SUBALULAR APTERIUM IN BIRDS

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An apterium, which evidently has remained undescribed, exists under the alula of many avian species but not by any means in all groups. We first noted it in the Snakebird (*Anhinga anhinga*) in which the unfeathered area, measuring about 850 sq mm, is created by an absence of most upper median and other small upper wing coverts associated with primaries 1 (innermost) through 6 (Figures 1A, 1B).

In an ordinary museum skin this apterium is apt to escape notice, being shut away behind a dry, inflexible alula. Details of subalular plumage are difficult to see in skins for the same reason, and at first we sought to limit our investigation to specimens in spirits and to freshly-collected and living birds. But this kind of material proved available for only a few forms. Consequently we often resorted to dampening the wings of skins with a weak solution of ethyl alcohol and examining as much of the subalular area as could be glimpsed by slightly deflecting the alula.

The present paper attempts to summarize our still very incomplete knowledge of the presence and absence of subalular apteria throughout the class. As used below, the term "apterium" refers to an absence or size reduction of coverts which, as we interpret the evolutionary evidence, converted a once almost fully feathered region into a partly naked expanse. A wide variety of conditions intermediate between a well-marked apterium, as seen in *Anhinga*, and a feathered subalular region, as seen in most species, of course exists. A show of skin may arise variously from loss of a few or many coverts, from size reduction of a few or many coverts, and from combinations of both these circumstances. Hence the problem of defining the term "subalular apterium" in any strict fashion is complicated from the start.

Subalular pterylography varies within the class and remains to be worked out for many groups. In addition to the greater upper primary coverts, almost all species we have seen show some sign of at least one row of coverts inserted at the base of the greaters—a row called "middle
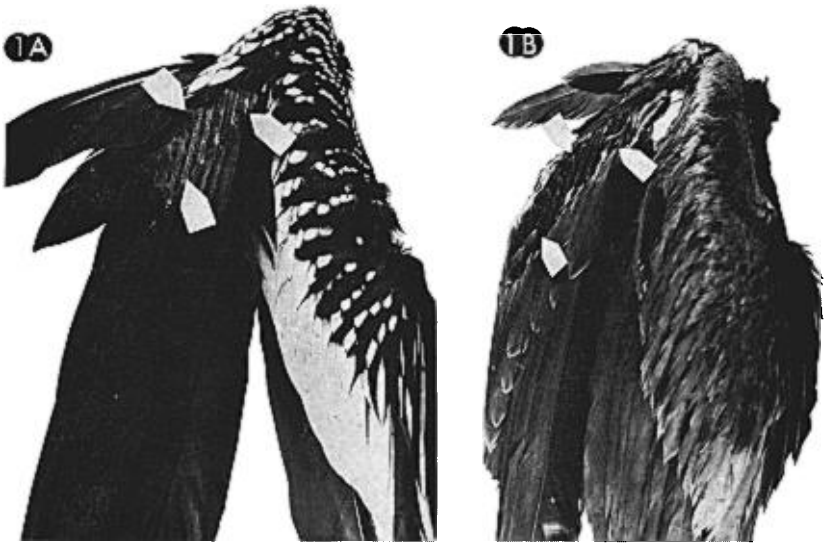
Figure 1. A, apterium in *Anhinga* ♂ fresh plumage. B, apterium in *Anhinga* ♀, worn plumage.

upper primary coverts" by some authors, such as Humphrey and Clark (1961), and termed "medians" herein. One or two, and even three or more rows may be present in some birds: a row of "lessers," and one or more rows of marginals, depending on the species. Table 1 shows the numbers of rows present in certain orders according to our determinations.

In rendering accounts of the subalular apteria, difficulties arise from not knowing truly how many rows of marginal coverts are present and whether a given marginal row in one species may be a row of lesser coverts in another. Homologies presumedly exist between the lesser row and one of the marginal rows in some birds, but not with reasonable certainty. As a result numerical or alphabetical codification of subalular feather follicles might produce misleading accounts if introduced as a basis for comparing the apteria of distantly related birds. We have nevertheless erected formulae below, but hasten to declare they are meant as reference points rather than homologic translations.

A detailed feather-by-feather catolog of subalular plumage is beyond the scope of this paper. Not that we could furnish such a treatment in any event, even if such a culmination were worth the effort, which it probably would not be because neither a functional nor phylogenetic explanation for the loss of subalular plumage has been determined (see "Origin and Function of the Apterium" below). Consequently a complete description of extant and missing plumes would be as apt to focus on

TABLE 1

NUMBER OF ROWS OF SUBALULAR UPPER WING COVERTS IN CERTAIN ORDERS OF BIRDS[1]

	Number of rows			
	4	3	2	1
Gaviiformes	x			
Podicipediformes		x		
Pelecaniformes		x		
Ciconiiformes		x (*Ardea*)	x	
Anseriformes	x (*Branta, Cygnus*) (?)	x		
Falconiformes		x	x	
Gruiformes		x		
Charadriiformes		x		
Cuculiformes			x	
Strigiformes		x (*Bubo*) (?)		
Piciformes			x	
Passeriformes		x (*Corvus*)	x	x (*Myrmochanes, Gymnocichla*)

[1] Not including the greater coverts.

the trivial or superficial as on the significant. For example, it might be assumed—probably rightly—that an apterium that automatically becomes exposed to the environment when the alula is extended, as proves to be the case in *Anhinga* (see below), is more likely to have a functional role than an apterium that remains concealed despite extension of the alula, as appears probably the case in formicariids. But in view of the unknown function of the apterium, one can not be sure of the relative importance of the loss and/or retention of a given series of plumes.

Pterylographic studies rarely have heeded the details of subalular plumage (Humphrey and Clark (1961) is one exception). Similarly, exacting observations on the behavior of species rarely have mentioned use of the alula. Anhingas seem always to flex the alula on assuming their famous spread-wing posture, yet despite many accounts of snakebird behavior and anatomy (i.e. Owre, 1967), no one seems to have commented on this phenomenon. The literature contains some fragments of information on the nonaerodynamic employment of the alula by a few birds, but without, as it happens, illuminating the apterium's significance within any species.

