIAL EXAMINED. *Anodorhynchus hyacinthus* 5*; *A. leari* 1*; *Ara*** *ararauna* 2; *A. militaris* 2; *A. macao* 4 (F, Z: 996·5, 0·05); *A. chloroptera* 3; *A. auricollis* 1; *A. severa* 1; *A. manilata* 3*; *Aratinga acuticaudata* 1; *A. guarouba* 1; *A. leucophthalmus* 1; *A. holochlora* 1; *A. jandaya* 1; *A. solstitialis* 2; *A. canicularis* 1; *A. aurea* 2; *Nandayus nanday* 1; *Conuropsis carolinensis* 1; *Rhynchopsitta pachyrhyncha* 1; *Cyanoliseus patagonus* 1; *Pyrrhura rhodogaster* 1; *P. molinae* 1; *P. hoffmanni* 1; *Myiopsitta monachus* 1; *Psilopsaigon aurifrons* 1; *Forpus conspicillatus* 1; *Brotogeris tirica* 1*; *B. versicolurus* 2*; *B. pyrrhyopterus* 1*; *B. jugularis* 2*; *B. cyanoptera* 2*; *B. chrysopterus* 4*; *B. st. thoma* 1*; *Pionites melanocephala* 2; *Graydidascalus brachyurus* 2*; *Pionus**** *menstruus* 2*; *P. maximiliani* 1*; *P. senilis* 1*; *P. chalcopterus* 1*; *Amazona leucocephala* 1*; *A. ventralis* 1*; *A. xantholora* 1*; *A. albifrons* 1*; *A. agilis* 1*; *A. vittata* 1*; *A. viridigenalis* 1*; *A. autumnalis* 1*; *A. barbadensis* 1*; *A. aestiva* 1*; *A. ochrocephala* 3*; *A. amazonica* 1*; *A. farinosa* 1*; *A. vinacea* 1*; *A. guildingii* 1*; *A. imperialis* 2*; *Triclaria malachitacea* 1; *Poicephalus senegalus* 2; *P. meyeri* 1; *P. ruppellii* 2; *Psittacus erithacus* 1; *Coracopsis nigra* 1; *Psittrichas fulgidus* 1; *Lorius roratus* 1; *Prioniturus discurus* 1; *Psittacula krameri* 5; *P. alexandri* 1; *P. cyanocephala* 1; *Polytelis swainsonii* 2; *P. alexandrae* 2; *Aprosmictus erythropterus* 3; *Psittinus cyanurus* 2; *Agapornis roseicollis* 2; *A. fischeri* 1; *A. lilianae* 3; *Loriculus vernalis* 1; *Platycercus elegans* 1; *P. eximius* 3; *P. icterotis* 2; *P. zonarius* 2; *Psephotus haematonotus* 3; *P. varius* 3; *Neophema elegans* 3; *N. chrysostomus* 1; *N. petrophila* 1; *N. pulchella* 7; *N. splendida* 3; *N. bourkii* 6; *Cyanoramphus auriceps* 2; *Melopsittacus undulatus* 1.

## Order Cuculiformes

**Gland characteristics.** Tufted or naked.

**Family Musophagidae** (Plantain-eaters)
MORPHOLOGY. Flattened and distinctly bilobed, papilla moderately developed, tufted (8 feathers). Verheyen (1956*b*) was evidently in error when he noted (p. 2) that touracos have a naked gland. Type I.
MATERIAL EXAMINED. *Tauraco corythaix* 1; *T. leucolophus* 1; *Gallirex porphyreolophus* 1; *Musophaga violacea* 3; *Crinifer leucogaster* 1; *C. africanus* 2.

**Family Cuculidae** (Cuckoos, Roadrunner, Anis)
MORPHOLOGY (family). Flattened and more or less distinctly bilobed, papilla large and often appearing double, naked.

**Subfamily Cuculinae**
MATERIAL EXAMINED. *Clamator glandarius* 1; *Cuculus canorus* 1; *Cacomantis merulinus* 1; *Chrysococcyx cupreus* 1; *C. klaas* 1; *C. caprius* 9; *Chalcites basalis* 1.

†gland absent, this study and Beddard (1898).
*gland absent, present study; Jacob & Ziswiler (1982, V. Ziswiler in litt.) found a gland in adult *Pionus fuscus*.
**gland present in *A. ambigua* and *maracana* (*fide* Garrod 1874*b*).
***gland also absent in *P. sordidus* (*fide* Garrod 1874*b*).

**Subfamily Phaenicophaeinae**
MATERIAL EXAMINED. *Coccyzus americanus* 4 (unsexed: 46·7, 0·09); *Piaya cayana* 2; *Saurothera vetula* 2; *Ceuthmochares aereus* 1; *Rhopodytes diardi* 1; *R. tristis* 2; *Rhamphococcyx curvirostris* 2; *Dasylophus superciliosus* 1.

**Subfamily Crotophaginae** (Anis, Guiras)
MATERIAL EXAMINED. *Crotophaga ani* 3 (M: 113·9, 0·03); *C. sulcirostris* 7; *Guira guira* 1.

**Subfamily Neomorphinae** (Roadrunners, Ground Cuckoos).
MATERIAL EXAMINED. *Tapera naevia* 1; *Morococcyx erythropygus* 2; *Geococcyx californiana* 3.

**Subfamily Couinae** (Couas)
MATERIAL EXAMINED. *Coua cristata* 1.

**Subfamily Centropodinae** (Coucals)
MATERIAL EXAMINED. *Centropus viridis* 2; *C. toulou* 1; *C. benegalensis* 2.

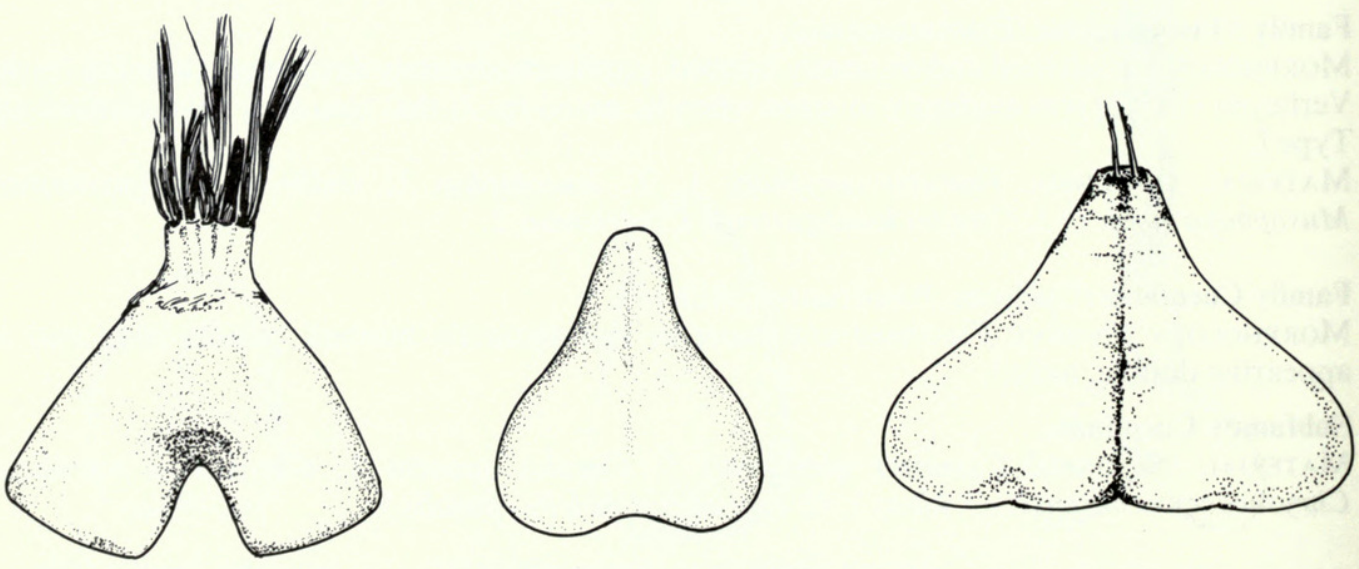
## Order Strigiformes

**Gland characteristics.** Naked or minutely tufted.
NOTE. Glands of various strigiform species have usually been described as 'naked' or 'nude' (Gadow 1893, Beddard 1898, Jacob & Ziswiler 1982). Nitszch (1840), Miller (1924), and I used magnification and identified 1 to 12 'rudimentary,' 'vestigial,' or 'minute' feathers on the papilla's tip in some individual specimens.

**Family Tytonidae** (Barn Owls)

**Subfamily Tytoninae**
MORPHOLOGY. Indistinctly bilobed, papilla moderately developed, tufted with minute feathers (1 or 2 5-mm feathers) or naked. Nitzsch (1867: 71) noted minute feathers on the papilla's apex in *Strix flammea, S. perlata,* and *S. furcata* (all = *Tyto alba*). Type I.
MATERIAL EXAMINED. *Tyto alba* 7* (M: 502·0, 0·07; 490·0, 0·04. F: 530·0, 0·12; 488·4, 0·11).

**Subfamily Phodilinae**
MORPHOLOGY. Like Tytoninae. Nitzsch (1867: 71) reported minute feathers at the gland apex in *Strix badia* (= *Phodilus badius*), but none were seen on 3 specimens in the present study.
MATERIAL EXAMINED. *Phodilus badius* 3.



*Tauraco corythaix* *Saurothera vetula* *Tyto alba*

*minute feathers in 3 specimens.

**Family Strigidae** (Typical Owls)
MORPHOLOGY (family). More superficial than in any other avian family, appearing to lie on top of the skin ('almost standing up,' Paris 1913: 180), bilobed, papilla large, tufted (up to 10 1-mm minute feathers) or naked. Type I.

**Subfamily Buboninae**
MATERIAL EXAMINED (naked unless otherwise indicated). *Otus spilocephalus* 1†; *O. scops* 1; *O. bakkamoena* 1; *O. asio* 26††, ††† (M: 103·2, 0·07; 107·7, 0·08. F: 149·3, 0·07; 108·4, 0·11); *O. trichopsis* 1†; *O. guatemalae* 1†; *O. choliba* 1†, †††; *O. watsonii* 1; *O. leucotis* 1; *Lophostrix cristata* 2; *Bubo virginianus* 8††† (M: 1207·0, 0·04; 1407·0, 0·04. F: 1887·0, 0·04; 1670·0, 0·03); *B. bubo* 1; *B. africanus* 1†††; *B. lacetus* 1†††; *Ketupa†††ketupu* 1; *Pulsatrix perspicillata* 1†††; *Nyctea scandiaca* 2†††; *Surnia ulula* 3 (M: 310·0, 0·07. F: 355·7, 0·04); *Glaucidium brasilianum* 2; *G. brodiei* 1; *Micrathene whitneyi* 1; *Ninox novaeseelandiae* 1†††; *N. philippensis* 1; *Athene noctua* 2; *A. brama* 1; *Speotyto cunicularia* 4; *Ciccaba virgata* 1†; *C. nigrolineata* 1; *C. woodfordii* 1.

**Subfamily Striginae**
MATERIAL EXAMINED (naked unless otherwise indicated): *Strix aluco* 1*; *S. varia* 20**, **** (M: 762·9, 0·09. $\bar{x}$ of 9 F: 775·4, 0·07); *S. nebulosa* 1*; *Rhinoptynx clamator* 1; *Asio otus* 5***, **** (F: 306·0, 0·09); *A. madagascariensis* 1*; *A. flammeus* 3*****; *Pseudoscops grammicus* 1; *Aegolius acadicus* 5 (M: 97·1, 0·10).

## Order Caprimulgiformes

**Gland characteristics.** Naked or rarely absent.

**Family Steatornithidae** (Oil-bird)
MORPHOLOGY. Indistinctly bilobed, papilla large, naked (first reported by Garrod 1873). Described by Paris (1913: 177) and Newton (1893–1896: 653) as 'large.' (See section on Weights and sizes of glands.)
MATERIAL EXAMINED. *Steatornis caripensis* 1.

**Family Podargidae** (Frogmouths)
MORPHOLOGY. *Podargus*—absent (see also Gadow 1893, Verheyen 1956*a*, Grassé 1950, Miller 1924). *Batrachostomus*—indistinctly bilobed, papilla large, naked. The implication by Van Tyne & Berger (1976) that the gland is absent in (all) Podargidae is incorrect.
MATERIAL EXAMINED. *Podargus strigoides* 2; *P. papuensis* 1; *P. ocellatus* 2; *Batrachostomus auritus* 1; *B. septimus* 2; *B. stellatus* 1; *B. javensis* 1.

**Family Nyctibiidae** (Potoos)
MORPHOLOGY. Very small, indistinctly bilobed, papilla large, naked.
NOTE. Miller (1924: 324) reported 'the loss of the oil-gland' in *Nyctibius*.
MATERIAL EXAMINED. *Nyctibius griseus* 3.

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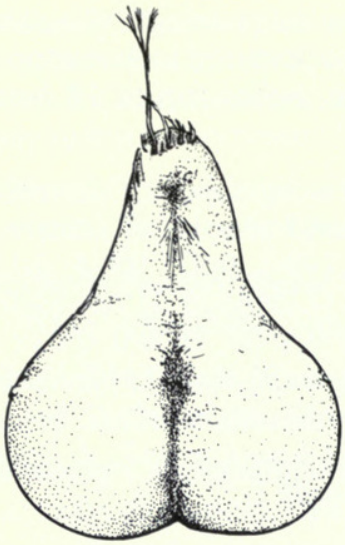
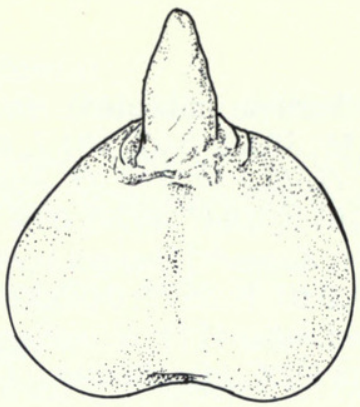
†minute tuft, present study.
††minute tuft, up to 8 1-mm feathers in 8 specimens.
†††some specimens with minute tuft *fide* Miller (1924: he also reported tufts in *Ketupa zeylonensis, Bubo bubo, Gymnoglaux lawrencii*).

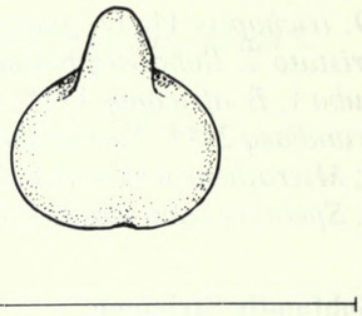
*minute tuft, present study.
**minute feathers in 6 specimens.
***minute feathers in 3 specimens.
****some specimens with minute tuft (Nitszch 1840, Beddard 1898, Miller 1924, or Verheyen 1956*a*).
*****'one or 2 very small white feathers,' Paris 1913: 182.



*Asio flammeus*



*Steatornis caripensis*



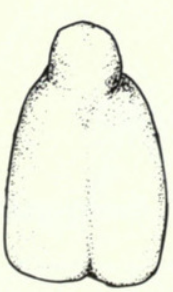
*Batrachostomus septimus*

**Family Aegothelidae** (Owlet-nightjars)
MORPHOLOGY. Broad, flattened and bilobed, papilla large, naked.
MATERIAL EXAMINED. *Aegotheles insignis* 1.

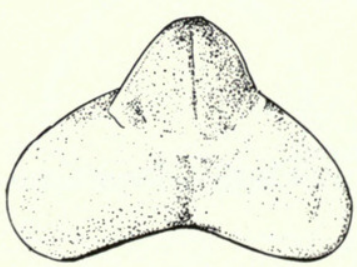
**Family Caprimulgidae** (Nighthawks, Goatsuckers)
MORPHOLOGY (family). Very small not apparently bilobed (see also Paris 1913: 173), papilla large, naked. I did not confirm the report by Arnall & Keymer (1975) that the gland is absent 'in nightjars.'

