THE SCLEROTIC RING IN NORTH AMERICAN BIRDS

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Plate 9

IT is well known to students of ornithology that a number of birds, particularly such larger forms as eagles, hawks, vultures and owls, have in the sclerotic coat of the eye a supporting ring of bony plates. Less well known is the fact that such a ring is developed to a greater or less degree in the eyes of all species of birds. Even in hummingbirds sclerotic rings are found, made up of minute osseous plates of almost the thinness of tissue paper. Comparatively little attention has been devoted to these rings, although according to Lemmrich (1931), who gives a history and rather complete bibliography of the subject, knowledge of their occurrence in birds of prey dates back to the thirteenth century, and a clear description of them was given by Volcher Coiter in 1645. Students of the osteology of birds, however, have as a rule merely referred to the sclerotic ring in passing, sometimes taking casual notice of the number of plates but giving no consideration to details of shape or arrangement.

Slonaker (1918, 1921) has given a careful description of the structure and embryonic development of the scleral plates in the eye of the English Sparrow. Heilmann (1927) has mentioned and figured the scleral ring in certain recent and fossil birds and reptiles. It remained for Lemmrich (loc. cit.) to point out, after examination of representatives of a considerable number of orders and families of birds, that a great deal of variation in the character of the sclerotic ring occurs in different groups, but that a degree of constancy usually prevails within given families or orders.

The present study was largely completed before Lemmrich's investigations came to our attention. The findings here reported, however, are in the nature of an extension rather than a duplication of that author's work, inasmuch as he dealt largely with European birds, and in cases where American species were considered his material was rather limited. In the present investigation 1404 pairs of sclerotic rings have been examined in considerable detail, including those of 235 species involving representatives of all of the orders of North American birds except one (no specimens of trogons having come to hand). In general we have several species represented in each order and in a few cases (English Sparrow, Mallard and Glaucous-winged Gull) enough individuals of one species have been available to permit a statistical study.

ACKNOWLEDGMENTS

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have been sent in by sixty individuals in different parts of the country. The larger number have been supplied by Mrs. Martha R. Flahaut, assistant in ornithology in the Washington State Museum, Mr. Adam Balmer of Westport, Washington, Mr. D. E. Brown of Bothell, Washington, Mr. Samuel J. Rathbun of Seattle, Dr. Ian McTaggert Cowan of Victoria, British Columbia, Mr. Kenneth Racey of Vancouver, British Columbia, Mr. Webster H. Ransom of Spokane, Dr. G. M. Sutton and Mr. A. L. Lindsey of Cornell University, Mr. A. R. Phillips of Flagstaff, Arizona, and Mr. Egmond Rett of Santa Barbara.

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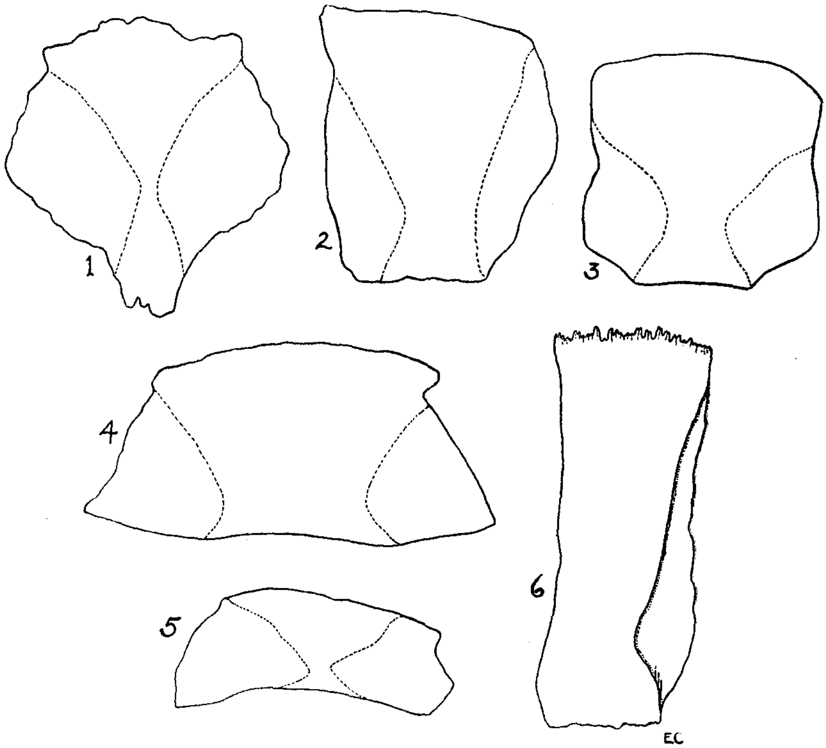
Description of the Sclerotic Ring

