

INFREQUENCY OF PINEAL ATROPHY AMONG BIRDS AND ITS RELATION TO NOCTURNALITY

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A recent resurgence of interest in the vertebrate pineal organ or epiphysis cerebri has provided new evidence of its systematic diversity, as well as of its probable functional significance in birds (Ralph 1970). Although embryologically derived from the roof of a part of the brain, the diencephalon, the pineal organ has a different and unique structure and composition. Microscopic and physiological studies have shown that, in general through the vertebrate series, as pineal photoreceptor activity decreases, an apparent secretory capacity increases (Quay 1970b). Among birds only abortive or vestigial photoreceptors have been identified so far in electron microscopic studies of the pineal organ (Oksche and Vaupel-von Harnack 1966; Collin 1966a, b, 1967, 1968; Renzoni et al. 1968; Bischoff 1969; Oksche et al. 1969; Oksche and Kirschstein 1969; and others). Similarly, electrophysiological investigations have been unsuccessful in detecting a direct response to light by avian pineals (Morita 1966; Ralph and Dawson 1968). Nevertheless, rapid biochemical changes occur in avian pineal organs in close correlation with the daily timing of environmental illumination (Axelrod et al. 1964; Quay 1966, 1970a; Ralph et al. 1967; Hedlund and Ralph 1968; Lauber et al. 1968; Sayler and Wolfson 1969). These changes are thought to be most likely mediated by the nervous system and the innervation of the pineal following photoreception by the lateral eyes. The pineal biochemical changes have been postulated most commonly to be related to a pineal endocrine secretory activity which may have some physiological significance in relation to adaptation to photoperiod, either on a short-term or seasonal basis. However, such postulations are in need of extensive additional supporting evidence (Ralph 1970).

With the recent advances in our knowledge of avian pineal composition and its primary correlations with light, the investigation of comparative pineal size in birds in relation to diurnality and nocturnality becomes of especial interest. Krabbe (1952) in comparative studies of the morphogenesis of the brain in birds found that the pineal gland or epiphysis cerebri varies in size and shape probably more than

any other part of the avian brain, and that it is smallest in owls (Strigidae). Owing to the hitherto relatively few species of adult birds whose pineal glands have been examined, it has not been possible until recently to effectively compare adult pineal development and structure in birds with their behavioral traits and daily times of activity. Although this situation has been improved, as can be ascertained from the data in table 1, it is still far from ideal. Two major areas of deficiency in our information can be cited. There are still many families and a few orders (Gaviiformes, Gruiformes, Coliiformes, and Trogoniformes) in which adult pineal size and structure are unknown. There are still comparatively few representatives of the Caprimulgiformes whose pineals are known. Behaviorally and physiologically, many of these may prove to be among the most interesting of the putatively nocturnal or crepuscular species. The second major area of informational deficiency is the fragmentary and largely subjective state of evidence for nocturnality in most species and the variability of supposedly nocturnal behavior in relation to seasonal activities, such as migration, incubation, feeding nestlings, and others. The present report, representing an extension of an earlier abstract for an oral presentation (Quay 1968), serves primarily to outline the degree of relation between the infrequent occurrences of pineal atrophy in birds and nocturnality.

METHODS AND MATERIALS

Table 1 lists the species whose pineals have been either described previously in publications or more recently examined by the author. Excluded are species whose pineals have been studied only in developmental stages or by electron microscopy, since doubt may remain concerning the size or final status of the pineal in adults of such species. Observations and conclusions in this study are based on published descriptions of adult pineal size and structure and on microscopic study of pineal specimens, some of which came from species whose pineal organs have not been studied or described before. Twenty-three orders, 58 families and 121 species are represented (table 1). Of these species, 89 have been examined histologically by the author, usually by means of serial sections of a median slice of the entire brain and its covering membranes. Techniques of preparation and histological staining have been noted previously (Quay and Renzoni 1963,

TABLE 1. Avian species whose pineals have been described in publication or (starred) examined microscopically by the author.

Taxa	Source
Struthioniformes	
Struthionidae	
<i>Struthio camelus</i>	Starck 1955
Rheiformes	
Rheidae	
<i>Rhea americana</i>	Starck 1955
Casuariiformes	
Dromiceidae	
<i>*Dromiceius n. hollandiae</i>	Cobb and Edinger 1962
Apterygiformes	
Apterygidae	
<i>Apteryx australis</i>	Craigie 1930; Krabbe 1959
Tinamiformes	
Tinamidae	
<i>*Crypturellus cinnamomeus</i>	
Sphenisciformes	
Spheniscidae	
<i>Aptenodytes patagonica</i>	Breucker 1967
Colymbiformes	
Colymbidae	
<i>*Aechmophorus occidentalis</i>	
<i>*Podilymbus podiceps</i>	Quay and Renzoni 1967
Procellariiformes	
Diomedidae	
<i>*Diomedea immutabilis</i>	
Procellariidae	
<i>*Puffinus pacificus</i>	
<i>*Pterodroma leucoptera</i>	
Hydrobatidae	
<i>*Oceanodroma homochroa</i>	Renzoni and Quay 1963; Quay and Renzoni 1967
Pelecaniformes	
Pelecanidae	
<i>*Pelecanus erythrorhynchos</i>	
<i>*Pelecanus occidentalis</i>	Quay and Renzoni 1967
Sulidae	
<i>*Sula sula</i>	
Phalacrocoracidae	
<i>Phalacrocorax carbo</i>	Charvát 1954
<i>*Phalacrocorax penicillatus</i>	Renzoni and Quay 1963; Quay 1965; Quay and Renzoni 1967
<i>*Phalacrocorax pelagicus</i>	Renzoni and Quay 1963; Quay 1965; Quay and Renzoni 1967
Ciconiiformes	
Ardeidae	
<i>Ardea cinerea</i>	Stammer 1961
Anseriformes	
Anatidae	
<i>*Anser albifrons</i>	Stammer 1961; Quay and Renzoni 1967
<i>*Anas acuta</i>	
<i>*Aythya americana</i>	Quay and Renzoni 1967
<i>*Melanitta deglandi</i>	Quay and Renzoni 1967
Falconiformes	
Cathartidae	
<i>*Cathartes aura</i>	Quay and Renzoni 1967
Accipitridae	
<i>*Buteo swainsoni</i>	Quay and Renzoni 1967
Falconidae	
<i>*Falco sparverius</i>	Quay and Renzoni 1967
Calliformes	
Phasianidae	
<i>*Lophortyx californicus</i>	
<i>*Gallus [domestic]</i>	Studnička 1905; Chiodi 1940; Spiroff 1958; Stammer 1961; Quay 1965; Quay and Renzoni 1967
Meleagrididae	
<i>Meleagris gallopavo</i>	Studnička 1905; Stammer 1961
Charadriiformes	
Haematopodidae	
<i>*Haematopus ostralegus</i>	
Charadriidae	
<i>*Squatarola squatarola</i>	Quay and Renzoni 1967
<i>*Charadrius vociferus</i>	Quay and Renzoni 1967
Scolopacidae	
<i>*Limosa fedoa</i>	Quay and Renzoni 1967
<i>*Catoptrophorus semipalmatus</i>	Quay 1965; Quay and Renzoni 1967