**Subfamily Chordeilinae** (Nighthawks)
MATERIAL EXAMINED. *Lurocalis semitorquatus* 1; *Chordeiles minor* 6 (M: 64·8, 0·01; 67·5, 0·01. F: 75·4, 0·01; 87·5, 0·01; 79·6, 0·01); *Podager nacunda* 2.

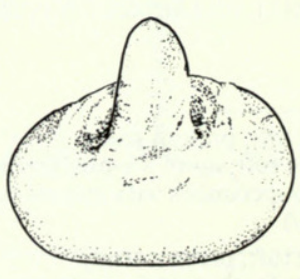
**Subfamily Caprimulginae** (Goatsuckers)
MATERIAL EXAMINED. *Eurostopodus macrotis* 1; *Nyctidromus albicollis* 4; *Phalaenoptilus nuttallii* 2; *Otophanes yucatanicus* 1; *Caprimulgus carolinensis* 10 (M: 113·0, 0·01; 80·7, 0·01; 124·8, 0.01. $\bar{x}$ of 4 F: 114·2, 0·01); *C. vociferus* 2 (M: 55·5, 0·02. F: 52·5, 0·02); *Scotornis climacurus* 1; *Semeiophorus vexillarius* 1; *Hydropsalis brasiliana* 1.



*Nyctibius griseus*



*Aegotheles insignis*



*Podager nacunda*

## Order Apodiformes

**Gland characteristics.** Naked.
NOTE. The reference by Elder (1954) and Pettingill (1985) to gland absence in 'certain species' of Apodiformes was unsubstantiated by me.

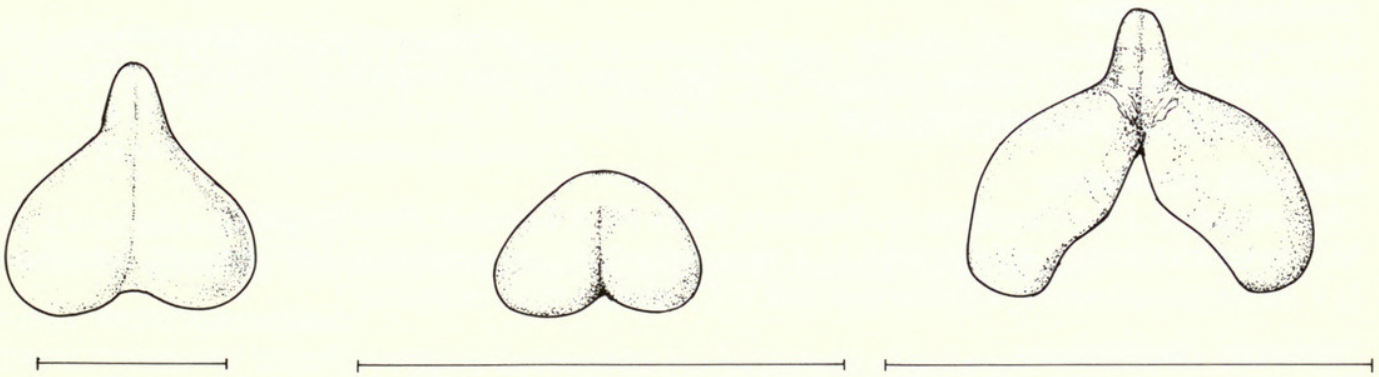
**Family Apodidae** (Swifts)
MORPHOLOGY (family). Indistinctly bilobed, papilla moderately developed, naked.

**Subfamily Chaeturinae** (Spine-tailed Swifts)
MATERIAL EXAMINED. *Collocalia inexpectata* 1; *C. vanikorensis* 1; *Hirund-apus giganteus* 2; *Streptoprocne zonaris* 1; *Chaetura pelagica* 3; *C. rutilus* 1.

**Subfamily Apodinae** (Typical Swifts)
MATERIAL EXAMINED. *Apus apus* 1; *Aeronautes saxatalis* 1; *Reinarda squamata* 1; *Cypsiurus parva* 1.

**Family Hemiprocnidae** (Crested Swifts)
MORPHOLOGY. Indistinctly bilobed, papilla absent, naked.
MATERIAL EXAMINED. *Hemiprocne mystacea* 1; *H. comata* 1.

**Family Trochilidae** (Hummingbirds)
MORPHOLOGY. Distinctly bilobed with lobes greatly separated, papilla large, naked.
MATERIAL EXAMINED. *Glaucis hirsuta* 1; *Phaethornis superciliosus* 2; *P. eurynome* 1; *P. longuemareus* 2; *Eutoxeres condamini* 2; *Phaeochroa cuvierii* 2; *Campylopterus curvipennis* 8; *C. hemileurcurus* 1; *C. ensipennis* 1; *Eupetomena macroura* 1; *Florisuga mellivora* 1; *Colibri serrirostris* 1; *Anthracothorax nigricollis* 1; *Chrysolampis mosquitus* 1; *Stephanoxis lalandi* 1; *Chlorestes notatus* 1; *Thalurania furcata* 1; *Hylocharis chrysura* 1; *Chrysuronia oenone* 1; *Leucochloris albicollis* 1; *Amazilia candida* 1; *A. versicolor* 1; *A. cyanocephala* 1; *A. rutila* 1; *A. tzacatl* 13; *Patagona gigas* 1; *Ensifera ensifera* 1; *Archilochus colubris* 3; *Selasphorus rufus* 1.



*Hirund-apus (Chaetura) giganteus*

*Hemiprocne comata*

*Glaucis hirsuta*

## Order Coliiformes

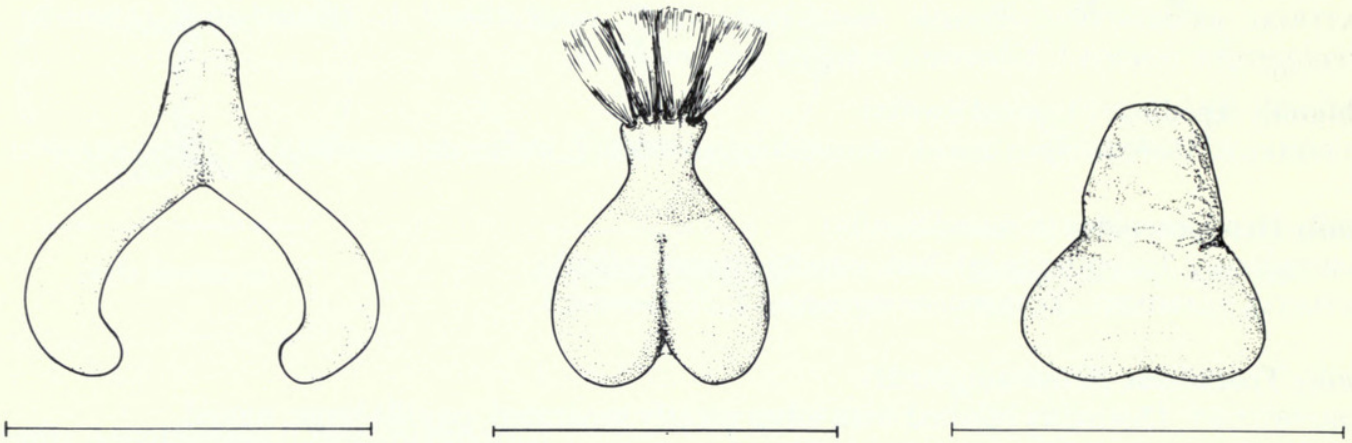
**Gland characteristics.** Tufted.

**Family Coliidae** (Colies)
MORPHOLOGY. Distinctly bilobed, papilla large, tufted. Verheyen (1956*e*) makes the unsubstantiated comment that the gland of *Urocolius* (= *Colius indicus* and *C. macrourus* of Peters) is naked. Both Nitzsch (1867) and Garrod (1876) reported that the gland of *Colius* is tufted. Type I.
MATERIAL EXAMINED. *Colius striatus* 4; *C. colius* 1; *C. indicus* 2; *C. macrourus* 1.

## Order Trogoniformes

**Gland characteristics.** Naked.

**Family Trogonidae** (Trogons)
MORPHOLOGY. Indistinctly bilobed, papilla large, naked.
MATERIAL EXAMINED. *Pharomachrus mocino* 2; *Priotelis temnurus* 1; *Temnotrogon roseigaster* 1; *Trogon strigilatus* 1; *T. citreola* 1; *Apaloderma marina* 1; *Harpactes erythrocephalus* 1.



*Patagona gigas* *Colius macrourus* *Pharomachrus mocino*

## Order Coraciiformes*

**Gland characteristics.** Much inter- and intrafamilial variation: naked, or sparsely to densely tufted.

**Family Alcedinidae** (Kingfishers)

**Subfamily Cerylinae**
MORPHOLOGY. Indistinctly bilobed, papilla absent or small, tufted (16 feathers in *C. alcyon*).
MATERIAL EXAMINED. *Ceryle torquata* 1; *C. alcyon* 6 (M: 102·5, 0·25. F: 104·5, 0·22); *C. rudis* 7; *Chloroceryle americana* 6; *C. aena* 4.

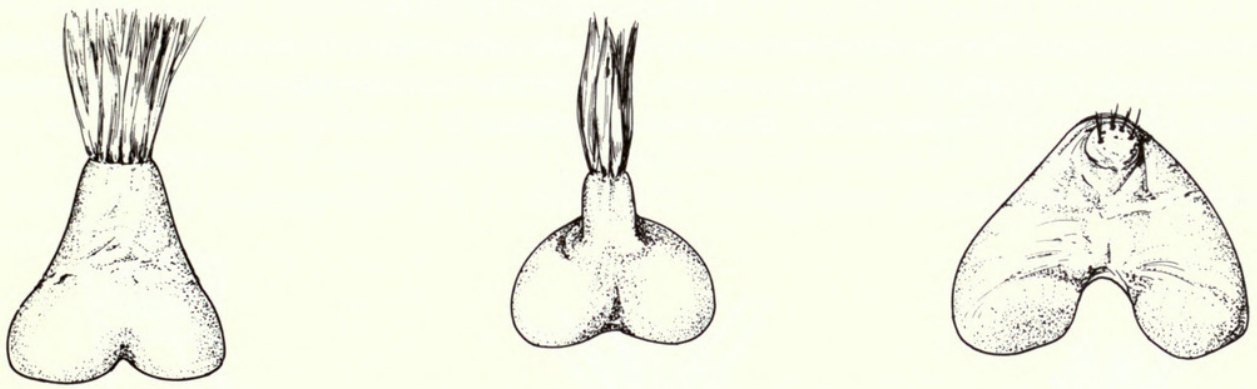
**Subfamily Alcedininae**
MORPHOLOGY. Like Cerylinae (12 feathers, Paris 1913, Jacob & Ziswiler 1982).
MATERIAL EXAMINED. *Alcedo atthis* 1; *A. meninting* 1; *A. euryzona* 1; *A. leucogaster* 1; *Ispidina picta* 1; *I. madagascariensis* 1; *Ceyx argentatus* 1; *C. azureus* 1; *C. erithacus* 1.

**Subfamily Daceloninae**
MORPHOLOGY. Indistinctly or distinctly bilobed, papilla absent (*Pelargopsis*) to large (*Tanysiptera*), tufted (small in *Lacedo*, large in *Halcyon*) or gland naked (*Tanysiptera*) (12 feathers in *Dacelo*). *Tanysiptera* species apparently have no distinctive ecological or behavioral traits that might be correlated with the unusual naked gland condition (Fry 1980). Type I.
MATERIAL EXAMINED. *Pelargopsis capensis* 1; *Lacedo pulchella* 2; *Dacelo novaeguineae* 3; *D. leachii* 1; *Clytoceyx rex* 1; *Melidora macrorrhina* 1; *Halcyon coromanda* 1; *H. smyrnensis* 1; *H. pileata* 1; *H. senegalensis* 1; *H. malimbica* 1; *H. albiventris* 1; *H. macleayii* 1; *H. cinnamomina* 1; *H. chloris* 1; *Tanysiptera galatea* 2; *T. sylvia* 1.

**Family Todidae** (Todies)
MORPHOLOGY. Indistinctly bilobed, papilla large, tufted (6 feathers in *T. subulatus*). Nitzsch (1867: 88) erroneously stated that *Todus* has a naked oil-gland, a point corrected by Forbes (1882). Type I.
MATERIAL EXAMINED. *Todus angustirostris* 1; *T. subulatus* 2.

*morphology reported here is, with exceptions noted below, consistent with the descriptions in Verheyen (1955, *a, b, c*).

**Family Momotidae** (Motmots)
MORPHOLOGY. Flattened and distinctly bilobed with lobes widely divergent, papilla moderately to well developed, minutely tufted or naked. Much difference of opinion is found in the literature concerning the feathered condition of glands in this family probably because some investigators failed to use magnification in their examinations of glands. By combining here the comments of Garrod (1878), Forbes (1882), Newton (1893–1896), Beddard (1898), Miller (1915), and Verheyen (1955*a*) plus microscopic examinations in the present study, it is apparent that any specimen of any species might have a gland that is naked or one that is tufted with 1–8 'vestigial,' 'rudimentary,' or very small feathers (ca. 1 mm). Type I.
MATERIAL EXAMINED. *Hylomanes momotula* 1; *Electron platyrhynchum* 1; *Eumomota superciliosa* 5; *Baryphthengus ruficapillus* 3; *Momotus momota* 5.



*Dacelo novaeguineae* *Todus subulatus* *Momotus momota*

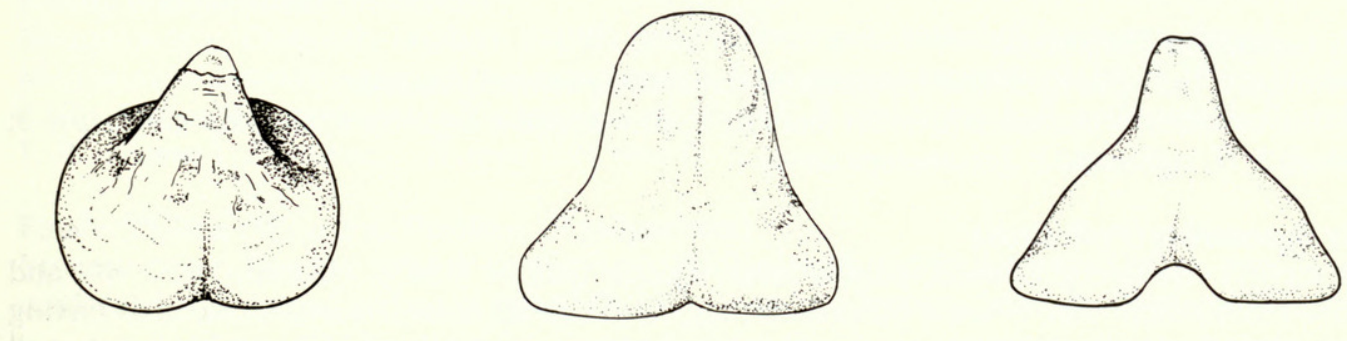
**Family Meropidae** (Bee-eaters)
MORPHOLOGY. Indistinctly bilobed, papilla large, naked (also reported by Paris 1913: 175).
MATERIAL EXAMINED. *Melittophagus pusillus* 1; *Merops apiaster* 2; *M. viridis* 1; *Nyctyornis amicta* 1.

**Family Leptosomatidae** (Cuckoo-rollers)
MORPHOLOGY. Indistinctly bilobed, papilla large, naked. The gland, about 10 mm in length, does not conform to Nitzsch's description of 'atrophy and almost total disappearance . . .' (1867:161).
MATERIAL EXAMINED. *Leptosomus discolor* 2.