Our primary purpose is to call attention to an overlooked feature existing, for whatever reason, in the main organ of flight of certain birds. To

achieve our objective we have adopted procedures calculated to indicate the species now known to us to exhibit obvious loss and/or size reduction of subalular plumage without, we trust, creating an impression either that our survey has removed a need of examining additional forms in any stated taxon, or that our survey has discerned every intermediate degree of subalular plumage modification in any group. To date we are aware of no evidence of an apterium involving the coverts for primaries 5 through 11 in over half the orders of birds, for example, in anseriforms and charadriiforms. It nevertheless can not be assumed that some duck or shorebird not seen by us lacks an obvious apterium, much less an obscure one. In an early survey of Formicariidae, encompassing a few of the better known species, we noted no apteria. When George carried the survey forward later to include an additional 40 species, he found the structure in a considerable number of genera. No doubt further investigation of certain groups will yield similar results.

RESULTS OF SURVEY

Brief accounts of variation within groups accompany the treatment of Anhingidae, Ramphastidae, and selected passeriforms of special interest. Formulae adhere to the following:

Neg. = no loss or size reduction of coverts was noted.

A = loss of some median coverts associated with primaries 4 through 9. All species appear to possess the median covert for primary 10. Loss or severe size reduction of median coverts for primaries 1, 2, and 3 characterizes most groups. Typically the loss of median coverts for primaries 4 through 9 is accompanied by size reduction of adjacent coverts and this is implied in formulae employing symbol A.

A^1 = severe reduction of some median coverts associated with primaries 4 through 9. Such coverts are vestigial, or very nearly so.

B = loss of some lesser coverts (as defined herein, the term "lesser" refers to a row of coverts lying on the dorsal surface of the wing immediately in front of the median coverts and behind the marginal coverts at the leading edge of the wing). Many species evidently lack such a series; perhaps in these species some lesser plumes have moved forward to the leading edge, merging with or supplanting marginal coverts. In any case, formulae never incorporate the symbol B unless the existence of this series seems demonstrable.

C = loss, severe size reduction or displacement of marginal coverts.

C^1 = apparent enlargement of some marginal coverts.

D = probable exposure of the apterium when the alula is extended.

As one example of formulae emerging from this treatment, Anhinga is ABCD. Some formulae given below are amplified by comments.

An examination of skins alone, as previously stated, yields less than an exhaustive appraisal of the subalular traits of a species, particularly in the case of large birds, so we have indicated skin-derived information by an asterisk after the appropriate name. Nomenclature generally follows Peters' "Check-list of the birds of the world" (1931), with some exceptions as noted. In most cases only one or two specimens per species were examined, but as will appear from some accounts

(see *Anhinga*) a single specimen ordinarily is sufficient to establish whether a species has lost a series of subalular plumes. To avoid any possible confusion between apteria and naked areas arising from molt, all information gleaned from wing-molting specimens has been excluded.

Struthioniformes*. Neg. *Struthio camelus.*
Rheiformes*. Neg. *Rhea americana, Pterocnemia pennata.*
Casuariiformes*. Neg. *Casuarius casuarius.* (Dromiceiidae not examined.)
Apterygiformes*. Neg. *Apteryx australis.*
Sphenisciformes*. Neg. *Megadyptes antipodes, Pygoscelis adeliae, Aptenodytes fosteri.*
Tinamiformes*. A¹B. *Eudromia elegans, Nothura darwinii.*
Gaviiformes. Neg. *Gavia immer, G. stellata.*
Podicipediformes. Neg. *Podiceps auritus, Aechmophorus occidentalis*, Podilymbus podiceps.*
Procellariiformes. Neg. *Diomedea immutabilis, D. nigripes*, Fulmarus glacialis*, Puffinus griseus, P. tenuirostris*, Pterodroma cookii*, Oceanodroma leucorhoa*, O. homochroa*, Oceanites oceanicus*.* (Pelecanoididae not examined.)
Pelecaniformes.

> Anhingidae. ABCD. *Anhinga anhinga, A. rufa*, A. melogaster*, A. novaehol-landiae*.*

> The extant subalular coverts in *Anhinga anhinga* and its congeners number 3 or 4 outer medians, the outermost lesser, and about 7 marginals. Most may be essential for maintaining an airtight surface at and just behind the wing's leading edge.

> In *A. anhinga* the apterium exists in all specimens of both sexes and all age classes, and in birds wearing both fresh (Figure 1A) and worn (Figure 1B) plumage. The months of year covered by the North American specimens we have seen include January, February, March, April, August, September, October, and December. A young bird (AMNH No. 349593) with most of its remiges and rectrices in sheaths, and most or all of its upper wing coverts mature, displayed an apterium seemingly identical to that of adults. Down-like feathers have been noted in the subalular region of some juveniles.

> Some minor variations in the North American birds have been noted. Median coverts 7, 8, and 9 are usually present, but various specimens lack 8 and a few lack 9. Individuals also may display or lack median coverts 2 and 4; such plumes are tiny, near vanishing vestiges. The largest median covert for primary 7 we have seen measured 18 mm (fresh, in the wing), the smallest 9 mm (worn, in the wing).

> Specimens examined: *Anhinga anhinga* (1 living ad. ♂ ; 1 ad. ♀ and 2 ad. ♂ in spirits; skins of 8 ad. ♀, 8 ad. ♂, 3 juv. sex ?, 1 nestling sex ?); *A. rufa* (skins of 1 ad. ♀, 2 ad. ♂); *A. melogaster* (skins of 1 ad. ♀, 2 ad. ♂, 1 ad. sex ?); *A. novaehollandiae* (skins of 1 ad. ♀, 1 ad. ♂).

> Phalacrocoracidae. Neg. All forms* listed by Peters (1931) except the extinct *Phalacrocorax perspicillatus.*

> An examination of two specimens of *Phalacrocorax auritus* in spirits failed to reveal any evidence of size reduction or loss of coverts.

> Pelecanidae. Neg. *Pelecanus occidentalis.*
> Phaethontidae. B. *Phaethon sp.*
> Sulidae. B. *Sula sula.*
> Fregatidae. B. *Fragata sp.*
Ciconiiformes.

> Ardeidae (nomenclature follows Bock, 1956). Neg. *Zonerodius heliosylus*,

Nycticorax nycticorax, N. violacea, Ardeola ibis. AC(D?). *Botaurus lenti-ginosus, Ixobrychus minutus, I. sinensis, Tigriornis leucolophus*, Nycti-corax sibilator, Cochlearius cochlearius, Ardeola ralloides, Butorides virescens, B. sundevalli, Hydranassa caerulea, Egretta sacra, E. thula, E. gularis, E. intermedia, Ardea purpurea, A. pacifica*, A. cinerea*, A. herodias*, A. cocoi*, A. melanocephala*, A. humbloti*, A. goliath*, A. sumatrana*, Agamia agami*.*

Fewer median coverts seemingly have been lost in *Ardea* than in the other species with formula AC. Some *Ardea* in fact may exhibit formula A¹C or just A¹, as also may *Tigriornis, Tigrisoma,* and *Agamia. Ardeola* (= *Bubulcus*) *ibis* is intermediate between A¹C and C, exhibiting a bit of bare skin.