TABLE 1. Continued.

Taxa	Source
<i>*Capella gallinago</i>	Quay and Renzoni 1967
<i>*Ereunetes mauri</i>	Quay 1965; Quay and Renzoni 1967
<i>*Erolia alpina</i>	Quay and Renzoni 1967
Burhinidae	
<i>*Burhinus capensis</i>	
Clareolidae	
<i>*Rhinoptilus cinctus</i>	
Laridae	
<i>Larus canus</i>	Wetzig 1961
<i>*Larus occidentalis</i>	Quay and Renzoni 1967
<i>*Sterna hirundo</i>	
Alcidae	
<i>*Uria aalge</i>	
<i>*Aethia cristatella</i>	Quay and Renzoni 1967
Columbiformes	
Columbidae	
<i>*Columba livia</i>	Quay and Renzoni 1967
<i>Columba oenas</i>	Renzoni 1970
<i>Streptopelia turtur</i>	Renzoni 1970
<i>Streptopelia decaocto</i>	Renzoni 1970
Psittaciformes	
Psittacidae	
<i>*Nymphicus hollandicus</i>	
<i>*Aratinga canicularis</i>	
<i>*Melopsittacus undulatus</i>	Renzoni 1964b, 1965a, b
Cuculiformes	
Cuculidae	
<i>Cuculus canorus</i>	Renzoni 1968
Strigiformes	
Tytonidae	
<i>Tyto alba</i>	Renzoni 1963, 1964a, 1968
Strigidae	
<i>Otus scops</i>	Renzoni 1963, 1964a, 1968
<i>*Glaucidium cuculoides</i>	
<i>Athene noctua</i>	Renzoni 1963, 1964a, 1968
<i>*Speotyto cunicularia</i>	
<i>Strix aluco</i>	Breucker 1967; Renzoni 1968
<i>Asio otus</i>	Renzoni 1963, 1964a, 1968
<i>*Asio flammeus</i>	Studnička 1905
Caprimulgiformes	
Caprimulgidae	
<i>*Phalaenoptilus nuttallii</i>	Quay and Renzoni 1967
<i>Caprimulgus europaeus</i>	Renzoni 1968
Apodiformes	
Apodidae	
<i>*Streptoprocne zonaris</i>	
<i>Apus apus</i>	Renzoni 1968
Trochilidae	
<i>Anthracothorax nigricollis</i>	Breucker 1967
<i>*Calypte costae</i>	Quay and Renzoni 1967
Coraciiformes	
Coraciidae	
<i>Coracias garrulus</i>	Renzoni 1965a
Upupidae	
<i>Upupa epops</i>	Renzoni 1965a
Piciformes	
Picidae	
<i>Jynx torquilla</i>	Renzoni 1965a
<i>*Colaptes cafer</i>	
<i>Picus viridis</i>	Renzoni 1965a
<i>*Dendrocopos pubescens</i>	
Passeriformes	
Tyrannidae	
<i>*Sayornis saya</i>	
<i>*Nuttallornis borealis</i>	Quay and Renzoni 1963
Alaudidae	
<i>*Eremophila alpestris</i>	Quay and Renzoni 1963
Hirundinidae	
<i>*Tachycineta thalassina</i>	Quay and Renzoni 1967
<i>Hirundo rustica</i>	Renzoni 1965a
Motacillidae	
<i>*Anthus spinoletta</i>	Quay and Renzoni 1967
Laniidae	
<i>*Lanius ludovicianus</i>	Quay and Renzoni 1967
Troglodytidae	
<i>*Salpinctes obsoletus</i>	Quay and Renzoni 1963, 1967
Muscicapidae	
<i>*Sialia mexicana</i>	Quay and Renzoni 1963, 1967
<i>*Myadestes townsendi</i>	Quay and Renzoni 1963, 1967
<i>Turdus merula</i>	Renzoni 1965a, Breucker 1967
<i>Turdus iliacus</i>	Renzoni 1965a
<i>*Turdus migratorius</i>	Quay and Renzoni 1963