**Family Coraciidae** (Rollers)
MORPHOLOGY (family). Flattened and indistinctly bilobed, papilla large, naked.

**Subfamily Brachypteraciinae**
MATERIAL EXAMINED. *Brachypteracias leptosomus* 1; *Uratelornis chimaera* 1.

**Subfamily Coraciinae**
MATERIAL EXAMINED. *Coracias garrulus* 1; *Eurystomus orientalis* 1.

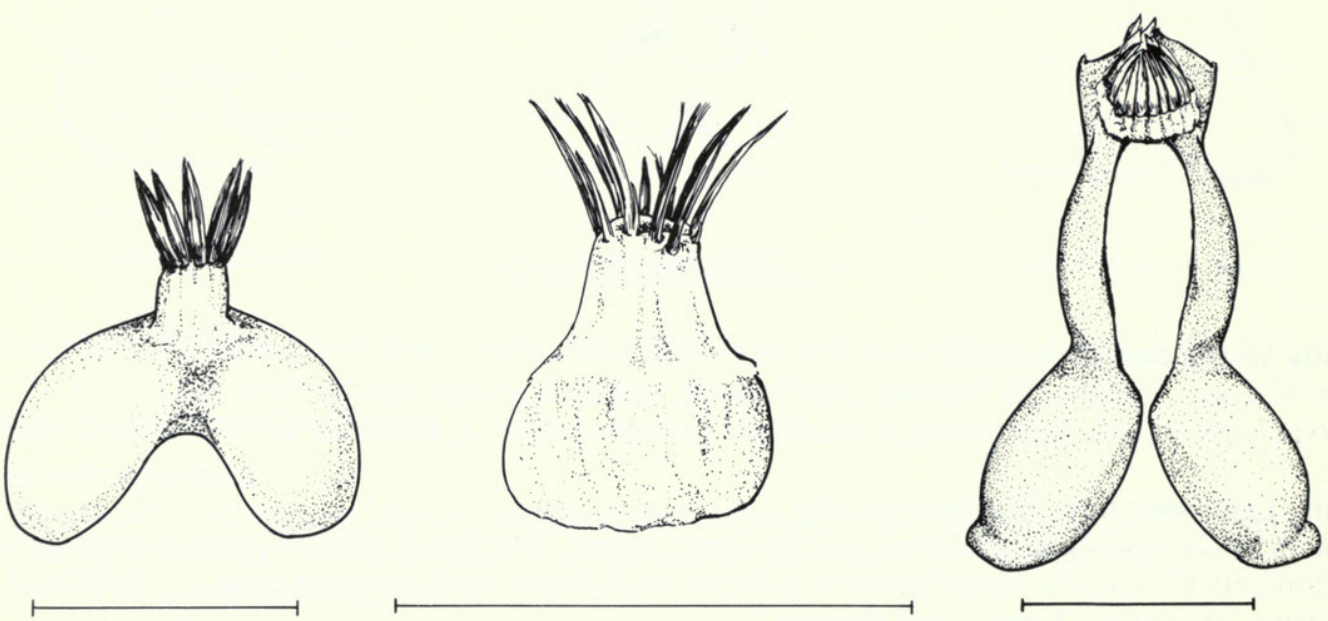


*Merops apiaster* *Leptosomus discolor* *Coracias garrulus*

**Family Upupidae** (Hoopoes)
MORPHOLOGY. Distinctly bilobed with widely diverging lobes, papilla large, tufted (10 feathers, Paris 1913, Grassé 1950; 14 feathers, Jacob & Ziswiler 1982). Type I.
MATERIAL EXAMINED. *Upupa epops* 2.

**Family Phoeniculidae** (Wood-hoopoes)
MORPHOLOGY. Small and not apparently bilobed, papilla large, tufted (10 feathers). Type IIa.
MATERIAL EXAMINED. *Phoeniculus purpureus* 1; *P. bollei* 1; *Rhinopomastus minor* 1; *R. cyanomelas* 1.

**Family Bucerotidae** (Hornbills)
MORPHOLOGY. Distinctly bilobed (lobes completely separated), papilla small, tufted (50 feathers, Paris 1913; 32–48 feathers in *T. erythrorhynchus*, Jacob & Ziswiler 1982). In *Tockus hartlaubi* the gland and its feather tuft are 'vestigial' (Verheyen 1955*a*). Type II.
MATERIAL EXAMINED. *Tockus alboterminatus* 1; *T. erythrorhynchus* 1; *T. flavirostris* 1; *T. deckeni* 1; *Aceros undulatus* 1; *A. plicatus* 1; *Anthracoceros malabaricus* 1; *A. coronatus* 1; *Ceratogymna atrata* 1; *Buceros bicornis* 1; *B. hydrocorax* 1; *Bucorvus abyssinicus* 2.




## Order Piciformes

**Gland characteristics.** Much inter- and intrafamilial variation: absent (rarely), naked, or sparsely to densely tufted.
NOTE. Differences (see figures) in gland morphology among the six families lend evidence to a polyphyletic origin of the Piciformes as suggested by Olson (1983).

**Family Galbulidae** (Jacamars)
MORPHOLOGY. Indistinctly bilobed, papilla moderately developed, naked.
MATERIAL EXAMINED. *Galbalcyrhynchus leucotis* 1; *Brachygalba lugubris* 1; *Galbula albirostris* 5; *G. galbula* 1; *G. ruficauda* 3; *Jacamerops aurea* 1.

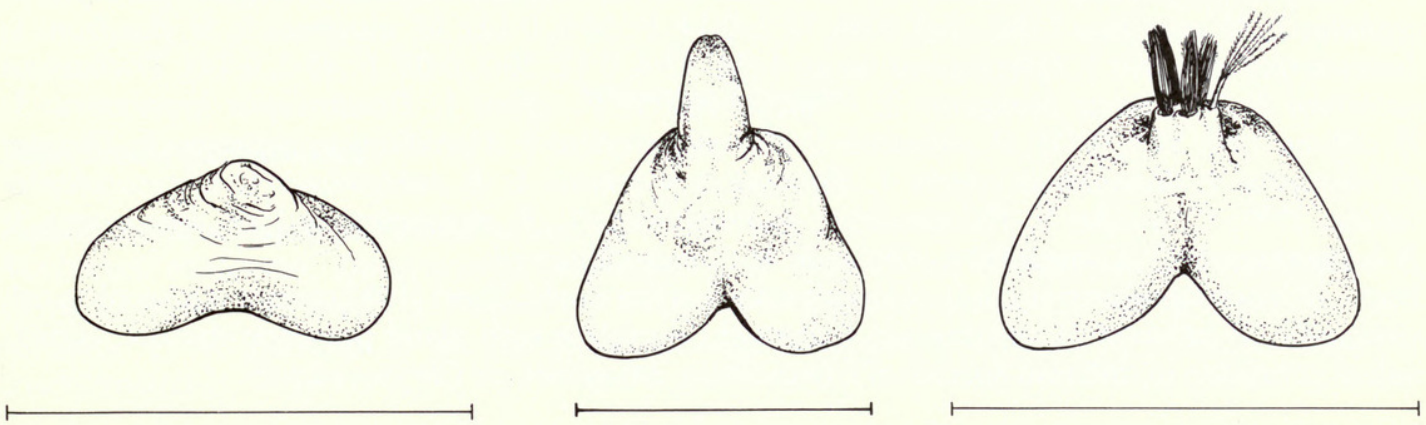
**Family Bucconidae** (Puff-birds)
MORPHOLOGY. Distinctly bilobed, papilla large, naked. Gadow (1893), Nitzsch (1867: 94), and Beddard (1898) each refer to some bucconids (e.g., *Malacoptila fusca, Bucco, Monasa*) as having glands with 'a few fine hairs at the apex' or 'feathered.' However, Miller (1915) and I found that all species and individuals in the Bucconidae that we examined had naked glands.

MATERIAL EXAMINED. *Notharchus macrorhynchos* 3; *Nystalus maculatus* 1; *Hypnelus bicinctus* 1; *Malacoptila striata* 1; *M. fusca* 1; *M. panamensis* 6; *Monasa nigrifrons* 1; *M. atra* 1; *M. morphoeus* 1; *Chelidoptera tenebrosa* 2.

**Family Capitonidae** (Barbets)

MORPHOLOGY. Distinctly bilobed, papilla moderately developed, naked or sparsely tufted (8–12 feathers in 2 species, Jacob & Ziswiler 1982). In addition to the species marked * below, the following species were reported by Miller (1924: 323) as having naked glands: *Stactolaema, Pogoniulus duchaillui, Trachyphonus cafer,* and *T. margaritatus.* Individual differences (naked vs. tufted) have been found in *Trachyphonus vaillantii, T. darnaudii,* and *Lybius torquatus.* A feathered gland was reported for *Pogonias* (*Lybius*) by Nitzsch (1867: 93). Beddard (1898: 168) noted that (all) capitonids have feathered glands. I did not confirm the statement by Verheyen (1955*b*) that different species in the Capitonidae lack a gland. Type I.

MATERIAL EXAMINED (tufted unless otherwise indicated). *Semnornis frantzii* 1; *S. ramphastinus* 1; *Psilopogon pyrolophus* 2; *Megalaima rafflesii* 2; *M. mystacophanos* 1; *M. flavifrons* 1; *M. asiastica* 1; *M. henricii* 1; *M. haemacephala* 1; *Gymnobucco bonapartei* 2*; *Smilorhis leucotis* 1*; *Pogoniulus simplex* 1; *P. bilineatus* 1; *P. subsulphureus* 1; *Tricholaema leucomelan* 1*; *T. diadematum* 1*; *Lybius guifsobalito* 1*; *L. leucocephalus* 1*; *L. dubius* 2*; *Trachyphonus purpuratus* 1; *T. vaillantii* 2*; *T. darnaudii* 1*.



*Galbula ruficauda* *Notharchus macrorhnychos* *Megalaima rafflesii*

**Family Indicatoridae** (Honey-guides)

MORPHOLOGY. Indistinctly bilobed, papilla moderately developed, tufted (2 feathers). Miller (1924: 323) correctly noted that the Indicatoridae are invariably tufted 'but the tuft is vestigial in *Prodotiscus.*' I did not confirm the statement by Verheyen (1955*b*) that different species in the Indicatoridae lack a gland. Type I.

MATERIAL EXAMINED. *Prodotiscus insignis* 2; Indicator exilis 1; *I. minor* 1; *I. maculatus* 2; *Melichneutes robustus* 1.

**Family Ramphastidae** (Toucans)

MORPHOLOGY. Distinctly bilobed, papilla poorly developed, tufted (8 feathers). Type I.

MATERIAL EXAMINED. *Aulacorhynchus prasinus* 1; *Pteroglossus torquatus* 2 (M, Z: 183·3, 0·14; 186·3, 0·12); *Andigena hypoglauca* 1; *Ramphastos vitellinus* 1; *R. discolorus* 1; *R. sulfuratos* 1; *R. swainsoni* 1; *R. tucanus* 1; *R. cuvieri* 1; *R. inca* 1; *R. toco* 2.

**Family Picidae** (Wryneck, Piculets, Woodpeckers)

MORPHOLOGY (family). Absent or distinctly bilobed with widely separated lobes, papilla usually moderately developed, naked or tufted (8–12 feathers in 3 species, Jacob & Ziswiler 1982). In some

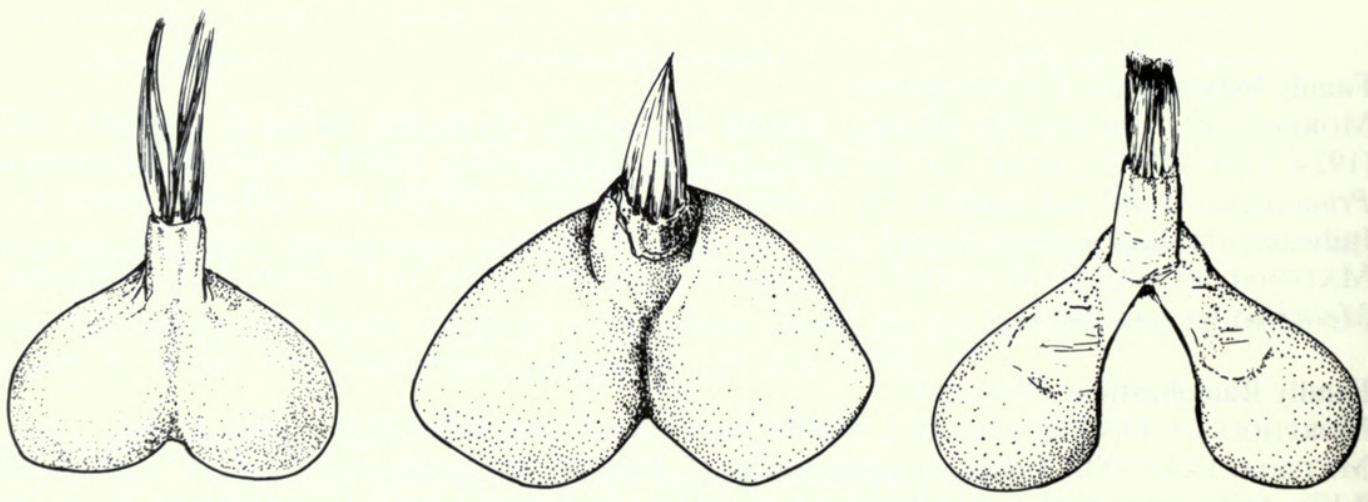
*naked, present study.

North American species (e.g., *Dryocopus, Colaptes*) each lobe narrows down to an extremely small 'band' before joining at the papilla, making dissection and removal of an intact gland difficult. Miller (1924) noted the gland's absence in *Campethera maculosa, permista, caroli,* and *nivosa,* these in addition to *C. cailliartii* in the present study. The gland is naked in *Dinopium* and *Gecinulus* and naked or tufted in specimens of *Chrysocolaptes validus fide* Miller (1924).

**Subfamily Jynginae** (Wrynecks)
MORPHOLOGY. 'Well developed and clearly bilobed' (Paris 1913: 168), tufted (8 feathers, Paris 1913). Type II.
MATERIAL EXAMINED. *Jynx torquilla* 1.

**Subfamily Picumninae** (Piculets)
MORPHOLOGY. Tufted.
MATERIAL EXAMINED. *Picumnus cirratus* 1; *Nesoctites micromegas* 1; *Sasia ochracea* 2; *S. abnormis* 1.

**Subfamily Picinae** (Woodpeckers)
MORPHOLOGY. Tufted, naked, or absent. Type I.
MATERIAL EXAMINED (tufted unless otherwise indicated). *Colaptes auratus* 7 (M: 100·9, 0·12. F: 131·9, 0·12; 137·7, 0.11; 98·5, 0·12); *Piculus simplex* 1; *Campethera punctuligera* 2; *C. nubica* 4; *C. bennettii* 1; *C. cailliautii* 2*; *C. abingoni* 2; *C. permista* 1*; *C. caroli* 2**; *C. nivosa* 7*; *Celeus flavescens* 2; *Micropternus brachyurus* 1; *Picus viridis* 1; *Dinopium beneghalense* 2***; *D. javanense* 1***; *Dryocopus pileatus* 5 (M: 240·8, 0·15. F: 220·8, 0·12); *Asyndesmus lewis* 1; *Melanerpes erythrocephalus* 2; *M. carolinus* 7 (M: 76·0, 0·09; 72·2, 0·14. F: 54·9, 0·12); *M. aurifrons* 3; *M. flavifrons* 1; *Leuconerpes candidus* 1; *Sphyrapicus varius* 4 (M: 43·4, 0·12; 50·3, 0·08. F: 45·5, 0·14); *Trichopicus cactorum* 2; *Veniliornis fumigatus* 2; *V. passerinus* 1; *V. affinis* 1; *Dendrocopos hyperythrus* 1; *D. villosus* 1 (F: 54·3, 0·11); *D. pubescens* 2; *Picoides arcticus* 1; *Xiphidiopicus percussus* 1; *Thripias pyrrhogaster* 1; *Hemicircus canete* 1; *Blythipicus pyrrhotis* 1; *B. rubiginosus* 1; *Chrysocolaptes validus* 2***; *C. lucidus* 8; *Phloeoceastes guatemalensis* 1; *P. melanoleucus* 1; *P. leucopogon* 1; *P. haematogaster* 1; *Campephilus principalis* 1; *C. magellanicus* 1.
NOTE. In his comprehensive study of woodpeckers of the world, Short (1982) presents no ecological, structural, or behavioral information that might correlate with gland presence/absence, tufted/naked condition in different species of *Campethera, Dinopium,* or *Chrysocolaptes.*



*Indicator maculatus* *Ramphastos toco* *Colaptes auratus*

*gland absent, this study; also absent in *C. maculosa* (Miller 1924).
**gland present (tufted) or absent in some specimens, this study.
***gland naked, this study. Tuft is individually variable in specimens of *Chrysocolaptes* (Miller 1924: 324).