The sclerotic ring of the avian eye is composed of a number of individual plates, placed side by side and overlapped to form a bony ring which surrounds the pupil of the eye and extends inward to a distance that is exceedingly variable in different orders of birds. The ring represents an ossification of a portion of the sclerotic coat and doubtless serves primarily for the protection of the eye-ball and for its support during contraction of the ciliary muscles (Slonaker, 1918, 1920). When removed from the eye, the ring has more or less the shape of a truncated cone, sometimes symmetrical, but in most cases having the aperture more or less eccentric, usually toward the nasal margin of the eye. The steepness of the ring is extremely variable. In some groups, as the herons, it is nearly flat; in others, as in the owls, it is so steep as to approximate Lemmrich's (1931) characterization of "tubular" (see Plate 9). There is, of course, much variation in the size of the rings. The largest ring we have examined, that of the Great Horned Owl, measures 36 mm. at its greatest diameter; the next in size, that of the Golden Eagle, 33 mm. The smallest, that of the Rufous Hummingbird, measures 4.5 mm.; next in order of size come the Green-backed Goldfinch, 4.6 mm., and the Coast Bush-tit, 5.5 mm.

The shape of the individual plates varies greatly (Text-fig. A). They are joined to one another in such a way that there is more or less overlapping of the border of one plate upon the next. This overlap is commonly more pronounced at the inner border of the ring, so that the plates are widest at the end proximal to the pupil. Occasionally the maximum overlap occurs near the middle of the plates, as in the auklet and the puffin. In the kingfishers and the woodpeckers overlapping occurs at the inner ends of the plates only. In owls, vultures and falcons the plates are joined with only a very small lap. Audubon's Caracara shows the least amount of overlapping of any species examined. The majority of orders show a large degree of overlapping.

The individual plates vary considerably in thickness. Slonaker (1918) says of the scleral plates of the English Sparrow: "Their thickness is greatest

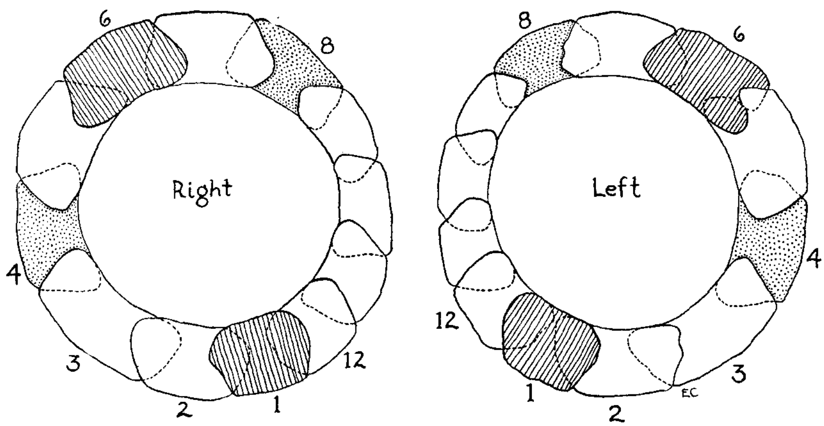


TEXT-FIG. A.—Various shapes of scleral plates: (1) Rhinoceros Auklet; (2) Golden Eagle; (3) Western Belted Kingfisher; (4) Northwest Coast Heron; (5) Domestic Pigeon; (6) Dusky Horned Owl. All drawings made with camera lucida. × 3.5.