Scopidae (not examined).

Balaenicipitidae. Neg. *Balaeniceps rex.*

Ciconiidae. Neg. *Xenorhynchus asiaticus*.*

Threskiornithidae. AC. *Threskiornis aethiopica, Plegadis falcinellus, Ajaia ajaja.*

Anseriformes. Neg. *Cygnus olor*, Olor columbianus*, Branta canadensis*, Anser albrifrons*, Chen hyperborea*, C. rossii*, Dendrocygna autumnalis*, Anas platyrhynchos, A. strepera*, A. acuta*, A. carolinensis*, A. discors*, Mareca americana, Spatula clypeata*, Aix sponsa*, Aythya americana*, A. collaris*, A. valisineria*, A. affinis*, Bucephala clangula*, Clangula hyemalis*, Histrionicus histrionicus*, Somateria mollissima*, Melanitta deglandi*, M. perspicillata*, Oidemia nigra*, Oxyura jamaicensis*, Lophodytes cucullatus*, Mergus merganser*, M. serrator*, Tachyeres patachonicus*, T. pteneres*, T. brachypterus*.*

Anhimidae (not examined).

Falconiformes.

Cathartidae. Neg. *Cathartes aura*, Coragyps atratus*.*

There appears to be some loss of plumage at or just behind the leading edge of the wing in these birds.

Sagittariidae. Neg. *Sagittarius serpentarius*.*

Accipitridae. Neg. *Accipiter cooperii, A. nisus, A. striatus, A. tachiro, Milvus milvus*, Ictinia misisippiensis, Buteo jamaicensis, B. lineatus, B. platypterus, B. magnirostris, Leucopternis melanops, Aquila chrysaetos*.* AB or A (B?). *Accipiter soloensis, A. badius, A. virgatus, Elanus caeruleus, E. leucurus, Aviceda leuphotes, Buteo leucorrhous.*

In these birds the missing median coverts include the innermost four or five. Only in *Elanus* is the apterium really well-marked.

Pandionidae. Neg. *Pandion haliaetus.*

Falconidae. Neg. *Falco columbarius, F. subbuteo, F. tinnunculus, F. naumanni, F. fuscocoerulescens, F. peregrinus, F. sparverius, F. newtoni.*

Galliformes. Neg. *Megapodius sp., Tetrao urogallus*, Dendragapus obscurus*, Lagopus leucurus*, Canachites canadensis*, Bonasa umbellus*, Pedioecetes phasianellus*, Tympanchus cupido*, Lophortyx californica*, Colinus virgin-ianus, Francolinus sp., Coturnix coturnix, Arborophila sp., Phasianus colchicus*, Pavo cristatus*, Numida meleagris*, Meleagris gallopavo*, Opisthocomus hoazin.* (Cracidae not examined.)

Gruiformes.

Mesoenatidae. A(B?)CD. *Mesoenas sp., Monias benschi*.*

Turnicidae. A(B?)CD. *Turnix sylvatica*, T. Tanki, T. suscitator, T. ocellata*, T. velox*, Ortyxelos meiffrenii*.*

Pedionomidae. Neg. *Pedionomus torquatus**.

Gruidae. Neg. *Grus*.

Aramidae. Neg. *Aramus scolopaceus**.

Psophiidae. Neg. *Psophia crepitans**.

Rallidae. A(B?)CD. *Rallus elegans, R. limicola*, Porzana carolina, Laterallus jamaicensis*, Coturnicops noveboracensis**. Neg. *Aramides cajanea, Fulica cristata*.

Heliornithidae (not examined).

Rhynochetidae. Neg. *Rhynochetos jubatus**.

Eurypygidae. Neg. *Eurypyga helias*.

Cariamidae. Neg. *Cariama cristata**.

Charadriiformes. Neg. *Pluvialis apricaria*, Charadrius vociferus*, Bartramia longicauda*, Numenius americanus*, Limosa lapponica*, Tringa solitaria, Totanus melanoleucus, Actitis macularia, Capella gallinago*, Philohela minor, Crocethia alba*, Ereunetes pusillus*, Erolia melanotos, E. bairdii*, E. minutilla, Phalaropus fulicarius*, Steganopus tricolor*, Burhinus oedicnemus, Larus argentatus*, L. delawarensis*, Chlidonias niger*, Sterna fosteri*, S. fuscata*, S. albifrons*, Thalasseus elegans*, Anous stolidus*, Plautus alle*, Uria aalge*, Cepphus columba, Fratercula artica**, (Jacanidae, Rostratulidae, Haematopodidae, Dromadidae, Glareolidae, Thinocoridae, Chionididae not examined.)

Columbiformes. A (B or C?) D. *Vinago calva**. Neg. *Columba livia, C. arquatrix*, Zenaidura macroura*.

Psittaciformes. ACD. *Micropsitta pusio**. Neg. *Melopsittacus undulatus**.

Coliiformes. Neg. *Colius colius**.

Cuculiformes.

Musophagidae. Neg. *Tauraco hartlaubi*.

Cuculidae. Neg. *Tapera naeva**. ACD. *Clamator glandarius, Cuculus solitarius*, C. canorus, C. poliocephalus, Cacomantis merulinus, C. variolosus, Chrysococcyx cupreus*, Chalcites basalis, Eudynamys scolopacea, Coccyzus erythropthalmus, C. americanus* (Figure 2A), *C. minor, Piaya cayana, Saurothera vetula, Ceuthmochares aereus, Rhopodytes diardi, R. tristis, Rhinortha chlorophaea, Zanclostomus javanicus, Rhamphococcyx curvirostris, Crotophaga ani, Guira guira, Geococcyx velox, Centropus sinensis, C. bengalensis, C. cuperciliosus*.

Strigiformes. Neg. *Tyto alba, Ninox philippensis, Otus asio, Bubo virginianus*, Nyctea scandiaca*, Strix varia, Asio otus*, A. capensis*, Aegolius acadicus**. A(B?)C. *Glaucidium gnoma, G. brodiei*.

The median covert for primary 5 is missing in the three specimens of *Tyto alba* we examined, whereas the rest of the plumes in the median series are present and well-developed. In owls generally the median coverts are better developed than in other birds.