TABLE 1. *Continued.*

Taxa	Source
* <i>Regulus calendula</i>	Quay and Renzoni 1963, 1967
<i>Phylloscopus collybita</i>	Renzoni 1965a
Aegithalidae	
* <i>Psaltriparus minimus</i>	Quay and Renzoni 1967
Paridae	
* <i>Parus rufescens</i>	Quay and Renzoni 1963
* <i>Parus inornatus</i>	Quay and Renzoni 1967
Sittidae	
* <i>Sitta canadensis</i>	Quay and Renzoni 1967
Certhidae	
* <i>Certhia familiaris</i>	Quay and Renzoni 1967
* <i>Certhia brachyactyla</i>	Renzoni 1965a
Emberizidae	
* <i>Melospiza melodia</i>	Quay and Renzoni 1963, 1967
* <i>Zonotrichia leucophrys</i>	Quay and Renzoni 1963, 1967
* <i>Zonotrichia atricapilla</i>	Quay and Renzoni 1963, 1967
* <i>Junco oreganus</i>	Quay and Renzoni 1967
* <i>Passerculus sandwichensis</i>	Quay and Renzoni 1963, 1967
* <i>Pipilo erythrophthalmus</i>	Quay and Renzoni 1963, 1967
* <i>Pipilo fuscus</i>	Quay and Renzoni 1963
Parulidae	
* <i>Dendroica auduboni</i>	Quay and Renzoni 1963, 1967
Vireonidae	
* <i>Vireo huttoni</i>	Quay and Renzoni 1967
Icteridae	
* <i>Agelaius phoeniceus</i>	Quay and Renzoni 1963, 1967
* <i>Agelaius tricolor</i>	Quay and Renzoni 1967
* <i>Sturnella neglecta</i>	Quay and Renzoni 1963, 1967
* <i>Euphagus cyanocephalus</i>	Quay and Renzoni 1963, 1967
Fringillidae	
* <i>Spinus pinus</i>	Quay and Renzoni 1963, 1967
* <i>Spinus lawrencei</i>	Quay and Renzoni 1963, 1967
* <i>Carpodacus mexicanus</i>	Quay and Renzoni 1963, 1967
<i>Coccothraustes</i> <i>coccothraustes</i>	Studnička 1905
Estrildidae	
* <i>Poephila guttata</i>	Quay and Renzoni 1963, 1967
* <i>Padda oryzivora</i>	Quay and Renzoni 1967
Ploceidae	
* <i>Passer domesticus</i>	Quay and Renzoni 1963; Renzoni 1965a; Ralph and Lane 1969
Sturnidae	
* <i>Sturnus pagodarum</i>	
Corvidae	
* <i>Aphelocoma coerulescens</i>	Quay and Renzoni 1967
<i>Garrulus glandarius</i>	Renzoni 1965a
* <i>Pica pica</i>	Renzoni 1965a
* <i>Pica nuttalli</i>	Quay and Renzoni 1967
<i>Corvus monedula</i>	Renzoni 1965a
<i>Corvus corone</i>	Renzoni 1965a
* <i>Corvus corax</i>	

1967). Generic and species names of North American birds follow the usage of the A.O.U. Check-list (1957). Names of birds from other regions follow, insofar as possible, those in Peter's Check-list (1931-1970). Major systematic groups and their order of presentation (table 1) follow, for convenience, the nomenclature and order in Peter's Check-list and in Mayr and Greenway (1956).

RESULTS

Without the necessity of going into anatomical or histological details for most species, it can be said that with the exception of the shearwaters and petrels (Procellariidae and Hydrobatidae) and the owls (Strigiformes), the pineal gland is well developed and cytologically active-appearing throughout the series of examined, living species (table 1). Individual and sexual variation in pineal size and structure within a species or population is slight or negligible in adult birds having well-

developed pineal organs, insofar as known (Quay and Renzoni 1963, 1967; Ralph and Lane 1969). Thus, although the samples representing particular species rarely contain more than two or three specimens, the pineal status in these can probably be judged as representative for the species.

Detailed observations here will concern two categories of birds, those that are found to have very small or atrophic pineal glands and those that are reputedly in some degree nocturnal. The remaining birds are both primarily diurnal and characteristically typified by pineal glands of medium to large size.

APTERYGIFORMES

Apteryx australis. Pineal microscopic structure in the kiwi is known particularly from descriptions by Craigie (1930) and Krabbe (1959). But the relative size and gross relations of the kiwi pineal are known from descriptions provided by others as well (Parker 1891; Starck 1955). For a bird of its general body size, the kiwi has a well-developed and active-appearing pineal which is only slightly smaller than that of the domestic chicken, whose body size is similar. Except for the qualification of some crepuscular activity (Williams 1963), kiwis are clearly nocturnal (Haeusler 1923; Stoner 1923; Buddle 1951; Oliver 1955; Bailey 1955; van Someren 1956; Wilson 1959; Falla 1964, 1966; and others).

PROCELLARIIFORMES

Personally examined specimens show a large and active pineal gland in the Laysan Albatross (*Diomedea immutabilis*) and very small or atrophic pineal organs in the Wedge-tailed Shearwater (*Puffinus pacificus*), White-winged Petrel (*Pterodroma leucoptera*), and Ashy Petrel (*Oceanodroma homochroa*). The atrophic pineals of the latter three species can be typified by what is observed in the three adult Ashy Petrels which have been examined. The distal part of the petrel pineal organ is small and atrophic (fig. 1A, B), and the pineal stalk is often difficult to trace and is variable in structure (Quay and Renzoni 1967).

Nocturnal habits have been suggested by Murphy (1936) as primitive among the Tubenares. But he noted as well the geographic or species variability in nocturnality among the small petrels that he studied. Diurnality has been demonstrated in captive Laysan Albatrosses, which moved little or not at all at night (Frings and Frings 1959). Nocturnal feeding, flying, and diving by large numbers of Wedge-tailed Shearwaters were observed at



FIGURE 1A. Sagittal section of the pineal region of the brain of an adult male Ashy Petrel (*Oceanodroma homochroa*) (Southeast Farallon Island, California; 22 May). The anatomical relations of the atrophic pineal organ (P) are seen in relation to the dural connective tissue covering (D) of the brain, cerebellar folia (CBE), cerebrum (CBU), lateral ventricle of the brain (LV), thalamus (T) and the posterior commissure (PC). Chrome alum hematoxylin and phloxine.

B. Pineal remnant from another section of the Ashy Petrel specimen shown in figure 1A. A series of small follicles of pineal parenchymal cells is shown encapsulated by connective tissue (CT) and containing a central lumen (L), some parenchymal cells with phloxinophilic apical cytoplasmic granules (G) and some with yellowish-brown globular pigment granules (PG). DP denotes the dorsal or distal end of the pineal remnant. Chrome alum hematoxylin and phloxine.

full moon by Gould (1967), and nocturnal activity typifies diverse species of shearwaters, particularly during the breeding and incubation periods (Lockley 1942; Dement'ev et al. 1951). A similar situation appears to be true for the more commonly studied species of

petrels (Forbush 1925; Dement'ev et al. 1951; Waters 1964), including the Ashy Petrel, as studied on Southeast Farallon Island (Ray 1904; Dawson 1923), the locality of origin for the specimens whose pineals have been studied here. Thus, an at least seasonally pronounced