in the middle portion and tapers off to a thin edge on their lateral sides. . . The combined thickness of the overlapping portion about equals the thickest portion of the plate. A ring of bone of practically uniform thickness is thus formed, completely surrounding the eye." This is true of all the rings we have examined. The thickest plate we have seen is that of the Great Horned Owl which measures 1.8 mm. in the heaviest part, while that of the Golden Eagle measures 1 mm. At the other extreme are the hummingbirds and the smaller passerine birds such as warblers, kinglets and bush-tits, with plates exceedingly thin and fragile. The density of the plates increases with the age of the birds, but even in adults of the types mentioned the plates are extremely thin and flexible. On the other hand, the diving birds show a rather heavy bony structure even in immature specimens.

RING PATTERN

Any number of plates may be arranged to form a circle, with each plate overlapping its neighbor in a clockwise or counter-clockwise direction, but this simplest pattern of overlapping we have not found in any ring examined. Instead, the regular overlapping is interrupted by what we term an *overplate*. This plate is similar in shape to its neighbors, but overlaps them on both sides (Text-fig. B). Using the clock face to show approximate



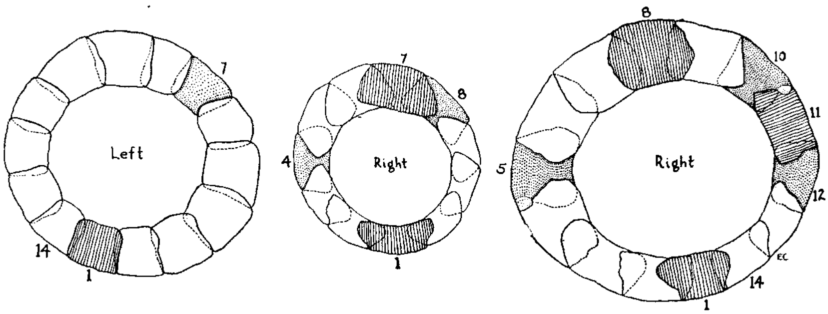
TEXT-FIG. B.—Scleral rings of the Rufous Hummingbird. Camera lucida, × 12.

position of certain plates in the ring, we find that an overplate occurs regularly in all rings in the position five to six o'clock in the right, and six to seven o'clock in the left eye. We call this overplate no. 1 and in counting always begin at this point.

Each *overplate* requires a corresponding *underplate* (Text-fig. C), as may easily be demonstrated by arranging playing cards in a circle. One overplate and one underplate occur regularly in the eye-rings of hawks and owls and usually in wrens. Lemmrich finds this true of the European Skylark also. In most species of birds there are two overplates and two underplates. The overplates lie in the position of five to six o'clock and eleven to twelve o'clock in the right, and six to seven and twelve to one in the left ring; the underplates occur at eight to nine, and one to two o'clock in the right ring.

Three overplates and underplates occur regularly in loons, and in six per cent of the ducks (see Table 1 for other examples). These three overplates occur at five to six, eleven to twelve, and two to three o'clock in the right ring, and in the reversed positions in the left. The three underplates occur at eight to nine, one to two and three to four o'clock in the right ring. In a very few cases (five single rings out of more than 1400 pairs) four overplates and underplates have been found. This condition has occurred in one eye only of a Lesser Loon, a Brown Pelican, a Bufflehead, and two Domestic Geese.

In recording the ring-pattern we have used Lemmrich's method in order to facilitate comparison with his findings. Beginning with the overplate which occurs in a ventral position, we count clockwise in the right, and counter-clockwise in the left ring (see Text-fig. B).



TEXT-FIG. C.—Scleral rings drawn to illustrate one, two and three overplates and underplates respectively (overplates ruled and underplates stippled). Left to right: Western Pigeon Hawk, Western White-winged Dove, Pacific Loon. Camera lucida, × 2.3.