Caprimulgiformes. Neg. *Chordeiles acutipennis, C. minor, Eurostopodus macrotis, Nyctidromus albicollis, Phalaenoptius nuttallii, Caprimulgus carolinensis*, C. vociferus, C. europaeus, C. madagascariensis, C. asiaticus, Hydropsalis brasiliana*. (Podargidae, Nyctibiidae, Aegothelidae not examined.)

Apodiformes. Neg. *Chaetura pelagica, Archilochus colubris*.

Trogoniformes. Neg. *Pharomachrus pavoninus*, Euptilotis neoxenus*, Priotelus temnurus*, Temnotrogon roseigaster*, Trogon massena*, Apaloderma narina*, Heterotrogon vittatus*, Harpactes diardii**.
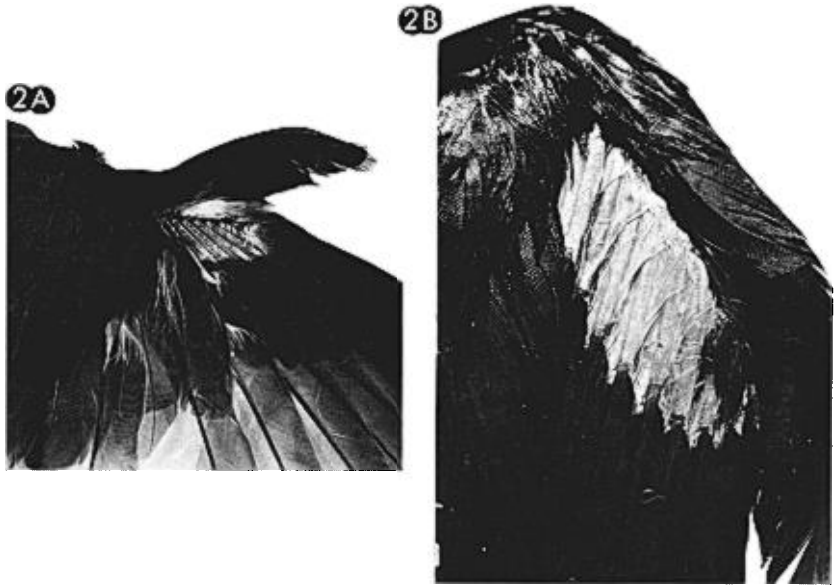
Coraciiformes.

Figure 2. A, apterium in *Coccyzus americanus*. B, apterium in *Ramphastos tucanus*.

Bucerotidae. A (B?)C. *Bucorvus abyssinicus.*

Alcedinidae. Neg. *Ceryle maxima*, C. torquata, C. alcyon, Chloroceryle inda, Alcedo atthis, Dacelo novaequineae, Halcyon smyrnensis.*

Phoeniculidae. AC. *Phoeniculus purpureus.*

Meropidae. Neg. *Melittophagus lafresnayii, Merops nubicus**. (Todidae, Momotidae, Leptosomatidae, Coraciidae, Upupidae not examined.)

Piciformes.

Galbulidae. A¹(B?). *Galbula tombacea.*

Bucconidae. Neg. *Notharcus pectoralis*, Malacoptila mystacalis**.

Capitonidae. A¹(B?). *Capito quinticolor, Megalaima sp., Lybius bidentatus.*

Indicatoridae. Neg. *Prodotiscus insignis, Indicator exilis, I. minor, I. variegatus*, I. indicator.*

A young specimen of *Indicator indicator*, its outer three primaries still in sheaths, exhibited an apparent apterium, but adults of the species have a fully feathered subalular region; evidently some young honeyguides acquire their subalular plumage late, a trait seen also in various woodpeckers and songbirds.

Ramphastidae. Neg. *Andigena bailloni*, A. lamnirostris*, A. hypoglauca*, A. cucullata*, A. nigrirostris**. Neg. or B. *Pteroglossus bitorquatus**. A'BCD. *Aulacorhynchus sulcatus*, A. calorhynchus*, A. derbianis*, A. prasinus*, A. haematopygus*, A. coeruleicinctis*, Pteroglossus castanotis*, P. viridis*, P. beauharnaesii*, P. mariae*, Selenidera spectabilis, S. culik*, S. reinwardtii*, S. langsdorffii*, S. nattereri*, S. maculirostris, Ramphastos sulfuratus*, R. ambiguus**, ABCD. *Pteroglossus torguatus*, P. erythropygus*, P. acari*, P. pluricinctus*, P. flavirostris*, Ramphastos vitellinus*, R. discolorus**,

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TABLE 2

VARIATION IN SUBALULAR PLUMAGE AND DISTRIBUTION IN RAMPHASTIDAE

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	Subalular plumage		
	Normal	Moderate loss	Great loss
Aulacorhynchus (upper tropical, subtropical, lower temperate)		All species	
Pteroglossus (tropical)	*bitorguatus*	*castanotis* *viridis* *beauharnaesii* *mariae*	*torguatus* *erythropygius* *acari* *pluricinctus* *flavirostris*
Selenidera (tropical)		All species	
Andigena (upper tropical, subtropical, temperate)	All species		
Ramphastos (tropical, occasionally subtropical)		*sulphuratus* *ambiguus*	All except *sulphuratus* and *ambiguus*

R. citreolaemus*, R. swainsonii*, R. tucanus (Figure 2B), *R. toco**.

In this small neotropical family (4 genera, about 40 species) the only genus that characteristically inhabits the temperate instead of the tropical zone is *Andigena*. It is also the only one whose members exhibit little or no loss of subalular plumage. This suggests that loss and retention of subalular plumes may be correlated with such factors as altitude and temperature. Among other puzzling cases is *Pteroglossus bitorquatus* which, as indicated above and shown in Table 2, displays an almost fully feathered subalular region, yet presumedly is no less tropical than its congeners. Indeed the heart of this species' range includes Amazonian Brazil along the Rios Madeira, Tapajoz, and Tocantins.

We examined 5 to 20 specimens of the listed species in an attempt to trace racial variation. But as skins composed the material, it was impossible to compare minor subalular refinements in detail, and a series of impressions instead of ac-curate measurements emerged from the work. Two impressions that one of us (George) received from examining the races of *Aulacorhynchus prasinus* may be worth mentioning: 1) size reduction and loss of lesser coverts is similar in the races from the northern end of the species range (*wagleri* in Mexico) to the southern end (*atrogularis* in Peru), while 2) size reduction and loss of median and marginal coverts varies, with the marginal coverts being longer and the median coverts shorter in the northern races (*wagleri, prasinus, stenorhabdus* and *virescens*) and the reverse condition being the rule in the remaining races (i.e. *cyanolaemus, albivita, atrogularis*).