## Order Passeriformes

**Gland characteristics.** Naked.

MORPHOLOGY (order). Indistinctly or distinctly bilobed, papilla moderately or well developed, naked. Although varying slightly in shape ('kidney-vs heart-shaped'), weight, and relative length of papilla (Jacob & Ziswiler 1982), glands of all passerines have been uniformly described by all authors as being present and naked. In the present comprehensive study, representatives of all passerine families (68, Peters 1931–1986) and subfamilies were examined: 1187 individuals of 349 genera and 482 species. Except for relative size (see Weights and sizes of glands section), I found no consistent, major morphological differences between or among any taxa. Paris (1913: 67) in his extensive study reported only slight variations in shape among at least 11 passerine families.

### Suborder Eurylaimi

**Family Eurylaimidae** (Broadbills)

**Subfamily Eurylaiminae**

MATERIAL EXAMINED. *Smithornis capensis* 1; *Eurylaimus javanicus* 1; *Psarisomus dalhousiae* 1.

**Subfamily Calyptomeninae**

MATERIAL EXAMINED. *Calyptomena whiteheadi* 1.

### Suborder Tyranni

**Superfamily Furnarioidea**

**Family Dendrocolaptidae** (Wood-hewers)

MATERIAL EXAMINED. *Dendrocincla anabatina* 8; *D. homochroa* 4; *Sittasomus griseicapillus* 4; *Glyphorhynchus spirurus* 10; *Drymornis bridgesii* 1; *Dendrocolaptes certhia* 7; *Xiphorhynchus ocellatus* 1; *X. guttatus* 2; *X. flavigaster* 3; *Lepidocolaptes souleyetii* 3; *Campylorhamphus trochilirostris* 1;

**Family Furnariidae** (Ovenbirds)

MATERIAL EXAMINED. *Geositta cunicularia* 1; *Upucerthia validirostris* 1; *Cinclodes fuscus* 1; *Furnarius leucopus* 1; *Aphrastura spinacauda* 2; *Phleocryptes melanops* 2; *Schizoeaca fuliginosa* 1; *Synallaxis albescens* 1; *S. erythrothorax* 2; *Poecilurus candei* 1; *P. scutatus* 1; *Asthenes hudsoni* 1; *Phacellodomus striaticollis* 1; *Coryphistera alaudina* 2; *Anumbius annumbi* 2; *Margarornis squamiger* 1; *Pseudoseisura lophotes* 2; *Ancistrops strigilatus* 1; *Syndactyla rufosuperciliata* 2; *Philydor erythrocercus* 1; *Automolus infuscatus* 1; *A. albigularis* 1; *A. ochrolaemus* 7; *Heliobletus contaminatus* 1; *Xenops minuta* 11; *Sclerurus guatemalensis* 4.

**Family Formicariidae** (Ant-thrushes)

MATERIAL EXAMINED. *Taraba major* 1; *Thamnophilus doliatus* 5; *T. aethiops* 1; *Myrmotherula surinamensis* 1; *Microrhopias quixensis* 2; *Formicivora grisea* 1; *Drymophila caudata* 1; *Cercomacra tyrannina* 5; *C. nigricans* 1; *Hypocnemis cantator* 1; *Myrmeciza longipes* 1; *Formicarius colma* 1; *F. analis* 5; *Chamaeza ruficauda* 1; *Pithys albifrons* 1; *Gymnopithys leucaspis* 1; *Hylophylax naevioides* 1; *Grallaria guatimalensis* 1.

**Family Conopophagidae** (Ant-pipits)

MATERIAL EXAMINED. *Conopophaga lineata* 1; *C. castaneiceps* 1; *Corythopis torquata* 1.

**Family Rhinocryptidae** (Tapaculos)

MATERIAL EXAMINED. *Pteroptochos tarnii* 1; *Scelorchilus rubecula* 1; *Rhinocrypta lanceolata* 1; *Teledromas fuscus* 1; *Melanopareia maximiliani* 1; *Scytalopus latebricola* 1.

**Superfamily Tyrannoidea**

**Family Tyrannidae** (Tyrant Flycatchers)

**Subfamily Elaeniinae**
MATERIAL EXAMINED. *Sublegatus modestus* 1; *Myiopagis viridicata* 2; *Elaenia flavogaster* 3; *E. pallatangae* 1; *Mionectes olivaceus* 1; *M. oleagineus* 28; *Leptopogon amaurocephalus* 7; *Oncostoma cinereigulare* 8; *Todirostrum sylvia* 1; *T. cinereum* 2; *Rhynchocyclus brevirostris* 1; *Tolmomyias sulphurescens* 4; *Platyrinchus cancrominus* 4; *P. mystaceus* 4.

**Subfamily Fluvicolinae**
MATERIAL EXAMINED. *Onychorhynchus coronatus* 3; *Terenotriccus erythrurus* 1; *Myiobius barbatus* 2; *Contopus virens* 1; *C. cinereus* 1; *Empidonax flaviventris* 3; *E. virescens* 1; *E. minimus* 5; *Sayornis phoebe* 2; *Ochthoeca fumicola* 1; *Myiotheretes striaticollis* 1; *Xolmis irupero* 1; *Muscisaxicola* sp. 1; *Knipolegus aterrimus* 1; *Fluvicola pica* 1.

**Subfamily Tyranninae**
MATERIAL EXAMINED. *Attila spadiceus* 7; *Rhytipterna simplex* 1; *Myiarchus tuberculifer* 2; *M. nuttingi* 2; *M. crinitus* 2 (M: 42·4, 0·08); *Pitangus sulphuratus* 3; *Megarhynchus pitangua* 2; *Myiodynastes bairdii* 1; *Tyrannus tyrannus* 2 (F: 40·0, 0·10); *T. melancholicus* 1.

**Subfamily Tityrinae**
MATERIAL EXAMINED. *Pachyramphus cinnamomeus* 1; *Tityra semifasciata* 2; *T. inquistor* 3.

**Family Pipridae** (Manakins)
MATERIAL EXAMINED. *Schiffornis turdinus* 3; *Chloropipo uniformis* 1; *Xenopipo atronitens* 1; *Manacus manacus* 10; *Chiroxiphia lanceolata* 1; *Pipra filicauda* 1; *P. mentalis* 40; *P. chloromeros* 1.

**Family Cotingidae** (Cotingas)
MATERIAL EXAMINED. *Ampelion rubrocristatus* 1; *Pipreola arcuata* 1; *P. chlorolepidota* 1; *Lipaugus vociferans* 1; *Gymnoderus foetidus* 1; *Querula purpurata* 1; *Pyroderus scutatus* 1; *Cephalopterus ornatus* 1; *Perissocephalus tricolor* 1; *Procnias nudicollis* 1; *Rupicola peruviana* 1.

**Family Oxyrunicidae** (Sharpbills)
MATERIAL EXAMINED. *Oxyruncus cristatus* 1.

**Family Phytotomidae** (Plantcutters)
MATERIAL EXAMINED. *Phytotoma rutila* 1.

**Family Pittidae** (Pittas)
MATERIAL EXAMINED. *Pitta erythrogaster* 1; *P. granatina* 1.

**Family Philepittidae** (Asitys)

**Subfamily Philepittinae**
MATERIAL EXAMINED. *Philepitta castanea* 1.

**Subfamily Neodrepanidinae**
MATERIAL EXAMINED. *Neodrepanis coruscans* 1.

**Family Acanthisittidae** (New Zealand Wrens)
MATERIAL EXAMINED. *Acanthisitta chloris* 2; *Xenicus longipes* 5; *X. gilviventris* 1.
NOTE. Most specimens available for examination were poorly preserved. I identified a gland in *Acanthisitta*, in only 1 of the 5 *Xenicus longipes*, and not in *X. gilviventris*.

## Suborder Menurae

**Family Menuridae** (Lyrebirds)
MATERIAL EXAMINED. *Menura novaehollandiae* 2.

**Family Atrichornithidae** (Scrub-birds)
MATERIAL EXAMINED. *Atrichornis clamosus* 1.
NOTE. B. Gillies (in litt., 4 April 1985) reported that this specimen (R11353) has a naked gland; another specimen (A15926) is illustrated in Zusi (1985) as having a naked gland.

## Suborder Oscines

**Family Alaudidae (Larks)**
MATERIAL EXAMINED. *Mirafra javanica* 1; *M. assamica* 1; *Eremopterix signata* 1; *Alaemon alaudipes* 1; *Melanocorypha yeltoniensis* 1; *Calandrella cinerea* 1; *Galerida cristata* 1; *Lullula arborea* 1; *Eremophila alpestris* 1.

**Family Hirundinidae** (Swallows)
MATERIAL EXAMINED. *Tachycineta bicolor* 2; *Progne subis* 7 (F: 63·1, 0·03); *Hirundo rustica* 3; *H. smithii* 1.

**Family Motacillidae (Wagtails, Pipits)**
MATERIAL EXAMINED. *Dendronanthus indicus* 1; *Motacilla alba* 2; *M. aguimp* 1; *Macronyx croceus* 1; *Anthus spinoletta* 1 (M: 19·2, 0·13).

**Family Campephagidae** (Cuckoo-shrikes)
MATERIAL EXAMINED. *Coracina novaehollandiae* 1; *C. striata* 1; *C. morio* 1; *C. panayensis* 1; *C. melaschistos* 1; *Lalage nigra* 1; *Campephaga phoenicea* 1; *Pericrocotus cinnamomeus* 1; *P. flammeus* 1; *Hemipus picatus* 1.

**Family Pycnonotidae** (Bulbuls)
MATERIAL EXAMINED. *Pycnonotus barbatus* 8; *P. goiavier* 1; *Chlorocichla flaviventris* 2; *Bleda eximia* 1; *Criniger phaeocephalus* 1; *Setornis criniger* 1; *Hypsipetes everetti* 1.

**Family Irenidae** (Leaf Birds)
MATERIAL EXAMINED. *Irena puella* 1.

**Family Laniidae** (Shrikes and Allies)

**Subfamily Prionopinae**
MATERIAL EXAMINED. *Eurocephalus ruppelli* 1; *Prionops plumata* 1.

**Subfamily Malaconotinae**
MATERIAL EXAMINED. *Dryoscopus cubla* 3; *D. sabini* 1; *Tchagra senegala* 1; *T. australis* 2; *Laniarius ferrugineus* 3; *L. barbarus* 1; *Telophorus sulfureopectus* 1; *T. multicolor* 1.

**Subfamily Laniinae**
MATERIAL EXAMINED. *Corvinella corvina* 1; *Lanius collurio* 1; *L. ludovicianus* 2.

**Subfamily Pityriasinae**
MATERIAL EXAMINED. *Pityriasis gymnocephala* 1.

**Family Vangidae** (Vangas)
MATERIAL EXAMINED. *Calicalicus madagascariensis* 1; *Vanga curvirostris* 1.

**Family Bombycillidae** (Waxwings)

**Subfamily Bombycillinae**
MATERIAL EXAMINED. *Bombycilla garrulus* 1; *B. cedrorum* 1 (F: 29·2, 0·10).

**Subfamily Ptilogonatinae**
MATERIAL EXAMINED. *Ptilogonys cinereus* 1.

**Subfamily Hypocoliinae**
MATERIAL EXAMINED. *Hypocolius ampelinus* 1.

**Family Dulidae** (Palm Chat)
MATERIAL EXAMINED. *Dulus dominicus* 1.

**Family Cinclidae** (Dippers)
MATERIAL EXAMINED. *Cinclus cinclus* 1; *C. pallasii* 1; *C. mexicanus* 4 (unsexed: 63·6, 0·48; 58·3, 0·65; 59·7, 0·71).
NOTE. Nitzsch (1867: 73) reported that the gland of *Cinclus* 'bears small down-feathers upon its surface,' but it is not clear that his 'surface' refers to the papilla's tip. All specimens examined in the present study had naked glands.

**Family Troglodytidae** (Wrens)
MATERIAL EXAMINED. *Campylorhynchus rufinucha* 1; *Cistothorus platensis* 2; *C. palustris* 2; *Thryothorus pleurostictus* 2; *T. maculiectus* 2; *T. ludovicianus* 1; *T. rufalbus* 1; *Troglodytes aedon* 2; *Uropsila leucogastra* 1; *Henicorhina leucosticta* 3.

**Family Mimidae** (Mockingbirds and Allies)
MATERIAL EXAMINED. *Dumetella carolinensis* 17 (F: 35·4, 0·18); *Mimus polyglottos* 5 (M: 47·6, 0·16); *Toxostoma rufum* 5 (M: 55·3, 0·07. F: 69·1, 0·14).

**Family Prunellidae** (Accentors)
MATERIAL EXAMINED. *Prunella collaris* 1.

**Family Muscicapidae***

**Subfamily Turdinae** (Thrushes)
MATERIAL EXAMINED. *Zeledonia coronata* 4; *Sialia currucoides* 1; *Catharus fuscescens* 2 (F: 28·1, 0·09); *C. minimus* 2; *C. ustulatus* 3; *C. guttatus* 2; *Hylocichla mustelina* 28 (F: 47·4, 0·09; 59·7, 0·07); *Turdus merula* 1; *T. iliacus* 1; *T. philomelos* 1; *T. viscivorus* 1; *T. grayi* 4; *T. migratorius* 4 (M: 85·3, 0·09. F: 72·4, 0·09; 85·7, 0·12).

**Subfamily Orthonychinae** (Logrunners)
MATERIAL EXAMINED. *Cinclosoma cinnamomeum* 1.

**Subfamily Timaliinae** (Babblers)
MATERIAL EXAMINED. *Trichastoma bicolor* 1; *Malacopteron magnum* 1; *Pomatorhinus schisticeps* 1; *Napothera brevicaudata* 1; *Chamaea fasciata* 2; *Turdoides squamiceps* 1; *Garrulax leucolophus* 3; *Actinodura ramsayi* 1; *Alcippe castaneceps* 1.

**Subfamily Panurinae** (Parrotbills)
MATERIAL EXAMINED. *Paradoxornis heudei* 1.

**Subfamily Picathartinae** (Picathartes)
MATERIAL EXAMINED. *Picathartes oreas* 1.

**Subfamily Polioptilinae** (Gnatcatchers and allies)
MATERIAL EXAMINED. *Ramphocaenus melanurus* 2; *Polioptila caerulea* 1.

*nomenclature and inclusive taxa according to Peters (Vol. X, 1964).

**Family Sylviidae** (Old World Warblers)
MATERIAL EXAMINED. *Locustella lanceolata* 1; *Acrocephalus scirpaceus* 1; *Cisticola erythrops* 1; *Sylvietta rufescens* 1; *Hylia prasina* 1; *Abroscopus schisticeps* 1; *Sylvia communis* 1; *S. hortensis* 1; *Regulus calendula* 6; *R. satrapa* 1.

**Family Muscicapidae** (Old World Flycatchers)**
MATERIAL EXAMINED. *Muscicapa dauurica* 1.

**Family Platysteiridae** (Puffback Flycatchers)
MATERIAL EXAMINED. *Batis molitor* 1.

**Family Maluridae** (Australo-Papuan Wrens)
MATERIAL EXAMINED. *Malurus lamberti* 1.

**Family Acanthizidae** (Australasian Warblers)

**Subfamily Acanthizinae**
MATERIAL EXAMINED. *Sericornis magnirostris* 1.

**Subfamily Mohouinae**
MATERIAL EXAMINED. Unavailable.

**Family Monarchidae** (Monarch Flycatchers)

**Subfamily Monarchinae**
MATERIAL EXAMINED. *Terpsiphone viridis* 1; *T. atrocaudata* 1; *Chasiempis sandwichensis* 1.

**Subfamily Rhipidurinae**
MATERIAL EXAMINED. *Ripidura albicollis* 1.

**Family Eopsaltriidae** (Australasian Robins)
MATERIAL EXAMINED. *Petroica phoenicea* 1; *P. vittata* 1; *Tregellasia leucops* 1.