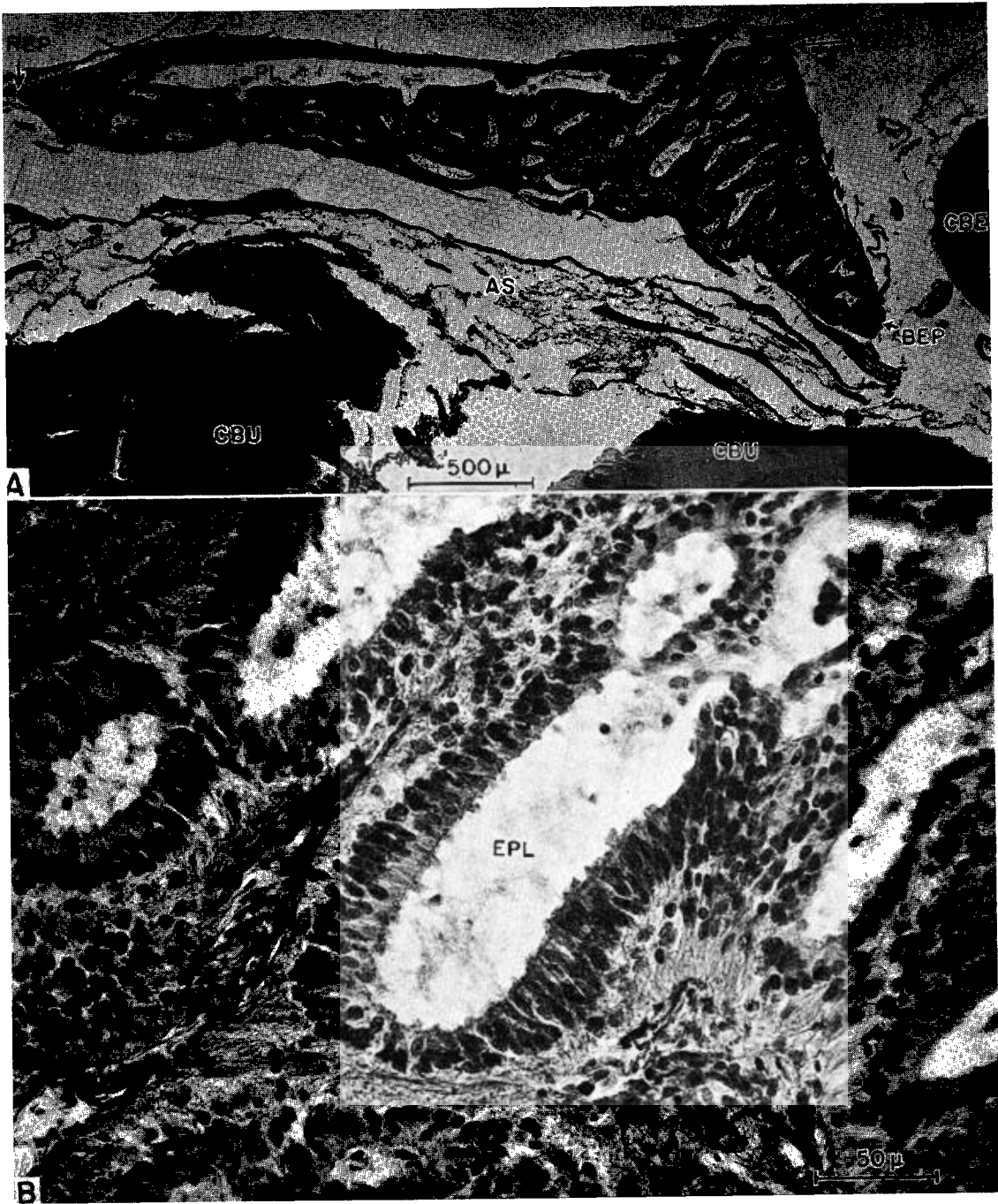


FIGURE 2A. Sagittal section of the most dorsal and superficial part of the pineal gland in a Cape Thick-knee (*Burhinus capensis*) (Sabi Valley, Rhodesia; 5 March). The glandular tissue lies close beneath the dural covering (D) of the brain and extends several millimeters from the basal (BEP) and caudal (CEP) extremities of the pineal gland near the cerebellum (CBE) to the rostral extremity (REP) overlying a median arachnoid space (AS) and the cerebral hemispheres (CBU). Within the gland is a central lumen (PL) with tubular and follicular extensions and derivatives. Chrome alum hematoxylin and phloxine.

B. A small area enlarged from the Cape Thick-knee pineal gland section shown in figure 2A. Epithelial and subepithelial organizations of pineal parenchymal cells are seen around each extension of the lumen (EPL).

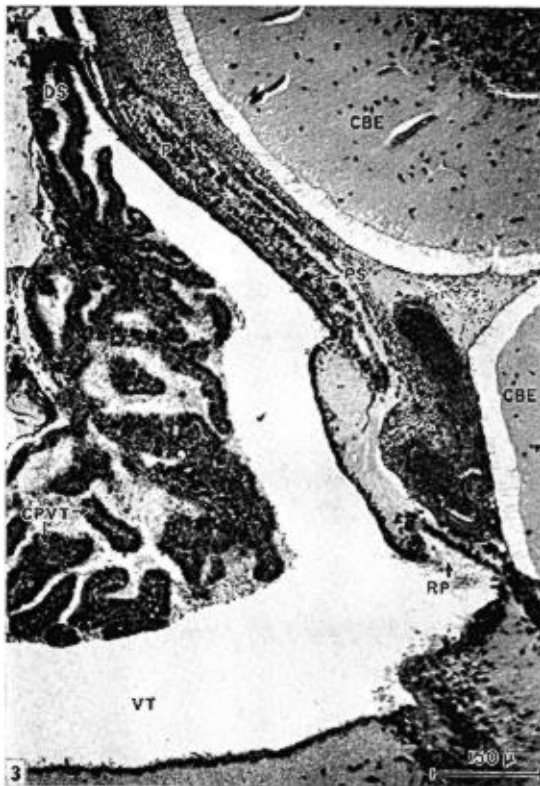


FIGURE 3. Sagittal section of the basal pineal region of a Three-banded Courser (*Rhinoptilus cinctus*) (Sabi Valley, Rhodesia; 5 March). The pineal stalk (PS) originates basally from the recessus pinealis (RP) and extends distally and dorsally into the pineal body (P), most of which lies out of this plane and dorsally farther beyond the tip of the dorsal sac (DS). Anatomical relations with cerebellar folia (CBE), third ventricle (VT) and choroid plexus of the third ventricle are shown. Chrome alum hematoxylin and phloxine.

nocturnality characterizes the procellariiform birds whose pineals are very small or atrophic.