Picidae. Neg. *Colaptes auratus, C. rupicola, Dryocopus pileatus, Melanerpes erythrocephalus, M. formicivorus, M. cruentatus, Sphyrapicus varius, Dendrocopos villosus, D. pubescens, D. mixtus, Picoides tridactylus.*

A^1(B or C). *Nesoctites micromegas, Piculus chrysochloros, P. rivolii, Campethera permista, Picus viridis, P. chlorolophus, Trichopicus cactorum, Blythipicus pyrrhotis, Chrysocolaptes lucidus.* A^1CD. *Jynx torquilla.*

Passeriformes.

  Eurylaimidae. Neg. *Smithornis capensis**, *Corydon sumatranus**, *Cymbirhynchus macrorhynchos**, *Eurylaimus javanicus**, *E. steerii**, *Serilophus lunatus**, *Calyptomena viridis**.

  Dendrocolaptidae. Neg. *Deconychura longicauda**, *Sittasomus griseicapillus**, *Glyphorhynchus pirurus**, *Drymornis bridgesii**, *Nasica longirostris**, *Xiphocolaptes albicollis**, *Xiphorhynchus picus**, *Lepidocolaptes affinis**, *Campylorhamphus trochilirostris*.

  Furnariidae.[1] Neg. *Geositta cunicularia*, *Upucerthia validirostris*, *U. serrana*, *Ochetorhynchus ruficaudus*, *Eremobius phoenicurus*, *Cinclodes patagonicus*, *C. oustaleti*, *C. fuscus*, *Furnarius rufus*, *F. torridus*, *F. cristatus*, *Limnornis curvirostris*, *Sylviorthorhynchus desmursii*, *Aphrastura spinicauda*, *Aphrastura spinicauda*, *Phleocryptes melanops*, *Leptasthenura andicola*, *Schizoeaca fuliginosa*, *Schoeniophylax phryganophila*, *Synallaxis ruficapilla*, *Cranioleuca albiceps*, *Siptornopsis hypochondriacus*, *Asthenes dorbignyi*, *Thripophaga macroura*, *Phacellodomus sibilatrix*, *Coryphistera alaudina*, *Anumbius annumbi*, *Siptornis striaticollis*, *Xenerpestes minlosi*, *Metopothrix aurantiacus*, *Roraimia adjusta*, *Margarornis squamiger*, *Premnornis guttuligera*, *Premnoplex brunnescens*, *Pseudoseisura lophotes*, *Hyloctistes subulatus*, *Ancistrops strigilatus*, *Anabazenops fuscus*.

  Considerable size reduction of the median coverts has occurred in the genus *Upucerthia* but without creating an apterium.

  Formicariidae*. Neg. *Cymbilaimus lineatus*, *Hypoedaleus guttatus*, *Mackenziaena leachii*, *Frederickena viridis*, *Sakesphorus bernardi*, *Biatas nigropectus*, *Thamnophilus doliatus*, *Pygiptila stellaris*, *Neoctantes niger*, *Clytoctantes alixii*, *Thamnistes anabatinus*, *Dysithamnus mentalis*, *Thamnomanes caesius*, *Myrmotherula surinamensis*, *Herpsilochmus longirostris*, *Microrhopias quixensis*, *Formicivora grisea*, *F. rufa*, *Drymophila genei*, *Terenura maculata*, *Cercomacra cinerascens*, *Sipia berlepschi*, *Pyriglena leuconota*, *Myrmoborus leucophrys*, *Hypocnemis cantator*, *Myrmochanes hemileucus*, *Gymnocichla nudiceps*, *Myrmoderus loricatus*, *Myrmophylax atrothorax*, *Formicarius colma*, *Chamaeza nobilis*, *Pithys albifrons*, *Gymnopithys rufigula*, *Rhegmatorhina melanosticta*, *Hylophylax naevioides*, *Phlegopsis nigro-maculata*, *Phaenostictus mcleannani*, *Pittasoma michleri*, *Grallaricula flaviorostris*, *Myrmothera campanisona*, *Grallaria squamigera*. AC[1]. *Batera cinerea*, *Taraba major* (part), *Megastictus margaritatus*, *Dichrozona cincta*, *Myrmochanes hemileucus*, *Gymnocichla nudiceps*, *Sclateria naevia*, *Percnostola rufifrons*, *Myrmeciza ferruginea*, *M. hyperythra*, *Pittasoma michleri*. A[1]C[1]. *Taraba major* (part).

  Typical antbirds possess two rows of subalular coverts (the medians and marginals), from which four general categories of subalular refinements have arisen: 1) vestigial medians, with an apterium present; 2) vestigial medians and no apterium; 3) medians gone entirely or in large part, with apterium present; and 4) medians gone entirely or in large part, with no apterium. The only species in which the latter condition (4) was noted were *Myrmochanes hemileucus*, *Gymnocichla nudiceps* and, less surely, *Formicivora grisea* and *F. rufa*. It would be interesting to know through which stages the subalular plumage of these birds passed. The fact some antbirds possess vestigial medians yet lack an apterium (i.e. *Drymophila genei*) suggests a species can lose an entire row of medians without developing a sizeable naked area.

The marginal coverts in this group appear relatively long and probably would have to be erected to expose the apterium. Erection of the marginal coverts might be required to expose the apterium in some birds of other groups as well.