**Family Muscicapidae*****

**Subfamily Pachycephalinae** (Whistlers)
MATERIAL EXAMINED. *Pachycephala lanioides* 1.

**Family Aegithalidae** (Long-tailed Tits, Bush Tits)
MATERIAL EXAMINED. *Aegithalos caudatus* 2.

**Family Remizidae** (Penduline Tits)
MATERIAL EXAMINED. *Auriparus flaviceps* 2.

**Family Paridae** (Titmice)
MATERIAL EXAMINED. *Parus atricapillus* 1; *P. carolinensis* 1; *P. bicolor* 1; *Hypositta corallirostris* 1.

**Family Sittidae**

**Subfamily Sittinae** (Nuthatches)
MATERIAL EXAMINED. *Sitta pusilla* 1; *S. canadensis* 1; *S. carolinensis* 1.

**Subfamily Daphoenosittinae** (Treerunners)
MATERIAL EXAMINED. *Neositta chrysoptera* 3; *Daphoenositta miranda* 2.

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**nomenclature and inclusive taxa according to Peters (Vol. XI, 1986).

***nomenclature and inclusive taxa according to Peters (Vol. XII, 1967).

**Subfamily Tichodromadinae** (Wallcreepers)
MATERIAL EXAMINED. *Tichodroma muraria* 1.

**Family Certhiidae** (Creepers)

**Subfamily Certhiinae** (Treecreepers)
MATERIAL EXAMINED. *Certhia familiaris* 2.

**Subfamily Salpornithinae** (Spotted Creeper)
MATERIAL EXAMINED. *Salpornis spilonotus* 1.

**Family Rhabdornithidae** (Philippine Creepers)
MATERIAL EXAMINED. *Rhabdornis mysticalis* 1.

**Family Climacteridae** (Australian Treecreepers)
MATERIAL EXAMINED. *Climacteris melanura* 1.

**Family Dicaeidae** (Flowerpeckers)
MATERIAL EXAMINED. *Rhamphocharis crassirostris* 1; *Prionochilus olivaceus* 1; *Dicaeum concolor* 1; *D. cruentatum* 1; *Oreocharis arfaki* 1; *Pardalotus rubricatus* 1.

**Family Nectariniidae** (Sunbirds)
MATERIAL EXAMINED. *Anthreptes malacensis* 1; *Hypogramma hypogrammicum* 1; *Nectarinia olivacea* 1; *N. senegalensis* 7; *N. sericea* 1; *N. jugularis* 2; *N. asiatica* 1; *N. venusta* 1; *N. talatala* 2; *N. habessinica* 1; *Aethopyga boltoni* 1; *Arachnothera longirostra* 1.

**Family Zosteropidae** (White-eyes)
MATERIAL EXAMINED. *Zosterops griseotincta* 1.

**Family Meliphagidae** (Honeyeaters)
MATERIAL EXAMINED. *Oedistoma iliolophum* 1; *Myzomela sanguinolenta* 1; *Meliphaga fusca* 1; *M. pencillata* 1; *Melithreptus brevirostris* 1; *Philemon citreogularis* 1; *Melidectes fuscus* 1; *Acanthorhynchus tenuirostris* 1; *Anthochaera carunculata* 1.

**Family Emberizidae**

**Subfamily Emberizinae** (Buntings and American Sparrows)
MATERIAL EXAMINED. *Emberiza flaviventris* 1; *Calcarius lapponicus* 1; *Zonotrichia melodia* 4 (M: 17·6, 0·12); *Z. georgiana* 3; *Z. albicollis* 7; *Junco hyemalis* 1; *Ammodramus sandwichensis* 3; *A. savannarum* 3; *Spizella passerina* 1; *S. pusilla* 1; *Pooecetes gramineus* 1; *Aimophila aestivalis* 2; *Sicalis olivascens* 1; *Volatinia jacarina* 2; *Sporophila torqueola* 6; *S. telasco* 1; *Camarhynchus crassirostris* 1; *Pipilo erythrophthalmus* 3 (M: 43·8, 0·26. F: 36·7, 0·22); *Arremon aurantiirostris* 3; *Arremonops rufivirgatus* 3; *A. chloronotus* 1.

**Subfamily Catamblyrhynchinae** (Plush-capped Finch)
MATERIAL EXAMINED. *Catamblyrhynchus diadema* 1.

**Subfamily Cardinalinae** (Cardinal-grosbeaks)
MATERIAL EXAMINED. *Pheucticus ludovicianus* 1; *P. melanocephalus* 1 (F: 40·5, 0·09); *Cardinalis cardinalis* 5 (M: 40·3, 0·09; 33·0, 0·07. F: 40·0, 0·09); *Saltator atriceps* 1; *S. maximus* 2; *S. aurantiirostris* 1; *Passerina cyanoides* 8; *P. caerulea* 2; *P. cyanea* 6.

**Subfamily Thraupinae** (Tanagers)
MATERIAL EXAMINED. *Eucometis pencillata* 2; *Lanio aurantius* 3; *Tachyphonus luctuosus* 1; *Habia rubica* 3; *H. fuscicauda* 16; *Piranga rubra* 2; *P. olivacea* 3 (F: 26·5, 0·06); *Ramphocelus sanguinolentus* 4; *R. passerinii* 4; *Thraupis episcopus* 1; *T. bonariensis* 1; *Euphonia affinis* 2; *Dacnis cyana* 1; *Cyanerpes cyaneus* 4; *Diglossa carbonaria* 1.

**Subfamily Tersininae** (Swallow-tanager)
MATERIAL EXAMINED. *Tersina viridis* 1.

**Family Parulidae** (Wood Warblers)
MATERIAL EXAMINED. *Mniotilta varia* 3; *Vermivora peregrina* 2; *Parula americana* 1; *Dendroica petechia* 4; *D. magnolia* 1; *D. coronata* 3; *D. cerulea* 1; *D. fusca* 3; *D. pensylvanica* 2; *D. castanea* 2; *D. striata* 1; *D. pinus* 1; *D. palmarum* 1; *Setophaga ruticilla* 4; *Seiurus aurocapillus* 6; *S. noveboracensis* 9 (M: 16·2, 0·15); *S. motacilla* 2; *Helmitheros vermivorus* 6; *Protonotaria citrea* 1; *Geothylpis trichas* 4 (M: 11·5, 0·09); *G. poliocephala* 1; *G. formosa* 20; *Wilsonia pusilla* 4; *Icteria virens* 4; *Coereba flaveola* 2.

**Family Drepanididae** (Hawaiian Honeycreepers)
MATERIAL EXAMINED. *Himatione sanguinea* 1; *Palmeria dolei* 1; *Vestiaria coccinea* 1; *Loxops virens* 1.

**Family Vireonidae** (Peppershrikes, Shrike-Vireos)

**Subfamily Cyclarhinae**
MATERIAL EXAMINED. *Cyclarhis gujanensis* 1.

**Subfamily Vireolaniinae**
MATERIAL EXAMINED. *Vireolanius pulchellus* 1.

**Subfamily Vireoninae**
MATERIAL EXAMINED. *Vireo griseus* 3; *V. flavifrons* 2; *V. solitarius* 2; *V. olivaceus* 3; *V. flavoviridis* 3; *V. gilvus* 1; *Hylophilus ochraceiceps* 4; *H. decurtatus* 1.

**Family Icteridae** (American Orioles and Blackbirds)

**Subfamily Icterinae**
MATERIAL EXAMINED. *Psarocolius montezuma* 2; *Amblycerus holosericeus* 1; *Icterus galbula* 1; *I. spurius* 2; *I. dominicensis* 1; *Agelaius phoeniceus* 26 ($\bar{x}$ of 16 M: 55·4, 0·17. $\bar{x}$ of 9 F: 42·8, 0·18); *Sturnella magna* 4 (M: 105·5, 0·11. F: 78·6, 0·13): *S. neglecta* 1; *Quiscalus mexicanus* 1; *Q. major* 23 ($\bar{x}$ of 14 M: 192·9, 0·17. $\bar{x}$ of 9 F: 91·0, 0·21); *Q. quiscula* 6 (M: 113·4, 0·16; 117·4, 0·14; 119·1, 0·14. F: 84·2, 0·17); *Euphagus carolinus* 1 (M: 66·0, 0·13); *Molothrus ater* 15 ($\bar{x}$ of 6 M: 47·5, 0·13. $\bar{x}$ of 8 F: 37·3, 0·14).

**Subfamily Dolichonychinae**
MATERIAL EXAMINED. *Dolichonyx oryzivorus* 12 ($\bar{x}$ of 10 M: 39·0, 0·09).

**Family Fringillidae**

**Subfamily Fringillinae** (Chaffinches and Brambling)
MATERIAL EXAMINED. *Fringilla coelebs* 1; *F. montifringilla* 1.

**Subfamily Carduelinae** (Serins, Goldfinches, et al.)
MATERIAL EXAMINED. *Serinus mozambicus* 14; *Carduelis pinus* 2 (M: 10·5, 0·10); *C. tristis* 1; *Carpodacus purpureus* 2 (M: 26·2, 0·03); *C. mexicanus* 2 (F: 23·2, 0·11); *Pinicola enucleator* 4 (F: 55·2, 0·06; 56·8, 0·05; 60·2, 0·03); *Coccothraustes vespertinus* 1 (M: 56·6, 0·05).

**Family Estrildidae** (Waxbills, Grass Finches, and Mannikins)
MATERIAL EXAMINED. *Pytilia melba* 2; *Uraeginthus angolensis* 8; *Estrilda caerulescens* 1; *Poephila acuticauda* 1; *P. cincta* 1; *Chloebia gouldiae* 1; *Lonchura cucullata* 1; *Amadina fasciata* 7.

**Family Ploiceidae**

**Subfamily Viduinae** (Indigo-birds and Whydahs)
MATERIAL EXAMINED. *Vidua paradisaea* 1.

**Subfamily Passerinae**
MATERIAL EXAMINED. *Passer domesticus* 14 (M: 24·5, 0·09; 24·8, 0·20. F: 22·3, 0·18; 25·1, 0·18); *P. griseus* 3.

**Subfamily Bubalornithinae**
MATERIAL EXAMINED. *Dinemellia dinemelli* 1.

**Subfamily Ploceinae**
MATERIAL EXAMINED. *Amblyospiza albifrons* 1; *Ploceus subaureus* 3; *P. xanthops* 1; *P. velatus* 4; *P. cucullatus* 25; *Euplectes hordeaceus* 1; *E. orix* 11.

**Family Sturnidae** (Starlings)

**Subfamily Sturninae**
MATERIAL EXAMINED. *Sturnus vulgaris* 5 (M: 78·3, 0·11; 80·5, 0·13; 89·7, 0·11); *Sarcops calvus* 1; *Gracula religiosa* 1.

**Subfamily Buphaginae**
MATERIAL EXAMINED. *Buphagus erythrorhynchus* 2; *Buphagus* sp. 1.

**Family Oriolidae** (Orioles)
MATERIAL EXAMINED. *Oriolus oriolus* 1; *O. chinensis* 1; *O. xanthornus* 1.

**Family Dicruridae** (Drongos)
MATERIAL EXAMINED. *Dicrurus remifer* 1; *D. hottentottus* 1; *D. paradiseus* 1.

**Family Callaeidae** (New Zealand Wattlebirds)
MATERIAL EXAMINED. *Callaeas cinerea* 1; *Creadion carunculatus* 1; *Heteralocha acutirostris* 1.

**Family Grallinidae** (Australian Mud Nest Builders)

**Subfamily Grallininae**
MATERIAL EXAMINED. *Grallina cyanoleuca* 1.

**Subfamily Corcoracinae**
MATERIAL EXAMINED. *Corcorax melanorhamphos* 1; *Struthidea cinerea* 2.

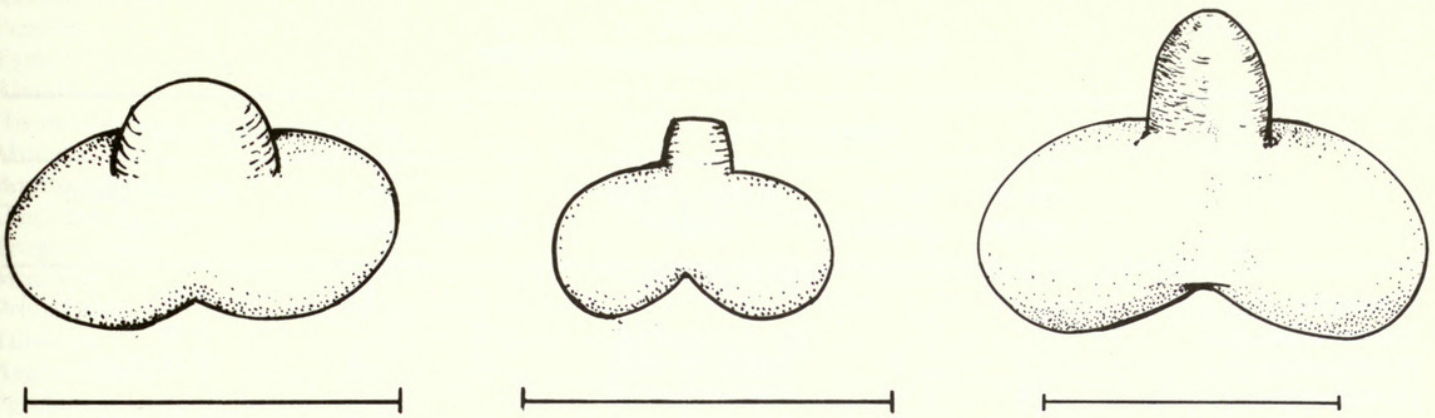
**Family Artamidae** (Wood-swallows)
MATERIAL EXAMINED. *Artamus fuscus* 1; *A. leucorhynchus* 1; *A. superciliosus* 1; *A. cinereus* 1; *A. minor* 1.

**Family Cracticidae** (Australian Butcherbirds)
MATERIAL EXAMINED. *Cracticus nigrogularis* 1; *Gymnorhina tibicen* 1; *Strepera graculina* 1.

**Family Ptilonorhynchidae** (Bowerbirds)
MATERIAL EXAMINED. *Ailuroedus crassirostris* 1; *Amblyornis macgregoriae* 2; *Sericulus chrysocephalus* 1; *Ptilonorhynchus violaceus* 1; *Chlamydera nuchalis* 2.

**Family Paradisaeidae** (Birds of Paradise)
MATERIAL EXAMINED. *Manucodia comrii* 1; *Semioptera wallacei* 1; *Astrapia stephaniae* 1; *Lophorina superba* 1; *Cicinnurus regius* 1; *Diphyllodes respublica* 1; *Paradisaea apoda* 1.

**Family Corvidae** (Crows, Magpies, Jays)
MATERIAL EXAMINED. *Cyanocitta cristata* 14 (M: 77·7, 0·20; 78·4, 0·10. F: 59·4, 0·08); *Aphelocoma coerulescens* 2 (M: 70·3, 0·11; 72·0, 0·07); *Garrulus glandarius* 1; *Pica pica* 2; *Corvus monedula* 1; *C. frugilegus* 2; *C. brachyrhynchos* 39 ($\bar{x}$ of 14 M: 563·1, 0·05. $\bar{x}$ of 11 F: 495·7, 0·05); *C. ossifragus* 4 (M: 330·0, 0·15. F: 232·0, 0·13); *C. corone* 2.