CHARADRIIFORMES

Three very different, reputedly nocturnal birds of this order have pineals that are very different in size and structure. They are considered separately.

Burhinus capensis. The pineal gland is large and active-appearing in the single available specimen of Cape Thickknee (fig. 2A, B). Most striking is the superficiality and radial extent of the distal part of the organ (fig. 2A). Field observations on this species generally concur on its being primarily crepuscular and nocturnal (Lane 1920; Pitman 1934; Mackworth-Praed and Grant 1962-3; Clancey 1964), but detailed behavioral investigation of a captive failed to mention significant nocturnal behavior (MacLean 1966).

Rhinoptilus cinctus. The single available specimen of Three-banded Courser has a pineal gland small in size and deep in position (fig. 3). Its distal pineal mass shows active-appearing parenchymal cells but far fewer, relatively, than in the preceding and following species. The field evidence for nocturnality in this species is similar to that for the preceding (Archer and Godman 1937; McLachlan and Liversidge 1957; Mackworth-Praed and Grant 1962-3).

Aethia cristatella. The pineal glands of three Crested Auklets of different ages have been studied (Quay and Renzoni 1967) and have been found to be well-developed and bipartite in structure. Field observations at the colony of origin for these specimens have provided evidence for abundant nocturnal activity by the species (Ray 1904; Dawson 1923; and others).

STRIGIFORMES

It is within this group, the owls, that the earliest and most frequent observations have been made on pineal atrophy among birds. Since different degrees of pineal reduction and behavioral nocturnality are suggested by available information, separate treatment of the examined species is appropriate.

Otus scops. Renzoni (1963, 1964a, 1968) studied the pineal organ in four embryos, two nestlings, and two adults of the Scops Owl. In adults, scarcely a trace of the organ was found; only a small nodule of possible pineal tissue occurred in one of them. This species is said to be mainly nocturnal, although sometimes abroad by day (Witherby 1940).

Tyto alba. Renzoni (1963, 1964a, 1968) looked for the pineal organ in six embryos, five nestlings, and four adults of the Barn Owl. Only atrophic traces were found in the adults, and these were often in the form of small nodules containing amorphous or apparently calcified material. This species is mainly nocturnal in diverse parts of the world, but it is sometimes seen flying before dusk or in daylight, depending on weather conditions and extended activity during the feeding of young (Howell 1932; Witherby 1940; and others).

Glaucidium cuculoides. Serial sections of the brains of two adult female Barred Pygmy Owls show atrophic nodular remnants of the pineal organ (figs. 4, 5). The pineal nodule in one specimen is considerably distal and dorsal in relation to the roof of the diencephalon (fig. 4A). In the other, the pineal remnant is basal in position (figs. 4B, 5A, B). Individual variation is shown not only in the pineal remnant's anatomical location but also

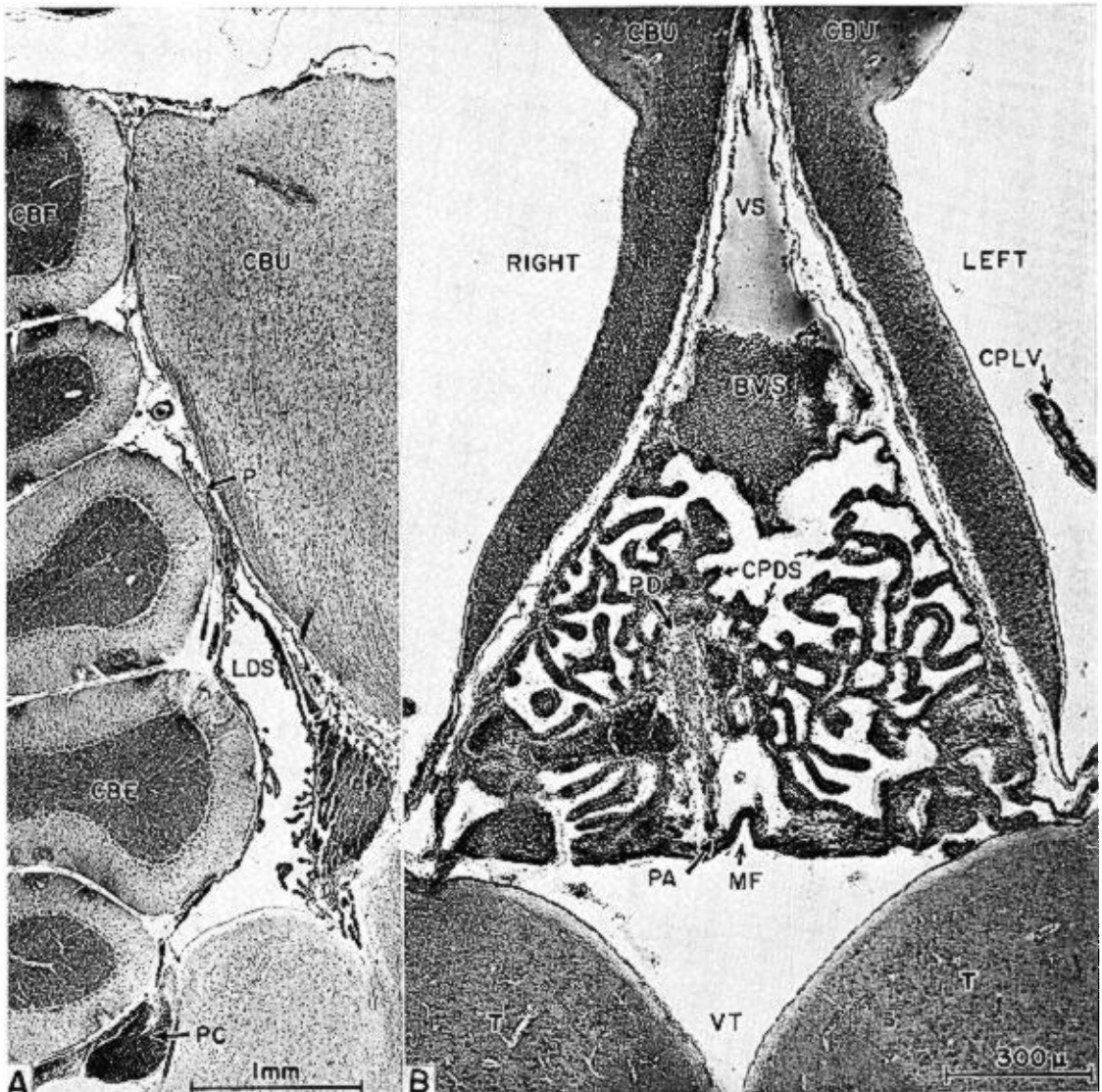


FIGURE 4A. Sagittal section of the pineal region of the brain of an adult female Barred Pygmy Owl (*Glaucidium cuculoides*) (near Bangkok, Thailand; 22 November). A distal pineal remnant (P) is seen between the cerebellum (CBE) and cerebrum (CBU) and distal to the posterior commissure (PC) and the lumen of the dorsal sac (LDS). Modified Bodian protargol method.