INTERLOCKING

Occasionally interlocking plates are found, in which the border of one partially overlaps and partially underlaps its neighbor (Text-figs. B and C). In such cases, the overlap at the inner or pupillary border has been arbitrarily considered to establish the status of the plate as an overplate or an underplate. As Lemmrich points out, interlocking tends to occur in a definite location in the ring. Thus we have found that in loons and herons, interlocking occurs most frequently between plates 4 and 5. In hawks the modal position for interlocking is between plates 6 and 7, for turkeys 8 and 9, chickens 9 and 10, gulls 7 and 8, horned owls 1 and 2, and flickers 5 and 6. Interlocking may, however, occur between any two plates, though it is found most frequently between an overplate or underplate and its neighbor in the ring. It may also occur several times in one eye.

Of the birds included in this study 41 per cent show interlocking plates in one or both eyes. In 22.4 per cent both eyes are involved, and in 7.5 per cent the interlocking is symmetrical in right and left eyes. Some orders show little or no interlocking. A single case has been discovered among the Columbiformes, and the condition has been found in only 12 per cent of Micropodiformes. Anseriformes are low with 21.1 per cent, and Passeriformes high with 56.8 per cent; the woodpeckers are highest with 81.5 per cent showing interlocking between two or more plates.

RING-PATTERN VARIATION IN RIGHT AND LEFT EYES

A question which presents itself for discussion is that of the constancy in number and arrangement of the plates in the sclerotic ring, first as regards the two eyes of the same individual, then as regards species and larger groups. In a large majority of cases the two eyes of individual birds are symmetrical as to number and arrangement of plates. Lemmrich reported 43 variants out of 148 pairs of rings, or 29 per cent variation between right and left eyes, considering number of plates alone. Of 1404 birds considered in the present study, only 326, or 16 per cent, showed variation in number of plates in right and left eyes. If arrangement of the plates be considered instead of the number, there is slightly more variation: 258 or 18.3 per cent show variation in pattern in the two eyes. If both the number of plates and the ring-pattern be considered, 334 individuals, or 23.7 per cent of the whole group, exhibit differences between the right and left eyes.

There is considerable difference in the amount of variation between right and left eyes in different groups. The orders Gruiformes, Columbiformes, and Micropodiformes show remarkable constancy in this respect, although our number of specimens in these groups is too small for statistical analysis. Anseriformes are fairly constant (see Table 2). while Piciformes and Strigiformes show the greatest amount of variation, 42.1 per cent and 38.7 per cent, respectively.

In Table 2a are shown the data for variation between right and left eyes in four species, selected by reason of the large numbers of individuals available.

DISCUSSION

The number of plates occurring in the sclerotic ring in birds considered as a class has been variously stated as from twelve to twenty (Coues, 1884), ten to seventeen (Heilmann, 1927), eleven to seventeen (Lemmrich, 1931). In the present study the range has been found to be from eleven to eighteen. The former number is characteristic of one entire order (Columbiformes), while the latter number was found in two individual birds (one Common Tern, one Baldpate) out of the 1404 examined. The modal numbers of different orders ranged from eleven to fifteen, with fourteen or fifteen the most common. No relation was found between the number of plates and the size of the ring. For example, the loons, herons, ravens, and bush-tits all characteristically have fourteen plates.

In so far as there is any overlapping of species considered by Lemmrich and by us, there is a fair measure of agreement in the findings. Seventeen of the 235 species (disregarding subspecific differences) considered in the present study have been reported on by Lemmrich; in the case of eleven of these we are in complete agreement. In the case of *Rissa tridactyla* we agree with Lemmrich as to number of plates in the ring, but he gives no pattern. As regards *Spatula clypeata* we disagree with Lemmrich as to the number of plates, and in *Mergus merganser* we disagree as to pattern. In *Aquila chrysaëtos, Nyctea nyctea,* and *Asio flammea* we disagree on both number and pattern.

Besides the foregoing cases of identical species, we find twenty-one additional genera on which Lemmrich and we have worked in common. Here we find about the same order of agreement, sixteen cases in which we are in complete agreement, and five in which we disagree. In most of these cases of disagreement, one specimen only (in some cases one ring only) was available either to Lemmrich or to us.