*Dendrocolaptes certhia* *Cinclus mexicanus* *Corvus brachyrhynchos*

## Weights and sizes of glands

Early accounts of uropygial glands included brief comments about relative size ('small,' 'large,' 'smaller than'; Willughby 1678; Burton 1822, Macgillivray 1837, Bartlett 1861). Such relative adjectives and phrases persist in the more contemporary literature (Austin 1961, Thomson 1964, Shortt 1977). Edwards Crisp (1860, 1862) was probably the first person to publish gland weights, and, by weighing birds and their glands separately, he presented the relative proportion of gland weight to the bird's body weight. He (1860: 258) presented data on 34 species of aquatic and terrestrial birds, showing relatively lightest glands in pigeons and heaviest ones in *Cinclus aquaticus* (*C. cinculus aquaticus* of Peters) and six species of waterfowl. The frequent assertion that the preen gland of water-birds is relatively larger than that of land-birds (e.g., Kennedy 1971) is probably derived from Crisp's results (see also Coues 1890), even though Frederick II in 1260 reported large glands in aquatic species (Wood and Fyfe 1943).

Subsequent authors have presented absolute or relative gland weights for many more species (Kossman 1871, Paris 1913, Kar 1947, Grassé 1950, Elder 1954, Kennedy 1971, Johnston 1979, Jacob & Ziswiler 1982). In these reports, differences in relative gland weights have variously been attributed to season (Kossman 1871, Kennedy 1971), habitat (Crisp 1860, Jacob & Ziswiler 1982), intergeneric body weight (Johnston 1979), nutrition (Kossman 1871), individual variation (present study and others), and sex (Groebbels 1932). Although Elder (1954) suggested that glands of diving ducks (*Aythya*) are relatively heavier than those of dabbling ducks (*Anas*), some of Jacob & Ziswiler's data (1982: 214) 'clearly refute this hypothesis.' Subsequently I compared relative gland weights from 7 species of dabbling ducks ($N=21$, $\bar{x}=0{\cdot}30\%$, $SD=0{\cdot}047$) with weights from 5 species of diving ducks ($N=20$, $\bar{x}=0{\cdot}29$, $SD=0{\cdot}065$); the differences were not statistically significant (d.f. $=40$, $t=0{\cdot}7560$, $p>0{\cdot}05$).

Jacob & Ziswiler (1982) presented gland weights from 574 individuals in 183 species, and I obtained gland weights from 544 individuals in 200 species. All these weights are presented in Table 1. A comparison of these two data sets shows reasonable agreement for the same taxon especially as regards mean values. Also apparent are variations in relative gland weights within and between species, variations that I attribute largely to individual body weight differences. The latter are probably due to sexual differences (see, for example, data for three species of Icterinae in the Systematic accounts) and variations in the amounts of subcutaneous fat.

From their analysis of relative gland weights, Jacob & Ziswiler concluded that 'the only thing that can be said with certainty regarding the size of the uropygial gland is that birds that swim and dive have, without exception, a large uropygial gland' (1982: 214). This statement should be expanded to include the earlier demonstrated correlations with season, nutrition, and sex by the other authors mentioned above.

I was able to examine the habitat-habit issue more thoroughly because of a much larger sample size, including birds living in most major habitat types. By grouping relative weights of birds at the family level and to broad habitat-habit categories (Fig. 2), I found that the largest (relative) glands

**Table 1**
**Summary of uropygial gland weights**

| | PRESENT STUDY | | | JACOB & ZISWILER (1982) | | |
|---|---|---|---|---|---|---|
| | No. of species | No. of glands | Relative gland weight* | No. of species | No. of glands | Relative gland weight* |
| Tinamidae | | | | 1 | 12 | 0·18 |
| Diomedeidae | | | | 1 | 1 | 0·30 |
| Procellariidae | 5 | 9 | 0·46 (0·30–0·67) | 2 | 4 | 0·24–0·27 |
| Hydrobatidae | 4 | 6 | 0·16 (0·07–0·37) | | | |
| Spheniscidae | 1 | 2 | 0·08 (0·06–0·12) | 2 | 3 | 0·21–0·26 |
| Gaviidae | 4 | 9 | 0·18 (0·09–0·30) | 2 | 3 | 0·14–0·20 |
| Podicipedidae | 2 | 6 | 0·26 (0·19–0·42) | 2 | 7 | 0·48–0·61 |
| Phaethontidae | 1 | 1 | 0·43 | | | |
| Fregatidae | 1 | 3 | 0·07 (0·06–0·07) | | | |
| Phalacrocoracinae | 1 | 10 | 0·25 (0·20–0·35) | 3 | 12 | 0·21–0·31 |
| Anhinginae | 1 | 8 | 0·15 (0·12–0·17) | | | |
| Sulidae | 1 | 1 | 0·38 | 1 | 2 | 0·35 |
| Pelecanidae | 2 | 4 | 0·36 (0·30–0·43) | 1 | 1 | 0·19 |
| Ardeidae | 9 | 20 | 0·14 (0·01–0·42) | 3 | 7 | 0·05–0·07 |
| Ciconiidae | 1 | 1 | 0·05 | 1 | 2 | 0·08 |
| Threskiornithidae | 3 | 4 | 0·15 (0·11–0·19) | 3 | 4 | 0·03–0·11 |
| Phoenicopteridae | | | | 2 | 4 | 0·18–0.21 |
| Cathartidae | 2 | 10 | 0·04 (0·01–0·05) | | | |
| Pandioninae | 1 | 2 | 0·25 (0·18–0·31) | 1 | 1 | 0·36 |
| Accipitrinae | 11 | 25 | 0·06 (0·01–0·13) | 7 | 17 | 0·04–0·22 |
| Falconidae | 4 | 15 | 0·07 (0·03–0·09) | 1 | 4 | 0·08 |
| Anatidae | 25 | 55 | 0·26 (0·10–0·42) | 15 | 55 | 0·08–0·54 |
| Anhimidae | 1 | 1 | 0·13 | | | |
| Megapodiidae | | | | 1 | 1 | 0·18 |
| Tetraonidae | 6 | 7 | 0·05 (0·02–0·18) | 3 | 11 | 0·09–0·15 |
| Phasianidae | 8 | 17 | 0·07 (0·02–0·16) | 5 | 12 | 0·08–0·11 |
| Meleagrididae | 1 | 3 | 0·03 (0·02–0·04) | 1 | 2 | 0·05 |
| Numididae | | | | 2 | 3 | 0·05–0·18 |
| Gruidae | 1 | 4 | 0·05 (0·03–0·05) | 1 | 1 | 0·05 |
| Aramidae | 1 | 7 | 0·28 (0·17–0·42) | | | |
| Rallidae | 6 | 27 | 0·19 (0·11–0·34) | 5 | 14 | 0·09–0·24 |
| Haematopodidae | | | | 1 | 1 | 0·20 |
| Charadriidae | 2 | 4 | 0·18 (0·07–0·22) | 1 | 2 | 0·16 |
| Scolopacidae | 9 | 25 | 0·12 (0·05–0·20) | 4 | 5 | 0·11–0·18 |
| Recurvirostridae | 1 | 1 | 0·24 | | | |
| Phalaropodidae | 2 | 4 | 0·59 (0·42–0·79) | | | |
| Burhinidae | | | | 1 | 1 | 0·09 |
| Chionididae | | | | 1 | 1 | 0·17 |
| Stercorariidae | 2 | 3 | 0·29 (0·28–0·37) | | | |
| Larinae | 3 | 5 | 0·20 (0·13–0·29) | 4 | 19 | 0·12–0·20 |
| Sterninae | 9 | 20 | 0·33 (0·18–0·57) | 4 | 5 | 0·19–0·44 |
| Rynchopidae | 1 | 1 | 0·20 | | | |
| Alcidae | 5 | 7 | 0·27 (0·18–0·47) | 3 | 7 | 0·17–0·29 |
| Pteroclididae | | | | 1 | 1 | 0·02 |
| Columbidae | 5 | 11 | 0·04 (0·01–0·10) | 4 | 5 | 0·02–0·04 |
| Psittacidae | 2 | 1 | 0·11 (0·05–0·16) | 41 | 125 | 0·04–0·19 |
| Cuculidae | 2 | 2 | 0·06 (0·03–0·09) | 2 | 4 | 0·12–0·16 |
| Tytonidae | 1 | 4 | 0·09 (0·04–0·12) | 1 | 7 | 0·08 |
| Strigidae | 6 | 22 | 0·07 (0·03–0·11) | 4 | 9 | 0·04–0·09 |
| Steatornithidae | | | | 1 | 1 | 0·22 |
| Caprimulgidae | 3 | 11 | 0·01 (0·01–0·02) | 1 | 1 | 0·01 |
| Apodidae | | | | 2 | 11 | 0.04–0·05 |
| Alcedinidae | 1 | 2 | 0·24 (0·22–0·25) | 1 | 2 | 0·18 |
| Upupidae | | | | 1 | 2 | 0·14 |
| Meropidae | | | | 1 | 1 | 0·11 |
| Bucerotidae | | | | 2 | 4 | 0·08–0·11 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Ramphastidae | 1 | 2 | 0·13 (0·12–0·14) | 2 | 5 | 0·08–0·10 |
| Picidae | 5 | 13 | 0·12 (0·08–0·14) | 4 | 9 | 0·09–0·12 |
| Tyrannidae | 2 | 2 | 0.09 (0·08–0·10) | | | |
| Alaudidae | | | | 1 | 1 | 0·28 |
| Hirundinidae | 1 | 1 | 0·03 | 1 | 6 | 0·21 |
| Motacillidae | 1 | 1 | 0·13 | 1 | 2 | 0·27 |
| Bombycillidae | 1 | 1 | 0·10 | | | |
| Cinclidae | 1 | 3 | 0·61 (0·48–0·71) | | | |
| Troglodytidae | | | | 1 | 3 | 0·58 |
| Mimidae | 2 | 4 | 0·14 (0·07–0·18) | | | |
| Prunellidae | | | | 1 | 1 | 0·28 |
| Turdinae | 3 | 6 | 0·09 (0·07–0·12) | 2 | 7 | 0·08–0·14 |
| Aegithalidae | | | | 1 | 2 | 0·21 |
| Paridae | | | | 2 | 23 | 0·14–0·15 |
| Sittidae | | | | 1 | 1 | 0·12 |
| Emberizinae | 2 | 3 | 0·20 (0·12–0·26) | 2 | 6 | 0·26–0·31 |
| Cardinalinae | 2 | 4 | 0·09 (0·07–0·09) | 1 | 2 | 0·18 |
| Thraupinae | 1 | 1 | 0·06 | | | |
| Parulidae | 2 | 2 | 0·12 (0·09–0·15) | | | |
| Icterinae | 6 | 55 | 0·15 (0·11–0·24) | | | |
| Dolichonychinae | 1 | 10 | 0·09 (0·06–0·13) | | | |
| Fringillidae | 5 | 7 | 0·06 (0·03–0·11) | 3 | 26 | 0·22–0·25 |
| Estrildidae | | | | 6 | 24 | 0·17–0·23 |
| Passerinae | 1 | 4 | 0·16 (0·09–0·20) | | | |
| Ploceidae | | | | 3 | 17 | 0·19–0·28 |
| Sturnidae | 1 | 3 | 0·12 (0·11–0·13) | 1 | 8 | 0·10 |
| Corvidae | 4 | 32 | 0·10 (0·04–0·20) | 7 | 40 | 0·08–0·12 |

*gland weight as percent of body weight; mean (extremes)

are found in nonpasserines that swim, dive or rest on water (N = 18 families, $\bar{x}$ = 0·28%). The smallest glands occur in terrestrial (non-aquatic) birds: nonpasserines (N = 15, $\bar{x}$ = 0·07%) and passerines (N = 16, $\bar{x}$ = 0·04%).

I found the largest relative gland weights in the Procellariidae (*Oceanodroma melania,* 0·69% *Fulmarus glacialis,* 0·67%) Phalaropodidae (*Phalaropus fulicarius,* 0·79%), Sterninae (*Sterna albifrons,* 0·57%), and Cinclidae (*Cinclus mexicanus,* 0·71%). The largest glands reported by Jacob & Ziswiler (1982) were for *Tachybaptus ruficollis* (0·61%) and *Troglodytes troglodytes* (0·58%). Because of its habit of plunging into water for fish, the Osprey expectedly has a larger (0·25%) gland than any other of the Falconiformes (Accipitrinae, 0·06% and Falconidae 0·07%). The smallest glands, which could be accurately weighed in the present study, were found in Caprimulgidae (11 individuals averaging 0·01%), Meleagrididae (3 individuals, $\bar{x}$ = 0·03%) and Columbidae (11 individuals, $\bar{x}$ = 0·04%).

Burton (1822: 4; and quoted by Murphy 1936) reported that the uropygial gland of *Fregata aquila* is a 'trifling size.' In my study, fresh weights of birds and glands of Fregatidae were available only for *F. magnificens,* so I could not compare relative gland weights among frigatebirds. However, the length of glands (sans feathers) were as follows: *F. magnificens,* 15 mm; *F. aquila,* 13 mm; *F. ariel,* 13 mm. The gland of *F. aquila* is thus no smaller than that of *F. ariel* which is the smallest species of *Fregata* (Nelson 1975). Frigatebirds have smaller glands relative to body weight (0·07%) than other nonpasserine birds that live on or in water (e.g., Procellariidae, 0·44%; Phaethontidae, 0·30%; Pelecanidae, 0·28%; Anatidae, 0·27%) with the exception of Spheniscidae (0·08%). The putative relationship between a small, 'insufficient' gland and feathers becoming so wet that frigatebirds drown (first proposed by Burton in 1822 and paraphrased by Welty 1962) lacks scientific verification (see related discussion on spread-wing posture in Clark 1969).

My findings enable me to correct several unverified statements in the literature on gland sizes. Gurney's (1913) assertion, paraphrasing Ticehurst, that the gland of *Sula bassana* 'is the largest proportionally' of all birds, now turns out to be incorrect. One relative gland weight for this species was only 0·38% (present study), compared with relatively much heavier glands in procellarids,

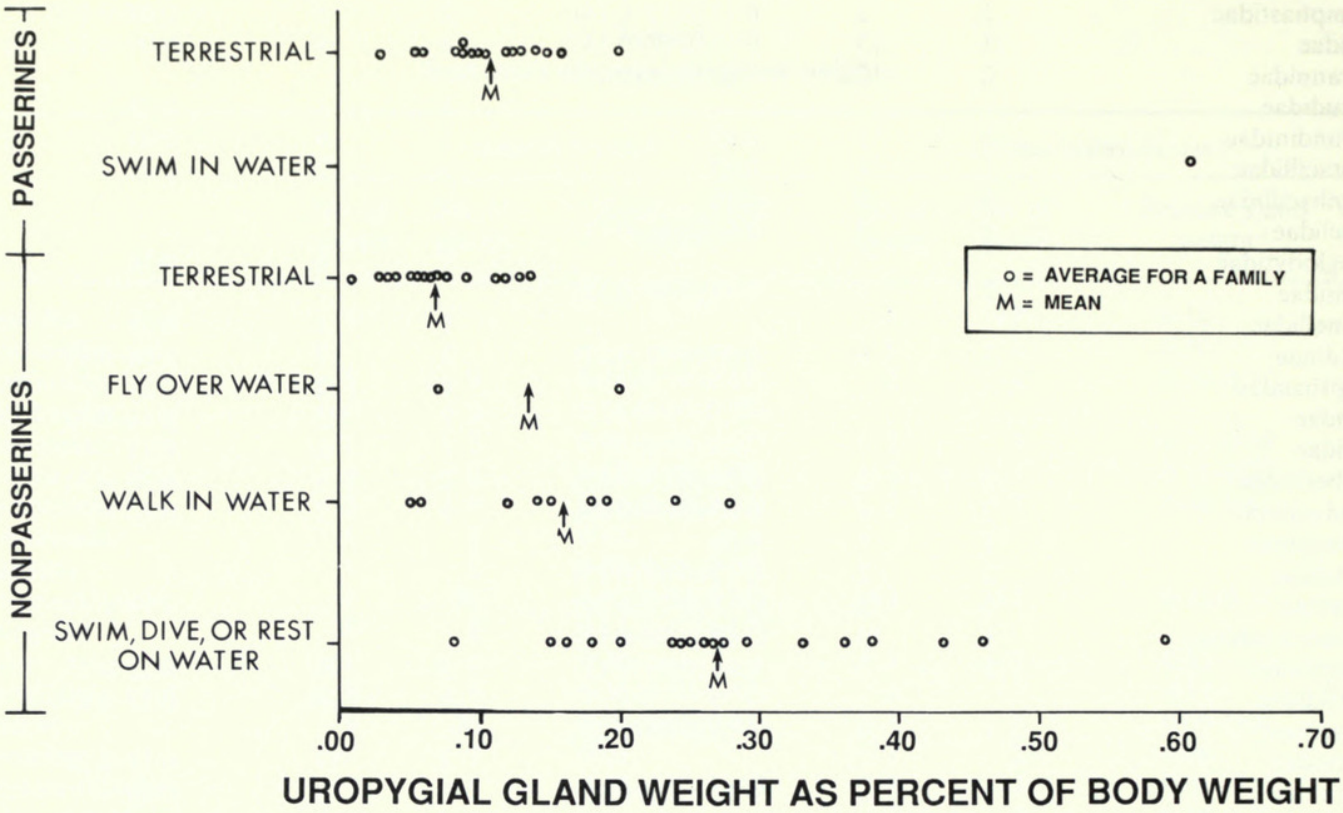



**Fig. 2** Relationships between uropygial gland weights and avian habitat-habits.

anatids, phalaropes, and others (above). Austin (1961) (see also Shortt 1977) wrote that dippers (Cinclidae) have a 'tremendous preen gland, ten times the size of that of any other passerine bird.' To be sure, the gland of *Cinclus mexicanus* ($\bar{x} = 0{\cdot}61$; 0·48–0·71%) is the largest yet reported for any passerine, but other passerine families (e.g., Emberizidae, Icteridae) have glands as large as 0·24–0·26% and *Troglodytes troglodytes* has a large gland (0·56–0·58%, Kennedy 1971; Jacob and Ziswiler 1982).