B. Transverse section of the basal pineal region of the brain of an adult female Barred Pygmy Owl (data as in fig. 4A, but specimen different). The pineal remnant's basal attachment (PA) is seen on the right side of a median furrow (MF) in the roof of the third ventricle (VT). The dorsal and distal extent of the pineal remnant (PD) is embedded on the posterior surface of the dorsal sac. BVS = blood cells in venous sinus; CBU = cerebral hemispheres; CPDS = choroid plexus of the dorsal sac; CPLV = choroid plexus of the left lateral ventricle; T = thalamus; VS = venous sinus. Modified Bodian protargol method.

in the microscopic organization of the parenchymal cells within the organ and their cytological characteristics. In both specimens some of the pineal cells appear degenerative, and others seem to be normal or active cytologically (fig. 5B). Cytochemical or *in vitro* metabolic studies on the pineal remnants are needed, however, in order to substantiate this last inference. This species is reported to show considerable diurnal activity (Caldwell and

Caldwell 1931; Deignan 1945), but the relative distribution or intensity of its activity according to day-vs.-night is not known.

Athene noctua. Pineal remnants in adults of this species, studied by Renzoni (1963, 1964a, 1968), also consist of small nodules, differing in location in different individuals. Although large neuronoid cells are reported to occur within such nodules in this species, it is not clear to what extent normal-appearing pineal

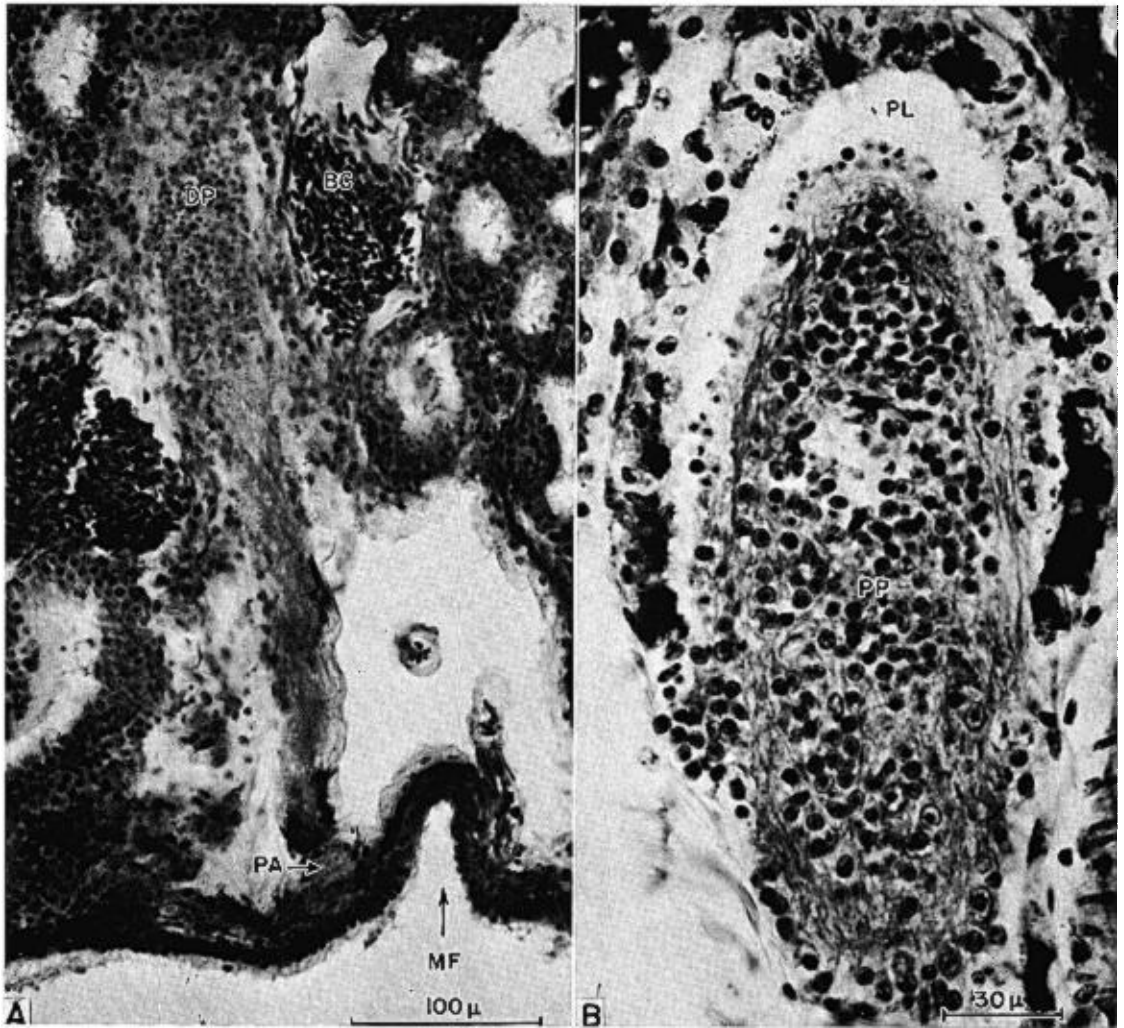


FIGURE 5A. Pineal remnant of *Glaucidium cuculoides* enlarged from figure 4B to show the relations of the distal pineal parenchyma (DP) and basal attachment (PA) to the dorsal sac's choroid plexus (BC = blood cells within plexus vessels) and the median furrow (MF) of the roof of the third ventricle. Modified Bodian protargol method.