Conophagidae*. Neg. *Conopophaga melanogaster, Corythopis torquata.*

Rhinocryptidae*. Neg. *Pteroptochus castaneus, Scelorchilus albicollis, Rhinocrypta lanceolata, Liosceles thoracicus, Merulaxis ater, Melanopareia elegans, Psilorhamphus guttatus, Scytalopus unicolor, Myornis senilis, Eugralla paradoxa.* AC[1] *Pteroptochos tarnii, Acropternis orthonyx.*

Cotingidae*. Neg. *Laniisoma elegans, Phibalura flavirostris, Tijuca atra, Carpornis cucullatus, Porphyrolaema porphyrolaema, Cotinga cotinga, Xipholena punicea, Carpodectes nitidus, Ameplion rubrocristatus, Pipreola arcuata, Ameplioides tschudii, Iodopleura isabellae, Calyptura cristata, Attila spadiceus, Pseudattila phoenicurus, Casiornis rufa, Laniocera hypopyrrha, Rhytipterna simplex, Lipaugus fuscocinereus, Chirocylla uropygialis, Platypsaris rufus, Tityra cayana, Haematoderus militaris, Querula purpurata, Pyroderus scutatus, Cephalopterus ornatus, Perissocephalus tricolor, Gymnoderus foetidus, Procneus alba, P. nudicollis, P. averano, Phoenicircus carnifex.*

Rupicolidae*. Neg. *Rupicola rupicola.*

Pipridae*. Neg. *Pipra aureola, P. cornuta, Teleonema filicauda, Antilophia galeata, Chiroxiphia linearis, Masius chrysopterus, Ilicura militaris, Corapipo gutturalis, Manacus manacus, Machaeropterus regulus, Allocotopterus deliciosus, Xenopipo atronitens, Chloropipo uniformis, Neopipo cinnamomea, Heterocercus linteatus, Neopelma pallescens, Tyranneutes stolzmanni, Piprites chloris, Sapayoa aenigma, Schiffornis virescens.*

Tyrannidae*. Neg. *Agriornis livida, Xolmis dominicana, Muscisaxicola rufivertex, Muscigralla brevicauda, Ochthoeca fumicolor, Sayornis phoebe, Colonia colonus, Knipolegus cyanirostris, Pyrocephalus rubinus, Tumbezia salvini, Muscivora forficata, Tyrannus tyrannus, Tyrannopsis sulphurea, Empidonomus varius, Legatus leucophaius, Conopias sp., C. parva, Megarhynchus pitangua, Myiodynastes luteiventris, Myiozetetes cayanensis, Pitangus sulphuratus, Myiarchus crinitus, Nuttallornis borealis, Nesotriccus ridgwayi, Blacicus latirostris, Contopus virens, Empidonax virescens, Cnemotriccus fuscatus, Terenotriccus erythrurus, Aphanotriccus capitalis, Myiobius barbatus, myiotriccus ornatus, Pyrrhomyias cinnamomea, Myiophobus fasciatus, hirundinea ferruginea, Onychorhynchus coronatus, Platyrinchus leucoryphus, Cnipodectes subbrunneus, Tolmomyias sulphurescens, Rhynchocyclus brevirostris, Ramphotrigon ruficauda, Todirostrum cinereum, Oncostoma olivaceum, Idioptilon nidipendulum, Snethlagea minor, Poicilotriccus ruficeps, Lophotriccus pileatus, Colopteryx galeatus, Atalotriccus pilaris, Myiornis ecaudatus, Pseudotriccus pelzelni, Hemitriccus diops, Pogonotriccus ophthalmicus, Phylloscartes ventralis, Capsiempis flaveola, Euscarthmus meloryphus, Pseudocolopteryx sclateri, Polystictus pectoralis, Culicivora caudacuta, Tachuris rubrigastra, Anairetes reguloides, Uromyias agilis, Stigmatura napensis, Serpophaga cinerea, Inezia subflava, Mecocerculus poecilocercus, Colorhamphus parvirostris, Elaenia flavogaster, Myiopagis gaimardii, Suiriri suiriri, Sublegatus modestus, Phaeomyias murina, Camptostoma obsoletum, Xanthomyias sclateri, Phyllomyias griseiceps, Tyranniscus viridiflavus, Acrochordopus burmeisteri, Ornithion inerme, Leptopogon amaurocephalus, Mionectes olivaceus, Pipromorpha oleaginea.*

Oxyruncidae*. Neg. *Oxyruncus cristatus*.

Phytotomidae*. Neg. *Phytotoma rara*.

Pittidae. Neg. *Pitta phayrei*, *P. kocki*, *P. maxima*.

Xenicidae. Neg. *Xenicus gilviventris*, *Acanthisitta chloris*.

Philepittidae. Neg. *Philepitta anerythra, Neodrepanis coruscans*.

Menuridae. Neg. *Menura superba*.

Alaudidae. Neg. *Eremophila alpestris*.

Hirundinidae. Neg. *Tachycineta thalassina*, *Progne subis, Stelgidopteryx rufi-collis*, *Riparia riparia*, *Hirundo rustica*.

Motacillidae. Neg. *Macronyx ameliae*, *Anthus spinoletta*.

Irenidae. Neg. *Chloropsis aurifrons, Irena puella*.

Laniidae. Neg. *Lanius ludovicianus*.

Bombycillidae. Neg. *Bombicilla cedrorum*.

Cinclidae. Neg. *Cinclus mexicanus*.

Troglodytidae. Neg. *Campylorhynchus turdinus*, *Odontorchilus branickii*, *Salpinctes obsoletus*, *Hylorchilus sumichrasti*, *Cinnycerthia unirufa*, *Cistothorus platensis*, *C. palustris, Thryomanes bewickii*, *Thryothorus atrogularis*, *Troglodytes aedon*, *T. rufulus*, *Uropsila leucogastra*, *Henicorhina leucosticta, Microcerculus marginatus*, *Cyphorhinus thoracicus*, *C. aradus*.

Mimidae. Neg. *Dumetella carolinensis*, *Melanoptila glabrirostris*, *Melanotis caerulescens*, *Mimus polyglottos, Nesomimus trifasciatus*, *Mimodes graysoni*, *Oreoscoptes montanus*, *Toxostoma rufum, T. bendirei*, *T. dorsale*, *T. lecontei*, *T. redivivum*, *Cinclocerthia ruficauda*, *Ramphocinclus brachyurus*, *Donacobius atricapillus*.

Turdidae. Neg. *Sialia sialis, Turdus migratorius*.

Timaliidae. Neg. *Chamaea fasciata*, *Yuhina flavicollis, Y. gularis, Y. nigrimenta*.

Polioptilidae. Neg. *Polioptila caerulea*.

Sylviidae. Neg. *Regulus satrapa*.

Parulidae. Neg. *Mniotilta varia, Vermivora pinus*, *V. peregrina, V. celata, Parula americana, Dendroica cerulea, D. dominica, D. virens, D. coronata, D. striata, Setophaga ruticilla, Seiurus aurocapillus, Limnothlypis swainsonii*, *Helmitheros vermivorus, Protonotaria citrea, Geothlypis trichas, Wilsonia citrina*, *Icteria virens*.

Vireonidae. Neg. *Vireo griseus, V. flavifrons*, *V. philadelphicus*, *V. olivaceus, V. gilvus*.

Icteridae. Neg. *Icterus galbula, I. spurius, Agelaius phoeniceus, Sturnella magna, Quiscalus quiscula*.