In the following pages, wherever it becomes necessary to take issue with conclusions set forth by Lemmrich, it should be understood that no criticism is intended of the carefulness of that author's work; but only that a larger amount of material leads to a different conclusion. Lemmrich draws the generalizations that (1) primitive groups of birds have a smaller number of plates in the ring; (2) that domestication (as in the Domestic Fowl) causes an increase in variability; (3) that higher groups have greater constancy in the number of plates. The first of these conclusions finds no support from our data (see Table 1). Thus the lowest order, Gaviiformes, has fourteen plates, the same number as Passeriformes, while the smallest modal number of plates is found in Columbiformes, a group rather well up in the scale.

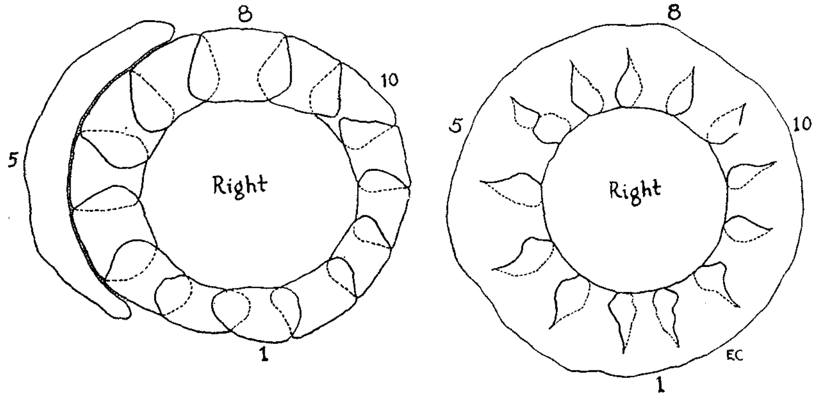
With regard to the conclusion that domestication increases variability, our data (Table 3) lend little support to Lemmrich's view. In comparing domestic races with their nearest relatives in the wild, we find in the case of Anatidae and Phasianidae that the wild forms show a greater variation in number of plates, while the domesticated forms show the higher degree of variation in *pattern.* It is to be noted also (Table 2a) in this connection that the white Leghorn Fowl shows a high percentage of variation between right and left eyes. The Domestic Turkey (Table 3) is remarkably constant in both number and pattern. It might be argued that the turkey has been so recently domesticated that it is still very close to its wild progenitor, or progenitors, and that the Domestic Turkey probably represents a blend of two or more distinct species. The Domestic Pigeon, however, shows very nearly the same degree of constancy, although it has been bred under domestication possibly as long as the Domestic Fowl. In Table 4 is shown the variation in number and pattern in sixteen species selected at random from ten different orders of birds, and in Table 4a is shown the variation among seven species of a single family. The amount of variation among wild birds shown in these tables is greater than that of any domesticated races of birds we have investigated.

These tables also cast doubt upon Lemmrich's suggestion that higher orders of birds exhibit greater constancy in the number of plates in the ring. This statement would be true if one considered only the modal number of plates in different families within an order, which is possibly what Lemmrich had in mind. In Passeriformes, for example (see Table 1), we find every family exhibiting a modal number of fourteen. However, when we consider *individual* variation within a species, this appears to be as great in higher as in lower forms.

FUNCTION OF THE RING

The function of the sclerotic ring constitutes something of a problem. It might be suggested that inasmuch as a similar ring is found in the eyes of many reptiles, the structure is merely one that has been carried over from the latter group. This suggestion, however, only pushes the explanation one step farther away. The universal presence and very considerable development of the sclerotic ring in birds suggests, moreover, that it is not simply a vestigial structure carried over from a more primitive group; to attain the degree of development it does, it must have some function in the bird today. To a certain extent the sclerotic ring may be regarded as a protection for the eyeball, although it would appear that, in general, injuries to the eye would occur in the pupillary area rather than through the sclerotic coat. Slonaker (1918, 1920) has suggested that the primary function of the ring is in connection with the mechanism of accommodation. It is his view that contraction of the ciliary muscles effects an increase in intraocular pressure, thus pushing the lens farther out to accommodate for near vision. He considers that some bending of the plates is involved in this process. It is not impossible that a certain amount of bending occurs in the scleral plates of the English Sparrow, as studied by Slonaker, and in some other cases where the ring is wide and flexible. Too much emphasis should not be placed, however, on the bending of the plates, or their possible sliding upon one another as a factor in accommodation. Interlocking of plates (Table 2) which has been mentioned above, would interfere with any such motion; and in certain cases there is a type of structure which would tend to prevent any motion. For example, in the eyes of the woodpeckers (Text-fig. D) the plates are firmly fused at the outer margin; and in some of the jays (Text-fig. D) there is an accessory bony plate developed along the temporal margin of the ring which would hold the plates rigid for at least a third of the circumference of the eye. In diving birds (vide infra) the ring is obviously too heavy and rigid to be warped by the pull of the ciliary muscles. The contraction of these muscles alone would appear adequate to effect the small increase in intra-ocular pressure necessary to move the lens, without requiring any bending of the plates or their sliding upon one another. It should be pointed out that the attachment of the muscles of accommodation is to the fascia and the scleral cartilage within the ring, not to the bony ring itself.