B. Section through the distal enlargement of the same pineal specimen shown in figures 4B and 5A. The pineal lumen (PL) is bounded dorsally and laterally by granulated ependymal cells and surmounts a mass of pineal parenchymal cells (PP) of variable consistency.

parenchymal cells survive within these structures.

Speotyto cunicularia. Of the several Burrowing Owl brains studied in serial sections, only one is completely satisfactory for analysis of the pineal region. In this specimen several nodules of degenerating pineal cells occur in the same general regions as those in *Glaucidium cuculoides*. The nodules range in diameter from about 50–100 μ and contain dense groups of degenerating parenchymal and glial cells and masses of flocculent material. No cytologically normal parenchymal cells are seen. Although Burrowing Owls sometimes hunt during the day, they are primarily crepuscular and

nocturnal (Bendire 1892; Howell 1932; Bent 1938).

Strix aluco. Renzoni (1968) has studied the pineal region in two embryos, three nestlings, and two adults of the Tawny Owl. The extremely small size of the developing pineal found by Krabbe (1952) in this species was confirmed by Renzoni. In one of the adults there was no trace of the pineal organ, and in the other only a thin cord of epithelioid cells. This is one of the most thoroughly nocturnal species (Witherby 1940; Hansen 1952).

Asio otus. Data concerning both the pineal organ and nocturnal habits are nearly identical in the Long-eared Owl to those noted for the

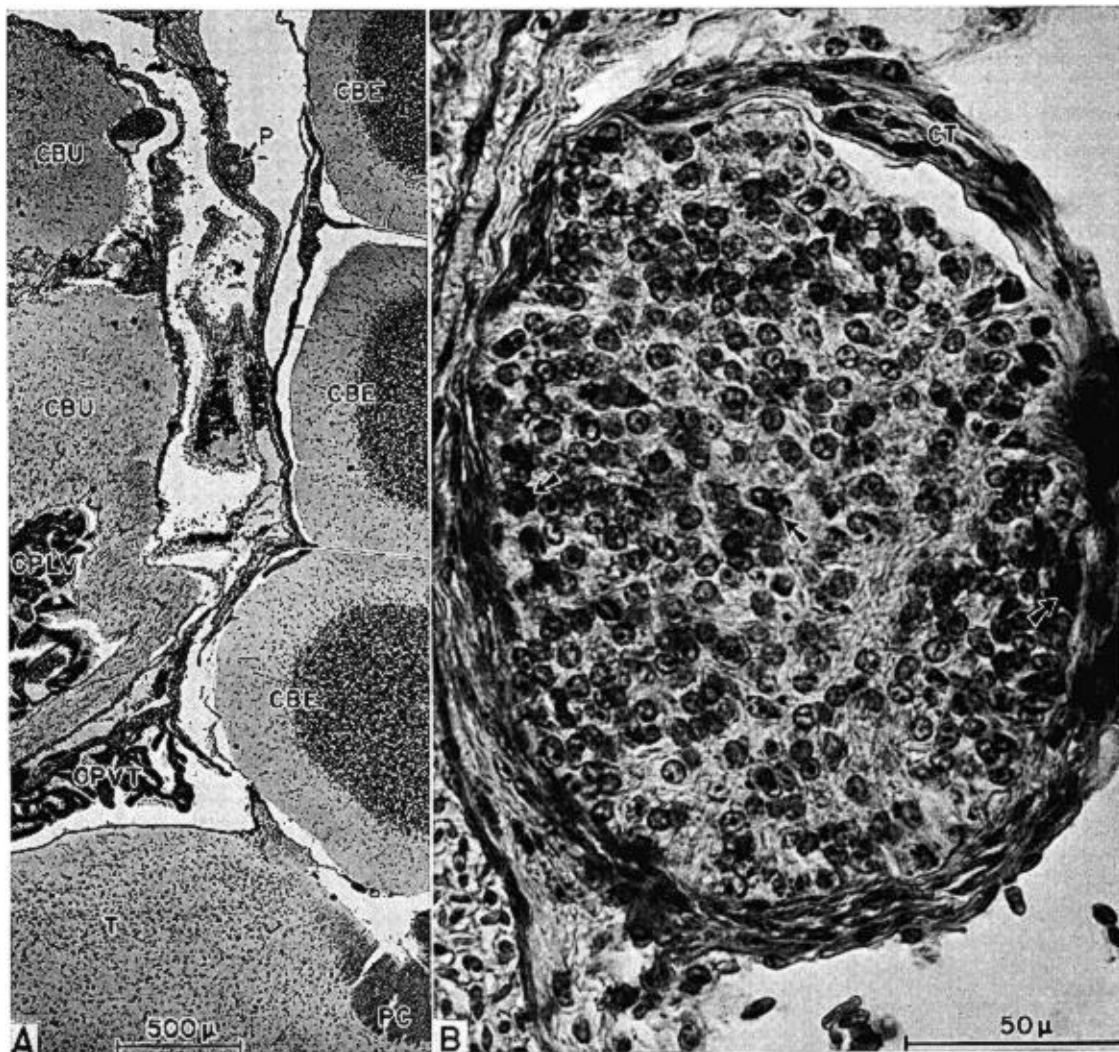


FIGURE 6A. Sagittal section of the pineal region of the brain of an adult female Short-eared Owl (*Asio flammeus*) (Hong Kong; 29 November). The pineal remnant (P) lies between the cerebrum (CBU) and the cerebellum (CBE). CPLV = choroid plexus of the lateral ventricle; CPVT = choroid plexus of the third ventricle; PC = posterior commissure; T = thalamus. Chrome alum hematoxylin and phloxine.

B. Enlargement of another section through the same pineal remnant shown in figure 6A. A thick connective tissue capsule (CT) surrounds the ball of pineal parenchymal cells, many of which contain cytoplasmic granules stained with chrome alum hematoxylin (arrows). Chrome alum hematoxylin and phloxine.

preceding species. Among the three adults examined microscopically by Renzoni (1963, 1964a, 1968), two had no trace of pineal tissue, and the third had a remnant in the form of a cord of epithelioid cells. Krabbe (1952) and Renzoni (op. cit.) found the pineal organ to be exceedingly small in developmental stages. Exclusively nocturnal activity for the species has been cited frequently (Grinnell and Storer 1924; Forbush 1927; Bent 1938; Witherby 1940).