Fringillidae. Neg. *Carduelis spinus, C. spinus, Carpodacus mexicanus, Richmondena cardinalis, Pheucticus melanocephalus, Passerina cyanea, Spiza americana, Ammodramus savannarum, Junco hyemalis, Spizella pusilla, Zonotrichia albicollis, Melospiza georgiana, M. melodia*.

Ploceidae. Neg. *Passer domesticus*.

Sturnidae. Neg. *Sturnus vulgaris*.

Oriolidae. Neg. *Oriolus sp*.

Dicruridae. Neg. *Dicrurus sp*.

Paridae. Neg. *Parus atricapillus, P. carolinensis, P. bicolor*.

Sittidae. Neg. *Sitta canadensis*, *S. carolinensis*.

Certhiidae. Neg. *Certhia familiaris*.

Dicaeidae. Neg. *Prionochilus olivaceus, Dicaeum hypoleucum*.

Nectariniidae. Neg. *Nectarinia sp., Arachnothera affinis.*

Zosteropidae. Neg. *Zosterops everetti.*

Meliphagidae. Neg. *Timeliopsis fulvigula*, Oedistoma iliolophum*, O. pygmaeum*, Glycichaera fallax*, Lichmera indistincta*, L. alboauricularis*, L. squamata*, Myzomela obscura, M. nigrita*, Meliphaga inexpectata*, M. lewinii, M. flava*, Oreornis chrysogenys*, Foulehaio carunculata*, Cleptornis marchei*, Melithreptus gularis*, Entomyzon cyanotis*, Notiomystis cincta*, Pycnopygius cinereus*, Philemon subcorniculatus*, P. eichhorni*, Ptiloprora plumbea*, P. guisei*, Melidectes nouhuysi*, M. torquatus*, Melipotes fumigatus*, M. ater*, Myza sarasinorum*, Gymnomyza samoensis*, G. aubryana*, Moho bishopi*, M. nobilis*, Phylidonyris pyrrhoptera*, P. melanops*, Ramsayornis fasciatus*, Plectorhynchia lanceolata*, Conopophila whitei*, C. albogularis*, C. picta*, Cissomela pectoralis*, Acanthorhynchus tenuirostris*, Manorina melanophrys*, Anthornis melanura*, Anthochaera chrysoptera*, A. carunculata*, Prosthemadera novaeseelandiae*.*

Corvidae. Neg. *Platylophus galericulatus*, Platysmurus leucopterus*, Gymnorhinus cyanocephala*, Cyanocitta cristata, C. stelleri, Aphelocoma coerulescens*, A. ultramarina*, Cyanolyca viridicyana*, Cissilopha melanocyanea*, C. beecheii*, Cyanocorax mystacalis*, C. dickeyi*, C. yncas*, psilorhinus morio*, Calocitta formosa*, Garrulus glandarius, Perisoreus canadensis*, Urocissa ornata*, Cissa thalassina*, Cyanopica cyana*, Dendrocitta vagabunda*, Crypsirina cucullata*, Pica pica, Zavattariornis stresemanni*, Podoces hendersoni*, Pseudopodoces humilis, Nucifraga columbiana*, Pyrrhocorax pyrrhocorax*, Ptilostomus afer*, Corvus kubaryi*, C. palmarum, C. brachyrhynchos, C. ossifragus.*

Corvus is an exceptional songbird genus in that it contains members (i.e. *C. brachyrhynchos, C. ossifragus*) that exhibit three rows of subalular coverts instead of the usual oscinine number of two. The extra row consists of three or four plumes lying between the medians and marginals associated with primaries 6, 7, 8, and 9. By our definition these are "lessers," but whether they are homologous with the lessers of more primitive birds is most uncertain.

(Not examined: Campephagidae, Pycnonotidae, Remizidae, Rhabdornithidae, Climacteridae, Dulidae, Prunellidae, Orthonychidae, Paruridae, Picathartidae, Muscicapidae, Drepanididae, Catamblyrhynchidae, Tersinidae, Geospizidae, Estrildidae, Grallinidae, Callaeidae, Artamidae, Cracticidae, Ptilonorhynchidae, Paradisaeidae).

ORIGIN AND FUNCTION OF THE APTERIUM

In trying to determine the evolutionary background and possible function of this apterium, we first considered the possibility of a physiological connection between the bare area, wettable plumage (see Rijke, 1968), and spread-wing posture of *Anhinga*. Wettable plumage may be an important asset to the underwater swimming of snakebirds (Owre, 1967: 107) but such a specialization has the apparent disadvantage of leaving a specimen so drenched as to hamper its ability to fly. In dry plumage Anhingas fly well and even soar in masterly fashion, whereas in wet plumage they rarely attempt flight. After swimming they ordinarily leave the water by crawling out soaking wet, then mount perches and

assume the spread-wing posture. Consequently we were impressed to discover that snakebirds extend the alula and expose the apterium while standing in an attitude surely useful in allowing the plumage to dry. One of us (Casler) observed repeatedly in a captive specimen at the National Zoological Park, Washington, D. C. the alula extended and the apterium exposed to sunlight. Published portraits and photographs (see Pearson, 1936: 94, bottom right photograph; or picture No. 602 in the slide series of the Everglades Natural History Association), which we earlier had scrutinized, showed birds in nature manifesting the same behavior. More recently an American Broadcasting Company television program titled "Arthur Godfrey's America: The Everglades," provided an excellent view of the entire sequence, the apterium plainly visible.

We attempted a histological examination of the skin of the subalular region of an Anhinga collected for an air sac study and fixed in a formalin solution too concentrated to serve well for microscopic tissue examination. The resulting slides, while poor in quality, revealed blood vessels and many melanocytes, but no evidence of exceptional beds of capillaries, or any unexplained feature except a thin layer of very small cell-like structures which has remained unidentified after failing to excite the curiosity of specialists. Mary E. Rawles (pers. comm.) directed our attention to this feature. She commented that the layer may represent only vestigial tissue, but that properly prepared fresh sections should be examined to establish its true nature.

Peter Stettenheim examined the slides and suggested (pers. comm.) that what they reveal does not prohibit the possibility of significant vascularization of the apterium. Walter Bock (pers. comm.) pointed out that a lack of cellular refinements in the apterium does not preclude the possibility of thermal information being transmitted via nerve cell endings near the skin surface.