My data show that large (i.e., heavy) birds have absolutely large uropygial glands. For 670 individuals, representing 61 families of passerine and nonpasserine birds, I found a significant correlation between body weight and gland weight ($r = 0{\cdot}694$, $P \leqslant 0{\cdot}01$). This correlation is important especially because of the inverse relation of plumage weight (as a percent of body weight) with body weight *per se* (Kossman 1871, Turcek 1966). Kennedy (1971: 370) correctly cautioned that 'this parallel could result from a functional connection between the preen gland [size and] secretion and the area of feathers which require anointing with it. Additionally, it is possible that relative to body weight, water-birds have a larger area of feather surface requiring anointing with secretion than land-birds of similar size, which may partly explain their larger glands.'

Conclusions drawn from size and weight relationships of glands must still be tentative. Despite the large numbers of weights and broad taxonomic coverage presented in this study and others (Kennedy 1971, Jacob & Ziswiler 1982), gland weights have never been reported from many birds—e.g., Apterygidae, wild Psittacidae, Trochilidae, Coliidae, most of the coraciiform and piciform families, and most of the passerines.

## Feathers on uropygial glands

Feathers attached to the papilla at the end of the uropygial gland are collectively termed *circulus uropygialis* by Lucas & Stettenheim (1972) and Baumel *et al.* (1979). Through the years these feathers have been variously described in different birds as 'contour' (Nitzsch 1867), 'down' or 'downy' or 'modified down' (Nitzsch 1867, Newton 1893–1896, Beddard 1898, Verheyen 1956*f*, 1958*c*, *d*, Grassé 1950, Lucas & Stettenheim 1972, Baumel *et al.* 1979), 'semiplumes' (Nitzsch

1840), 'plumules' or 'plumulets' (Paris 1913), 'plumes' (Beddard 1898), with or without a rachis and/or hyporachis (Paris 1913, Verheyen 1959*c*). Some of the earlier publications (e.g., Nitzsch 1867) even described 'fine hairs' at the tip of certain glands. Miller (1924) was apparently the first investigator to use magnification in determining the number and type of feathers on a gland.

The number of feathers per gland ranges from 1 (minute) to 90 (Jacob & Ziswiler 1982, the present study). Jacob & Ziswiler provided a thorough discussion of the number, arrangement, density, and length of the feathers. Because of some individual variation in number of feathers and other considerations, Jacob & Ziswiler (correctly in my opinion) cautioned against the use of feather number for taxonomic or diagnostic criteria. Rather, from a functional standpoint, they noted a general tendency for waterbirds to have more and longer feather tufts than landbirds. They also believed that the proportional length of the papilla to that of the tuft is taxonomically specific (see also Schumacher 1919).

Lucas and Stettenheim (1972) classified uropygial gland feathers as 'modified down,' defining down as feathers with a rachis shorter than the longest barbs and semiplumes having a rachis that exceeds the longest barbs. My microscopic study of gland feathers from 70 families containing tufted glands revealed the presence of three feather types (Fig. 3). Most of the family representatives (62) had feathers of type I which, by the definition of Lucas & Stettenheim (1972), are down.

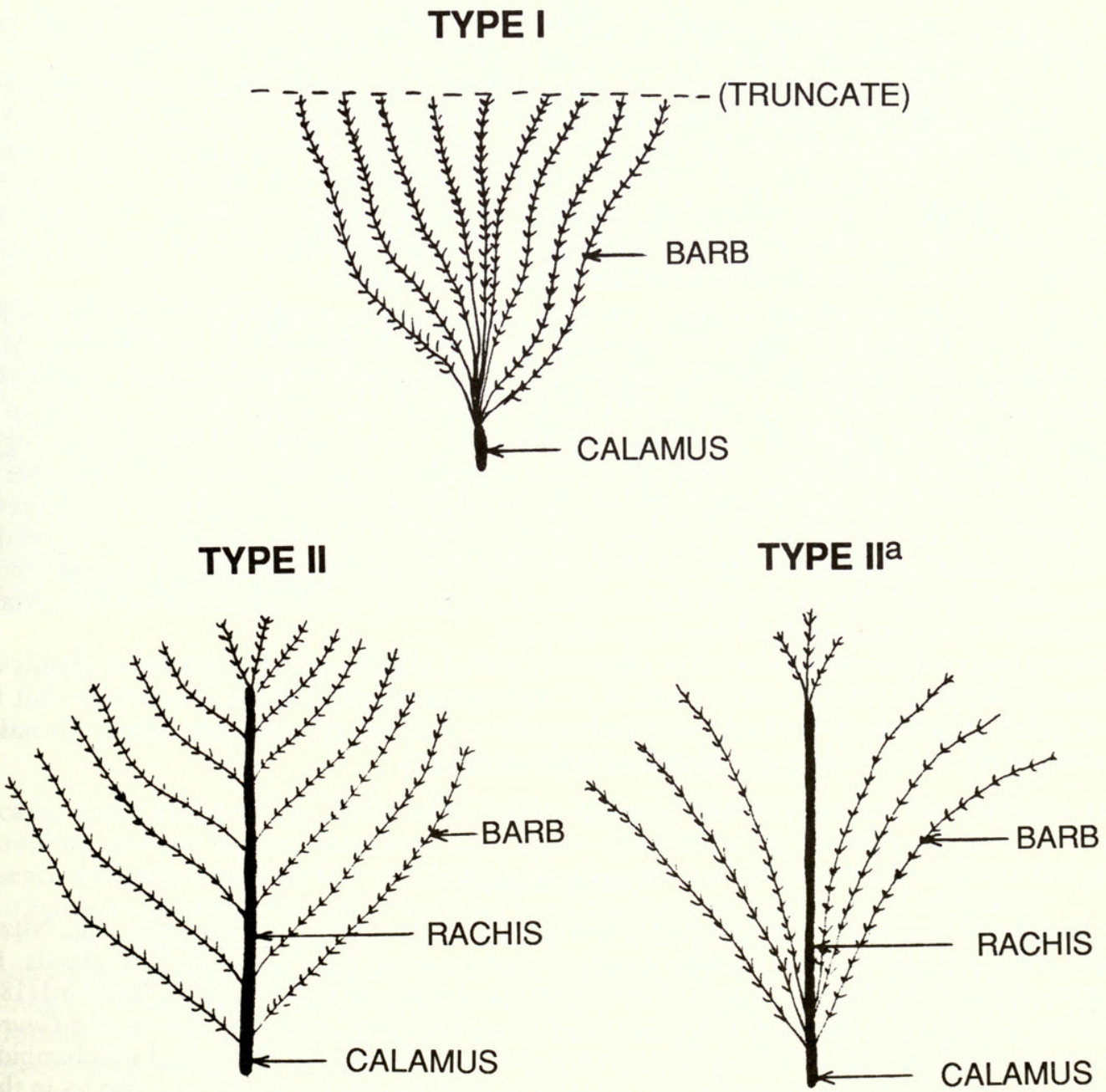



**Fig. 3** Diagrams of typical uropygial gland feathers.

Three families each had feathers of Types II and IIa, both defined here as semiplumes. Nodal structures on barbules on these feathers differed from those on true down and contour feathers (Douglas Deedrick and Roxie Laybourne, pers. comm.). Therefore, the most appropriate terms for describing the *circulus uropygialis* are modified down or modified semiplumes.

Contrary to the reports of some other investigators (e.g., Lucas & Stettenheim 1972), I found no afterfeathers on any gland feathers. Even in groups (e.g., Galliformes) renowned for having afterfeathers on body contour feathers, afterfeathers were not found. This difference might be attributable to the criterion for identifying an afterfeather. Lucas & Stettenheim (p. 252) regarded any group of outgrowths on the rim of the superior umbilicus as an afterfeather; outgrowths were not identified in the present study.

## Naked and tufted glands

Most early investigators such as Nitzsch (1867), Beddard (1898), and Paris (1913) generally categorized glands as either tufted or naked (nude, bare), that is, with or without feathers on the papilla. For the most part, the glands that they examined were 'obviously' (unmagnified) tufted or naked, although occasional references were made to a 'fine hair' at the tip of some glands (Nitzsch 1867). This dichotomous difference apparently served well until some putative 'naked' glands were examined with magnification by Miller (1924) and were found to possess 1–2 mm feathers.

It is now desirable to establish three categories of glands with respect to the degree of feathering on the papilla: naked (no feathers observable, even with magnification), minutely tufted (feathers detected only with magnification), and tufted (feathers observable without magnification). Glands previously considered to be naked by Paris (1913) and others but now known to be 'minutely tufted' include species in the families Apterygidae, Opisthocomidae, Tytonidae, Strigidae, and Momotidae. In each of these families, considerable individual variation has been found between the naked and minutely tufted conditions (see Systematic accounts).

Naked glands are also morphologically variable, particularly as regards the length and width of the papilla. In all passerine birds, for example, the papilla is distinct and well defined. Most nonpasserine naked glands, on the other hand, either have no papilla (Rhinochetidae, Columbidae, Hemiprocnidae, Galbulidae) or the papilla is so ill-defined and broad that it appears to be continuous with the glandular lobes (e.g., Apterygidae, Cathartidae, Cuculidae). Although I believe the passerine gland shape is distinctive, some nonpasserine glands superficially resemble the passerine type—Cariamidae, Steatornithidae, *Batrachostomus*. Close examinations of figures in the Systematic accounts will show the distinctiveness of the naked passerine gland as opposed to the several naked nonpasserine ones. Jacob & Ziswiler (1982) recognized different shapes among many passerine glands (heart-shaped, kidney-shaped, etc.), but these designations were so variable between and within families that I could not use them.

The majority of nonpasserines have obviously tufted glands, whereas passerine glands are uniformly naked. From an examination of all nonpasserine gland types, I conclude that the tufted gland is primitive. Derived types include those that are (1) minutely tufted, (2) naked (nonpasserine), and (3) naked (passerine).

## Gland absence

The absence of uropygial glands in certain species of birds has been known at least since Nitzsch (1840). As more species were examined over the years, more were found to lack glands. For example, in the Columbidae, Garrod (1874*a*) noted gland absence in only 4 genera, Beddard (1898) and Grassé (1950) in 6 genera, and Verheyen (1957*a*) added 'new' species in *Treron* and *Goura*. I made a special effort to examine as many species and individuals as available in the Columbidae, Psittacidae, and Picidae because of earlier discrepancies in reports for genera and species in these families. Nearly every published account containing any information on the absence of uropygial

glands (Beddard, Paris, Grassé, Elder, VanTyne & Berger, and others) include at least one factual error on the subject, sometimes simply by omission and frequently by uncritically copying a statement from an earlier author.

The glandless condition varies markedly at every taxonomic level: absent from entire orders, families, genera, species, and individuals. A gland might be present in some species of a genus, yet absent in others. At the individual level, for example in each of three species of *Ptilinopus* (*coronulatus, pulchellus, rivoli*), some individuals possess glands, whereas others do not. Darwin (1900) and Levi (1941) reported the gland's absence in certain varieties of *Columba livia.*

I found the gland to be absent in the following taxa (see Systematic accounts for details and pertinent comments): Struthionidae (all age groups), Rheidae (adults), Casuariidae (all age groups), Dromaiidae (adults), Mesoenatidae (all 3 species), Otidae (all 5 species examined), Columbidae (9 genera, 28 species), Psittacidae (6 genera, 31 species), *Podargus* (3 species examined), and Picidae (1 genus, 4 species).

Some minor discrepancies exist between my findings and earlier reports. Although Garrod (1874*b*) reported no gland in *Cacatua sulfur* (*Kakatoe sulphurea*), a live bird that I examined had a conspicuous, tufted gland. Nitzsch (1840), Beddard (1898), and others noted no gland in *Argusianus* (*Argus*); 5 specimens in the present study contained a gland. I suspect these discrepancies, as well as those in *Ara* and *Cacatua roseicapella*, can be attributed to individual variation among the specimens examined, most or all of them being captive birds.

Because the glandless condition is found in such a wide diversity of species and other taxa, a quest for causal relationships is appropriate. Why, for example, do some parrots have glands whereas others do not? No single attribute (distribution, climate, ecology, flight, etc.) has been found to be consistent as an explanation, a conclusion also reached by Kossmann (1871) who stated that he could find no relationship between gland absence and 'way of life of the bird.' Some flightless birds lack glands; others do not. Some insular pigeons have glands; others do not. Some neotropical parrots lack glands; others have well-developed glands. In my opinion, uropygial glands have apparently been secondarily and independently lost in a variety of birds, but these losses remain unexplained.

Although Beddard (1898: 232) stated that 'presence or absence cannot be made use of as a fact of great systematic importance,' he (pp. 313–314 and elsewhere) nonetheless used the 'fact' as a family characteristic. Similarly, Garrod (1874*b*), Nitzsch (1840), Paris (1913) and many others have used presence or absence of glands (in addition to naked vs. tufted conditions) as distinctive family and generic characteristics. This is a valid use of uropygial gland data except in cases of known individual variation. Gland absence in all species of the Mesoenatidae is just as good a family characteristic as is their singular limited distribution. On the other hand, in the Picidae, and especially in only a few species of *Campethera,* gland absence is probably of little taxonomic importance at the family level.

## Glands in flightless birds

Because some authors (e.g., Elder 1954) have suggested relationships among uropygial gland secretions, normal feather functions, and flight capabilities, an analysis of gland presence/absence in flightless birds is desirable. Elder's experiments on ducks essentially showed that gland extirpation resulted in reduced feather waterproofing, thus rendering the birds flightless.

The first consideration has been to determine if a relationship exists between a flightless condition and gland presence in nature. In Table 2, flightless species identified from several literature sources are listed along with the presence or absence of the gland. Except for most of the ratites (Struthionidae, Rheidae, Casuariidae, Dromaiidae), only one other taxon (all three species of Mesoenatidae) is known wherein flightless species lack a gland. Overall, this analysis reveals virtually no correlation between a flightless condition and gland absence: for 42 flightless species examined, only 8 lacked a gland in the adult.