Asio flammeus. Serial sections of an adult Short-eared Owl's brain reveals a relatively large nodule of normal and active-appearing

pineal parenchymal cells (fig. 6A, B). These are organized in several layers around a small central lumen and include some with cytoplasmic granules staining heavily with chrome alum hematoxylin. This pineal "organ," measuring about 0.15 mm in width (antero-posterior) and 0.20 mm in length (dorso-ventral), with its normal cytology, represents the largest and most normal of the pineal structures reported here in the Strigiformes. The present specimen, however, does not approach the 6-mm length claimed by Studnička (1905) for the pineal gland in a specimen supposedly of this species.

Behaviorally, Short-eared Owls are not so strictly nocturnal as most other species of owls. Beyond this generalization there is disagreement, probably due in part to effects of season, climate, and weather on the birds' timing of hunting activity (Forbush 1927; Caldwell and Caldwell 1931; Howell 1932; Hendrickson and Swan 1938; Bent 1938; Witherby 1940; Irving 1955; Short and Drew 1962). Even the metabolic evidence for this species presents inconsistency. Irving (1955) found that captive Short-eared Owls in Alaska were still at night and awake by day, and that their temperatures ranged about as would be expected among birds which rest at night in lower latitudes. He found that, although most of them were distinctly cooler at night, they did not appear to be drowsy at the depressed nocturnal temperatures. On the other hand, Graber (1962) found in Short-eared Owls, as well as in two other owl species, a peak in oxygen consumption near the middle of the night period and depressions during the daytime.

CAPRIMULGIFORMES

The pineal organ is well developed in adults of the two species of nightjars (family Caprimulgidae) which have been examined (Quay and Renzoni 1967; Renzoni 1968). The personally better known of these, the Poor-will (*Phalaenoptilus nuttallii*), is peculiar in pineal structure (Quay and Renzoni 1967) and in its daily rhythmicity. Onset and cessation of Poor-will activity at dusk and dawn coincide with a light intensity usually less than one foot candle (Brauner 1952). A marked fall in body temperature during the daytime sleeping period occurs even in summer (Miller 1950). Further study of the daily temperature curve reveals two high points (near 06:00 and 18:00) and two low points (near 02:00 and noon), with the lowest near noon (Brauner 1952). This is a pronounced departure from what would be observed in either diurnal or nocturnal birds under most conditions.

APODIFORMES

Consideration of this group is prompted by popular attributing of nocturnal activity to the European Swift, *Apus apus*. Renzoni (1968) has shown the pineal to be well-developed in this species. Recent behavioral studies show it to be unquestionably diurnal (von Haartman 1949; Lack and Lack 1952).

DISCUSSION AND CONCLUSIONS

Three tentative general conclusions can be drawn from this survey of avian pineal organs

with respect to nocturnality: (1) The only major groups (Procellariiformes, Strigiformes) in which pineal atrophy is presently known to occur are also the groups that are believed to have been primitively primarily nocturnal, on the basis of various adaptive features, and to have today probably the most intensive utilization of this temporal category of niche. (2) Within each of these two groups, species with the largest pineals and those with the most atrophic appear, respectively, to be more diurnal and more nocturnal in habits. Thus, among the examined Procellariiformes, the Laysan Albatross is the most diurnal and has the largest pineal, and the petrels are the most nocturnal and have the smallest pineal organs. Among the examined Strigiformes, the Short-eared Owl (*Asio flammeus*) is behaviorally probably the most often diurnal and has the largest pineal remnant, and the Tawny and Long-eared Owls (*Strix aluco* and *Asio otus*) are the most strictly nocturnal species and have the least evidence of any pineal tissue. (3) Nocturnal behavioral activity in birds of other and very diverse groups is not associated with any apparent reduction or peculiarity in the pineal organ.

Another conclusion, perhaps a corollary of the extreme pineal reduction in owls, concerns variability of the organ. While in no avian species or population having pineals of moderate to large size is there much variation in pineal size or morphology, within the owls as a group, and more especially within each of their examined species, marked individual variation occurs in the adult position(s) and size of the pineal remnants. This may serve to forewarn investigators of pineal structures in owls and other groups and species in which the organ is reduced or atrophic. Worthwhile and accurate appraisals of pineal status in such birds are possible only with complete series of serial sections through the entire pineal region of the brain, with meninges intact and in place. On the other hand, personal studies of large numbers of pineal glands in many common species show dependability and consistency in the location and size of the organ in species in which it is moderately to well developed.

Contrasting with the large number of random observations on reputedly nocturnal birds is the paucity of objective, systematic, and quantitative data concerning nocturnal behavior and its basis in any avian species. Comparative studies of daily temperature (Baldwin and Kendeigh 1932) and activity cycles (Aschoff 1964, 1967) in birds should be extended to include more species that are nocturnal or that

are not strictly diurnal. This problem is aggravated by the apparent adaptive and seasonal differences in such behavior as related to migration, breeding, nesting, feeding young, and the avoidance of predators. Moreover, conflicts inherent in the available data on nocturnality in such species as the Short-eared Owl present additional serious problems of interpretation. Undoubtedly the physiological and behavioral mechanisms for special timing of events in an avian species' daily cycle are not only very poorly known but may hold some surprises for us. Our survey suggests that although pineal reduction, where it occurs in certain birds, has no obligatory relationship with nocturnality, there may be some, perhaps indirect, adaptive relationship with such behavior. Another and perhaps more direct posing of this situation is that diurnality in birds is associated with pineal organs of moderate to large size, and species with extensive nocturnal, and perhaps facultative, departures may have small or atrophic pineal organs. An analogous correlation is unlikely in mammals, since many of them are both nocturnal and have relatively large and metabolically active pineal glands (Quay 1965, 1970a).

SUMMARY

A survey was made of the size and state of the pineal organ in adult birds representing 23 orders, 58 families, and 121 species with particular reference to possible association with nocturnal behavioral activity. Pineal reduction or atrophy was found to occur only within two groups, Procellariiformes and Strigiformes, and within these an inverse relationship between pineal size and nocturnality was suggested. Although pineal atrophy occurred only in these primitively and most conspicuously nocturnal groups, it was not found in nocturnal species representing other and diverse genera from *Apteryx* to *Burhinus*. The relation of pineal atrophy in birds with nocturnality is thus not obligatory and is likely to be indirect, although possibly of adaptive significance.

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