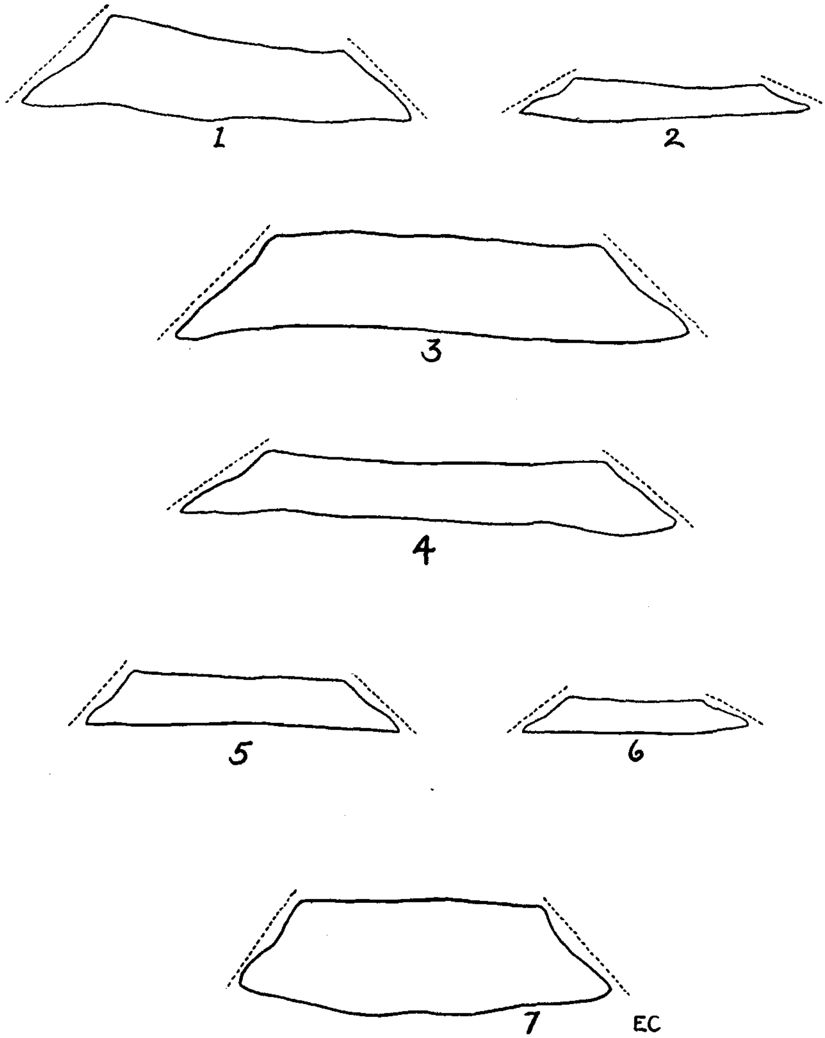
With regard to the reason for the persistence of individual plates in the ring, the best view seems to be that this is essential to growth in size of the ring from early to adult life. Lemmrich (1931) has pointed out that growth



TEXT-FIG. D.—Left: scleral ring of California Jay, showing accessory bony plate at temporal margin. Right: scleral ring of Northwestern Flicker, showing fusion of plates along outer margin. Camera lucida, × 3.5.

of the rings occurs by increase in size of the individual plates in exactly the same way that growth of the skull occurs through enlargement of the individual bones at their margins.