Heat loss from the apterium surely would appear inevitable, and not surprisingly species that characteristically inhabit cold environments or, unlike snakebirds, spend lengthy periods in water (loons, grebes, cormorants, waterfowl, alcids) lack the apterium. In groups displaying the structure, loss of plumage seems to be most extensive in the tropical forms, the Ramphastidae being one example. Furthermore, tropical or semitropical antecedents is a common denominator of the species exhibiting a subalular apterium. Thus a thermoregulatory function for this apterium remains one of the possibilities deserving future study.

Correlations between loss of subalular plumage and both behavioral and morphological traits may exist but so far we have not encountered any unvarying or convincing cases.

Of the birds known to spread their wings while perched or on the

ground, whether for wing-drying or sun-bathing purposes, a few have
the apterium (*Anhinga, Butorides virescens, Coccyzus americanus, Cro-
tophaga ani*) while a much larger number lack it (*Phalacrocorax, Pele-
canus, Nannopterum, Cathartes aura*, and many other species including
a long list of songbirds; see Bent, 1940: 23; Hauser, 1957; Cracraft,
1964; Clark, 1969).

Wing size and phylogeny.—Neither size of wing nor closeness of
phylogenetic relationship appears a fundamental factor regulating the
origin of subalular apteria in bird groups. Distantly related species have
the apterium, while more often than not it is absent in their kin, whatever
the size of the species: large (some herons and diurnal birds of prey
have it, others do not), medium-sized (some pigeons, cuckoos, wood-
peckers and antbirds have it, others do not), or small (some antbirds
have it, others do not).

Phylogeny and wing size, however, cannot completely be ignored because
as shown in Table 1, there evidently has been an overall decrease in
the number of rows of subalular coverts within the class, with the more
primitive groups of larger species tending to exhibit more rows than
the groups of more recent and generally smaller forms. Some apteria, then,
may reflect in part a phylogenetic process of reduction and also in part
a reduction based on size.

The perching birds, showing more variation in the number of rows
than any other group, seem to offer the best chance of descrying whatever
progression of phylogenetic and size factors may influence the reduction
(and/or addition) of subalular coverts. Such large passerines as crows
(*Corvus*) have three rows of these coverts, while most of the species,
including jays (*Cyanocitta*), have two, and a few have one (*Myrmo-
chanes hemileucus* and *Gymnocichla nudiceps*, both formacariids). Un-
fortunately perching bird relationships are obscure at the suprageneric
levels; correspondingly the evolution of passeriform subalular traits is
unclear. Size seems implicated in the subalular difference noted between
the crows and jays, but at the same time one can not help noticing
that some of the smallest perching birds, including kinglets (*Regulus*)
and other diminutive members of the most advanced passeriform sub-
order, Oscines, retain two rows of coverts while the presumed more
primitive suboscines contain the few birds that have "advanced" beyond
the two-row complement and today have but one.

The argument that wing size may be an unimportant factor in re-
duction and loss of subalular coverts is further strengthened by noting
that in herons the largest birds (*Ardea*) seemingly have lost the fewest
coverts; the same is true in owls, with *Glaucidium* exhibiting an ap-
terium in contrast to such large species as *Bubo* and *Strix*, which appear

to have not only retained their subalular plumage but undergone no change resulting in attenuated plumes.

In any case, and whatever the origin of the apteria in the different groups, *Anhinga* and some other species of undoubted antiquity have more than merely lost a few coverts in the course of bending to natural selection. They have retained the resulting apterium. Why this should be so unless the apterium has a function is hard to say.

Length and functional efficiency of the alula.—A relatively long alula characterizes many species that have the apterium (*Anhinga,* various cuckoos), but also many species that do not (swans and geese, various gallinaceous birds, the cuckoo *Tapera,* the cotinga *Cephalopterus ornatus*).

It might seem a loss of subalular plumage could arise from a need to clear out feathers in the way of the alula's primitive claw, but this claw, in reduced form at least, occurs in almost all specimens of Bobwhite (*Colinus virginianus*) (George and Brown, 1968), a species which, though missing several innermost median coverts, lacks the apterium.

A possibility nevertheless exists that loss of subalular plumage is a natural response to the need to suppress or remove plumage near the wrist and the joint between the alula and the hand; numerous species indeed either lack, or possess in stunted form, the median coverts between primaries 1 and 3, but this creates only a very obscure patch of bare skin, concealed not only by the alula itself but by such feathers as the carpal remex and/or carpal covert. Various species, moreover, do exhibit coverts in this region (i.e. *Corvus*).

Displays.—In living Anhingas the apterium is a blue-gray color and conspicuous against the background of the wing plumage. As there is evidence (Owre, 1967: 107) that snakebirds seek their prey while swimming very slowly beneath the water surface (are they stalking or ambushing prey at this time?), with the wings "held incompletely folded" (Owre, op. cit.: 61), we have considered and continue to imagine the apterium could be used as a fish lure, "flashing" with the flexing of the alula. Regrettably we have to date been unable to observe the underwater behavior of snakebirds closely enough to determine whether swimming individuals ever extend the alula; nor have we been able to determine whether this species extends the alula during courtship or in other displays. Allen's (1961) account of the breeding postures of snakebirds does not mention movements of the alula, and as said earlier, few reports on displaying birds mention the alula even in passing. Yet use of the apterium in displays is a possibility. Because they tend to be the color of the skin, apteria often constrast with the surrounding plumage. The apteria of *Butorides virescens* and *Coccyzus americanus*, for example, are yellowish and if exposed might contribute to the pro-

duction of a spectacle. In this connection, it might as well be pointed out, the subalular plumage of an impressive number of birds differs markedly in color and pattern from the adjacent plumage. In many furnariids and cotingas the rows of subalular coverts are unlike each other in markings, shade, and even basic color.

A rather remarkable number of species that exhibit an apterium also display areas of colored naked skin on the face (*Anhinga*, toucans, the formacariids *Myrmeciza hyperthyra* and *Gymnocichla nudiceps*); yet there are many exceptions to this, and a large number of birds with naked facial patches lack a subalular apterium (Phalacrocoracidae, the formacariids *Rhegmatorhina*).

Taxonomic significance.—That the presence and absence of the subalular apterium will prove a useful taxonomic character we think unlikely, without however dismissing the possibility of a taxonomic application in some groups.

SUMMARY

Many bird species exhibit, but many more do not, an apterium stemming from loss, or acute reduction in size, of upper wing coverts beneath the alula.

This apterium has been noted in 12 of 27 orders examined. Its presence and absence is often variable within families and genera but constant within a species.

Neither functional nor phylogenetic explanations for its existence have been determined.

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