**Table 2**
The Relationship between the flightless condition*
and presence of uropygial glands

Struthionidae**
*Struthio camelus*—absent in adult

Rheidae**
*Rhea americana*—absent in adult
*Pterocnemia pennata*—absent in adult

Casuariidae**
*Casuarius bennetti*—unavailable
*Casuarius casuarius*—absent in adult
*Casuarius unappendiculatus*—unavailable

Dromaiidae**
*Dromaius novaehollandiae*—absent in adult

Apterygidae
*Apteryx australis*—gland present, essentially naked (but see Beddard 1898, 1899)
*Apteryx owenii*—gland present, naked
*Apteryx haastii*—gland present, naked

Spheniscidae
16 species—gland present and tufted in all 10 species examined

Podicipedidae
*Rollandia microptera*—gland present, tufted
*Podilymbus gigas*—gland present, tufted

Phalacrocoracidae
*Phalacrocorax harrisi*—gland present, tufted

Anatidae
*Tachyeres pteneres*—gland present, tufted
*Tachyeres brachypterus*—gland present, tufted
*Anas aucklandica*—gland present, tufted
*Mergus australis*—gland present, tufted (but perhaps capable of flight, see Weller 1980)

Mesoenatidae
*Mesoenas variegata*—gland absent
*Mesoenas unicolor*—gland absent
*Monias benschi*—gland absent

Rallidae***
*Rallus owstoni*—gland present, tufted
*Rallus wakensis*—gland present, tufted
*Cabalus modestus*—unavailable
*Atlantisia rogersi*—gland present, tufted or naked
*Tricholimnas lafresnayanus*—unavailable
*Tricholimnas sylvestris*—gland present, tufted
*Dryolimnas cuvieri aldabranus*—gland present, tufted
*Cyanolimnas cerverai*—gland present, tufted
*Nesoclopeus poeciloptera*—unavailable
*Gallirallus australis*—gland present, tufted
*Habropteryx insignis*—unavailable
*Habroptila wallacii*—unavailable
*Megacrex inepta*—unavailable
*Porzanula palmeri*—gland present, tufted
*Pennula sandwichensis*—unavailable
*Aphanolimnas monasa*—unavailable
*Tribonyx mortierii*—gland present, tufted
*Porphyriornis nesiotis*—gland present, tufted
*Porphyriornis comeri*—gland present, tufted
*Notornis mantelli*—gland present, tufted

Rhynochetidae
*Rhynochetos jubatus*—gland present, naked

Alcidae
*Pinguinus impennis*—gland present, tufted

Psittacidae
*Strigops habroptilus*—gland present, tufted

Acanthisittidae
*Xenicus lyalli*—unavailable (see Systematic accounts for other species).

*Flightless species names taken from Thomson (1964), Greenway (1958), Austin (1961), Van Tyne & Berger (1976), Olson (1973*a, b*), Weller (1980), and Mlikovsky (1982).
**Several authors (e.g., Beddard 1898, Jacob 1978) have reported the absence of a gland in all ratites except *Apteryx*, although the species examined were usually not identified by the author.
***Opinions differ on the flight capability of some of these species. Ripley and Beehler (1985: 7), for example, reported that *Rallus owstoni* 'can fly as high as one or two meters above the ground, but they seldom do so.'

A second consideration concerns a possible relationship between gland size and a flightless condition. Although fresh gland weights from flightless species were unavailable to me, sizes (linear measurements) of glands of flightless species in the Podicipedidae, Phalacrocoracidae, Anatidae, and Rallidae were compared with glands from closely related (often congeners) species that fly. These comparisons revealed no major size differences in glands between flightless and flying birds.

## General taxonomic considerations of glands

The use of the uropygial gland as a character in avian systematics has been both commonplace and controversial for many years. As early as 1840, Nitzsch identified general gland features (e.g., tufted vs. naked conditions) as characteristics of different avian taxa, and the gland was subsequently much used in classification by ornithologists such as Coues (1890) and Beddard (1898). This use in taxonomy has continued to date by some investigators (e.g., Olson & Steadman's 1981 characterization of *Pedionomus*), but others have excluded gland morphology in taxonomic considerations (e.g., Cracraft, 1985). Thomson (1964) stated that the gland is 'unsatisfactory as a taxonomic character,' and Jacob & Ziswiler (1982) noted that the gland 'has little systematic importance. . . .'

From the systematic accounts of this monograph, it can be seen that the gland's presence or absence, tufted vs. naked condition (and variations thereof) might vary at any taxonomic level: intraspecific to interordinal. At the ordinal level, the gland is present and naked (with distinctive papilla) in all the Passeriformes, thus adding, as it were, another passerine characteristic. On the other hand, the several morphological variations in glands of the piciform families lend credence, I believe, to Olson's (1983) suggestion for a polyphyletic origin of the Piciforms (see also Burton 1984).

The morphological gland characteristics that could be used in taxonomic analyses are:

1. ontogeny—e.g., gland present in embryos and young of some ratites, but absent in all age groups of other ratites.
2. presence or absence of the gland—e.g., absent from families (Mesoenatidae in the Gruiformes) and genera (*Amazona* in the Psittacidae).
3. lobe shape—e.g., cf. Apodidae and Trochilidae in the Apodiformes.
4. tufted vs. naked condition—
   a. degree of feathering (cf. Momotidae and Meropidae)
   b. shape, size, and length of papilla (cf. Leptosomatidae and Coraciidae).
5. histology—little is known about histological variations, but features such as the number of gland openings are mentioned by Jacob & Ziswiler (1982).

The value for a cladistic taxonomic scheme would depend on the number of variable features of the gland that could be analyzed and the incidence of multiple evolutions of those features. The recent chemo-taxonomic approach of Jacob & Ziswiler (1982), based on chemical differences in uropygial secretions among different taxa, has as yet received little attention in avian taxonomic schemes.

I believe that gland morphology is just as important a diagnostic taxonomic character as are muscle variations, osteological minutiae, incubation patterns, syringeal structures, and the like. The question is, of course, the degree of importance that one assigns to gland morphology in a large suite of taxonomic characters. Because of significant variations in gland morphology in different taxa, as identified in the present study, the least that could be said here is that gland morphology should be considered especially in cladistic taxonomic approaches.

## Functions of glandular secretions

Uropygial gland functions (actually, the functions of glandular secretions) have been controversial ever since the gland was first described in the 13th century. Form and function of glands are biologically interrelated features, but, because the present report concentrates on gland morphology, only a brief summary of secretion functions is included here. (More detailed accounts can be found in Law (1929), Elder (1954), Thomson (1964), and Jacob & Ziswiler (1982)). At least 8 functions have been ascribed to the gland, and the interested reader is referred to the appropriate publications:

1. water-repellent action (Stubbs 1910, Elder 1954, Rijke 1970),
2. preserve physical structure of feathers (Rutschke 1960),
3. maintain horny sheath of bill (Thomson 1964),
4. as a scent organ (Giebel 1857, Jackson 1938, Mackworth-Praed and Grant 1970),
5. pheromone-producing (Balthazart and Schoffeniels 1974),
6. antirhachitic action (Hou 1928),
7. prevent growth of skin microorganisms (King and McLelland 1984),
8. dislodge feather lice (Morris 1836*a*).

Apparently any one or some combination of these functions could be ascribed to the secretions of an individual species but also the functions might not be identical for all birds. Most of the research on water-repellency ('waterproofing') has been appropriately conducted on aquatic birds, but virtually nothing is known about 'waterproofing' in landbirds. Indeed, Rutschke (1960) believed that the gland is only indirectly involved in 'waterproofing' of plumage in aquatic birds (see also Clark 1969), and Spearman (1971) made the unsupported comment that the glandular products are 'not essential for terrestrial birds.' Hou's studies (1928) on rickets and vitamin D were conducted only on chickens, pigeons, and, later, ducks. A scent-organ function for the gland has been reported for a variety of birds (e.g., *Anas moschata, Phoeniculus bollei*), but it is not clear how the 'foul-smelling' (to humans) secretions actually function. Contrary to the research reported by Elder (1954) on ducks, a number of reports have indicated that some birds from which glands had been surgically removed nonetheless had 'normal, bright plumages' (Arnall and Keymer 1975). As early as 1910, Pycraft expressed 'grave doubts' as to the function of the gland primarily because (1) he believed that some birds (e.g., *Anastomus*) presumably could not remove oil from the gland because of their peculiar bill structure and (2) birds lacking glands presumably keep their feathers in as good condition as those species possessing those glands.

Throughout much of the literature on uropygial glands, one finds the recurring suggestion that powder down somehow fulfills the function of oil from glands in those species where the gland is small or absent (Bartlett 1861, Nitzsch 1867, Newton 1893–1896, Verheyen 1956*f*, Voitkevich 1966, Jacob 1978, Goodwin 1983). This presumed correlation arose, I believe, because observers were seeking functional replacements in those birds either lacking glands or possessing small glands. Goodwin (1983: 27), for example, reports for pigeons, 'The powder down . . . appears to

function in lieu of preen oil to aid in waterproofing of the feathers.' Verheyen (1956*f*, 1957*a*) variously describes the glands of Psittaciformes and Columbidae as being in a 'phase of regression' or 'deficient,' somehow compensated by 'a lot of powder.' This correlation argument contains a number of basic flaws, i.e., unproven assumptions (1) that a small gland produces insufficient oil and (2) that the oil and powder down are used more or less interchangeably for waterproofing feathers especially in land birds. It should be emphasized that virtually nothing is known about the quantity, rate of production, or rate of secretion of uropygial oils. Without experimental documentation, it cannot be assumed that small glands have any reduction in rate or quantity of secretion, whether the bird has powder down or not.

It is true that birds known to produce a significant amount of powder down (Gadow 1891, Chandler 1916, Thomson 1964, Jacob 1978, Baumel *et al.* 1979) tend to have relatively small glands: (gland weights as a percent of body weight) Ardeidae ($N=20$, $\bar{x}=0{\cdot}29\%$), Psittacidae ($N=41$, $\bar{x}=0{\cdot}10\%$, *fide* Jacob & Ziswiler 1982 for zoo birds), Ramphastidae ($N=3$, $\bar{x}=0{\cdot}12\%$), and Tinamidae ($N=1$, 0·18% *fide* Jacob & Ziswiler 1982). Relative gland weights are unavailable for other species that produce powder down: Podargidae, Cotingidae, Leptosomatidae, Artamidae, Ptilonorhynchidae, and others. The Mesoenatidae, which have five pairs of powder down patches (Olson 1978), lack a gland. According to Schuz (1927), 'powder downs are lacking, or nearly so, in ratite birds;' among the ratites, only *Apteryx* possesses a gland as an adult. Powder downs, produced in various amounts are known from a wide variety of other birds including Columbidae, Rhynochetidae, Eurypigidae, Podargidae, Otididae, and Accipitridae. This body of circumstantial evidence lends some support to the view that birds with well-developed powder down production have reduced (or no) uropygial glands.

A cause-and-effect functional relationship remains unproven, however. Furthermore, the function of powder remains conjectural probably because several types of powder (down) are known: as a waterproof dressing (Bartlett 1861), preserving feathers (Welty 1962), and cleaning feathers (Thomson 1964). Although the powder has a nonwettable property, it is composed largely of keratin, so its functional equivalence to uropygial oils must await experimental proof (see also Lucas & Stettenheim 1972).

All this information strongly argues that more research on functions of glandular secretions is badly needed before physiological generalizations can be asserted. Particularly open to question is the function of secretions in terrestrial birds and in bird taxa containing some glandless members (e.g., doves, parrots).

## Future studies

Several biological aspects of uropygial glands merit further investigations because results therefrom could help to explain some of the morphological variations identified in the present monograph. Johansson's studies (1927) indicated a strong genetic component in the inheritance of uropygial glands in *Columba livia,* as is also suggested from the fact that certain varieties of this pigeon lack glands (Darwin 1900, Levi, 1941, Goodwin 1983). Hutt (1949) reported that mutation of a dominant gene in chickens causes bifurcation of the gland's papilla and that most heterozygotes have no uropygial gland at maturity. The rumpless chickens of Waterton (1836*a*) presumably had no glands and might have been genetic mutants. Inheritance of double gland papillae were discussed by Kessel (1945) for domestic fowl. Apparently these are the only investigations pertaining to the inheritance of uropygial glands, and further genetic studies might reveal biological relationships to the absence of glands in taxa of wild birds.

Another aspect in need of experimental studies is the physiology of gland production, secretion, and its relationship to preening. Nothing is known about either the quantity or rate of secretion of uropygial oils. Some information is available on histology, vascular supply and innervation (Kossman 1871, Paris 1913, Kanwar 1961). Many additional questions are unanswered, however: (1) do birds with large glands (e.g., waterbirds) produce more oil than birds with small glands (e.g., landbirds); (2) is gland oil production stimulated, and at what rate, by physical manipulation with the bird's bill; (3) is there either seasonal or daily variation in the quantity or rate of secretion?

Despite some papers that address preening activities in birds (e.g., in penguins, Bekoff *et al.* 1979, and references therein), little is known about the relationship between gland secretion and types or rates of preening activities that involve this gland. A case in point was the radical statement by Gurney (1913) that *Sula bassana* does not use its gland in preening, a statement since disputed by Nelson (1978).

As indicated in the previous account, attention should be given to functional attributes of glandular secretions, especially in terrestrial birds.

Little is known about any relationship between gland shape and the underlying muscles and rectrices. Future research could focus on explaining the several different gland shapes identified in this study especially as those shapes might be related to muscle differences or to placement of the rectrices.

A final research need is in embryology, especially post-hatching development as it might relate to function in certain species (a review of the gland's embryology is found in Jacob and Ziswiler 1982). Prior to the report by Pycraft in 1900, it was believed that ratites, with the exception of *Apteryx,* lack uropygial glands. He found, however, that in both *Dromaius novaehollandiae* and *Rhea americana,* a gland exists in both the embryo and nestling, but is absent in the adult. (Those conditions have been verified in the present study). Apparently no one has examined those embryonic glands histologically or functionally. Although no glands have been found in any age group of *Struthio* or *Casuarius*, might some trace or anlage be found by an embryonic-histological study? In other adult birds lacking glands (e.g., Mesoenatidae, Otidae) is there any early embryological development of a gland?

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## Summary

The primary goal of this study has been to assemble a complete analysis of the uropygial gland's morphology in representatives of all bird families and subfamilies. Particular attention has been given to correcting erroneous information about glands in the existing literature. Morphological data are included from many avian taxa not previously reported.

The largest glands, relative to body weight, are found in birds that swim, dive or rest on water. Progressively smaller glands occur in birds that walk in water, those that habitually only fly over water, and lastly, terrestrial species. Glands are now known to be absent in the Struthionidae (all age groups), Rheidae (adults only), Casuariidae (all age groups), Dromaiidae (adults only), Mesoenatidae, Otidae, Columbidae (9 genera, 28 species), Psittacidae (6 genera, 31 species), *Podargus* spp., and Picidae (1 genus, 4 species). The absence of glands in these taxa is believed to be a secondary and independent loss. Because only 17 percent of flightless species lack a gland, this study revealed no significant correlation between gland absence and a flightless condition.

Many nonpasserine taxa possess tufted glands, whereas others have manifestly naked (non-tufted) glands. Apparently naked glands of others, e.g. Strigidae, actually might bear minute feathers. All species of the Passeriformes have naked glands. Feathers attached to the uropygial gland are more numerous in waterbirds than landbirds and are of two principal types, modified down or modified semiplumes. Only circumstantial evidence was found to support the oft-expressed hypothesis that power down is a substitute for gland secretions in glandless species.

The present complete study provides sufficient morphological characteristics for their consideration in avian taxonomic schemes.

Future investigations should focus on gland function, especially in terrestrial birds, the quantity and rate of secretion of uropygial oils, relationships between gland production and preening activities, details of feather structure, genetics, and embryological development.

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