Concerning the matter of protection and support of the eye, it may be pointed out that diving birds have the sclerotic ring developed to an extraordinary degree. The ring in murres, loons and puffins is more heavily bony in proportion to size than in any other forms studied. It is to be noted also that the slope of the ring is steeper in diving birds than in their immediate relatives that have not this habit. Thus the ring of the coot is steeper than that of the rail, the ring of a scoter steeper than that of a mallard, and the ring of the dipper notably steeper than that of the wren (see Text-fig. E). Rapid fliers, such as swifts and swallows, also have steep-sided rings, although it cannot be observed that the ring is particularly heavy. It would appear that the steeper-sided ring gives greater support to the outer part of the eyeball, which would be advantageous alike to diving birds, whose eyes are subjected to pressure from the water, and to swift-flying birds whose eyes are subjected to the pressure of rushing air.



TEXT-FIG. E.—Outlines of scleral rings (nasal margin), showing variations in steepness: (1) American Coot; (2) Sora; (3) White-winged Scoter; (4) Common Mallard; (5) Dipper; (6) Tule Wren; (7) Black Swift. Camera lucida, × 5.

ECCENTRICITY OF THE RING AND BINOCULAR VISION

Monocular vision is generally regarded as characteristic of birds, although Chievits (1891, 1899), Slonaker (1897, 1918), and Wood (1917) have pointed out that there is often a well-developed temporal fovea which permits more or less acute vision of objects directly in front of the bird. The present writers have given no attention to the problem of binocular vision, except casually to consider its possible relation to eccentricity of the aperture of the sclerotic ring. When the aperture is off center, it is usually displaced toward the nasal margin (Text-fig. D). While a majority of birds exhibit a certain degree of eccentricity of the aperture, the condition is most marked in pelicans, turkeys, herons, coots, pigeons and doves, owls, swifts, and jays. Of these, at least, the pelicans, herons, and owls may be presumed, from the position of the eyes, habitually to bring them both to bear on the same object. Eccentricity of the aperture may thus be regarded, at least in certain cases, as an adaptation to facilitate convergence of the eyes in binocular vision.

TAXONOMIC VALUE OF THE SCLEROTIC RING

The present study was motivated primarily by the thought that a careful comparative study of the sclerotic ring in different orders of birds might yield data of definite taxonomic value. The results, however, considered from that standpoint, have frankly been somewhat disappointing. There is usually close agreement in the number of plates in different genera within a family, but different families in one order may have a different modal number.

Rings as distinctive as those of hawks, owls or woodpeckers may be recognized by anyone; and a person thoroughly familiar with large numbers of sclerotic rings can generally group them on sight, even in many cases assigning an unlabelled ring to its proper genus. But the differences upon which such recognition is based, including such variables as size, shape, curvature, slope, color, texture, regularity or eccentricity, degree of overlapping, are difficult to describe and impossible to tabulate. The attempt to organize the data concerning such relatively simple matters as number and arrangement of the plates (Table 1) leads to a rather complicated tabulation. It does not appear practicable at present to attempt to systematize the more subtle differences.

In certain specific cases, the structure of the sclerotic ring may be of assistance in determining relationships between species, or larger groups. One or two illustrations may be cited. In the first jays examined it was noted as a matter of some interest that an additional bony plate is attached to the temporal margin of the ring, extending about one-third of its circumference (Text-fig. D). This was not found in the Crow. Further investigation showed that the condition does not exist in any of the members of the subfamily Corvinae that we have examined (*Corvus*, *Cyanocephalus*, *Nucifraga*) but is uniformly present in the genera *Cyanocitta* and *Aphelocoma* of the subfamily Garrulinae. Of fourteen magpies examined, four showed a rudiment of such a plate in one or both eyes. The genus *Perisoreus* shows no trace of such a structure. One may conclude that, so far as eye-rings may be used as a guide, the subfamilies Garrulinae and Corvinae are natural groups, with *Cyanocitta* and *Aphelocoma* more closely related to each other than to *Pica*. The status of *Perisoreus* is left undetermined on this basis.

In Micropodiformes, it is to be noted that the number of plates in the scleral ring, fifteen in swifts and twelve in hummingbirds, affords additional justification for the division of this group into the two suborders Micropodii and Trochili.

It is strongly to be urged that persons collecting birds give attention to the sclerotic ring and carefully preserve it, either with the skeleton, or with the skin if a skeleton is not made.

TABLE 1

A Systematic Survey of the Structure of the Sclerotic Ring

Order, Suborder and Family	No. of species examined	No. of pairs of eye-rings examined	Modal no. of plates	Range of no. of plates	Segregation according to number of over- and underplates[1]				Typical position of over- and under-plates (ring pattern)	
					1	2	3	4	O	U
GAVIIFORMES										
Gaviidae	3	10	14	14–15			9.5	.5	1–8–11	5–10–12
COLYMBIFORMES										
Colymbidae	3	8	15	11–15	3.5	4.5			Not dete	rmined
PROCELLARIIFORMES										
Procellariidae	3	7	15	14–15		7			Not dete	rmined
Hydrobatidae	2	2	13			2			Not dete	rmined
PELECANIFORMES										
Pelecani										
Pelecanidae	1	1	14				0.5	0.5	Not dete	rmined
Phalacrocoracidae	3	8	13	12–14		8			Not dete	rmined
Fregatae										
Fregatidae	1	1	15		1				1	6
CICONIIFORMES										
Ardeidae	2	8	14	14–15		8			1–8	5–10
ANSERIFORMES										
Anatidae	26	331	15	13–18		310.5	19	1.5	1–9	5–11
FALCONIFORMES										
Cathartae										
Cathartidae	2	3	15	13–15	1.5	1.5			Not dete	rmined
Falcones										
Accipitridae	13	48	15	14–17	43	5			1	6
Falconidae	5	21	14	14–16	17.5	3.5			1	7

[1] In this column are listed the number of pairs of rings having one overplate, two overplates, etc.; e. g., in the Gaviidae, of ten pairs examined all had three over- and three underplates, except one, in which one eye exhibited three and the other eye four.

TABLE 1 (cont.)

A Systematic Survey of the Structure of the Sclerotic Ring

Order, Suborder and Family	No. of species examined	No. of pairs of eye-rings examined	Modal no. of plates	Range of no. of plates	Segregation according to number of over- and underplates[1]				Typical position of over- and underplates (ring pattern)	
					1	2	3	4	O	U
GALLIFORMES										
Galli										
Tetraonidae	6	10	14			10			1–9	6–10
Perdicidae	2	19	14	13–15		17	2		1–9	6–10
Phasianidae	2	92	14	13–16	17.5	74	0.5		1–9	6–10[2]
									1–9	7–10[3]
Numididae	1	3	14	13–14		3			1–9	6–10
Meleagrididae	1	34	14			34			1–9	6–10
GRUIFORMES										
Rallidae	3	26	13	12–14		26			1–8	6–9
CHARADRIIFORMES										
Charadrii										
Charadriidae	3	9	15	15–16		9			1–9	5–11
Scolopacidae	5	16	15	12–16		15.5	0.5		1–9	5–11
Recurvirostridae	1	1		15–16		1			Not determined	
Phalaropodidae	2	2	13			2			1–8	5–10
Lari										
Stercorariidae	3	13	15	14–16		12.5	0.5		1–9	6–11
Laridae	8	91	15	13–18		89.5	1.5		1–9	5–11
Alcae										
Alcidae	7	34	13	13–15		32	2		1–8	5–10
COLUMBIFORMES										
Columbidae	4	17	11	11–12		11			1–7	4–8
PSITTACIFORMES										
Psittacidae										
Australian Paroquet	1	18	12			17.5	0.5		1–7	4–9

[2] White Leghorn Chicken.
[3] Ring-necked Pheasant.

TABLE 1 (cont.)

A Systematic Survey of the Structure of the Sclerotic Ring

Order, Suborder and Family	No. of species examined	No. of pairs of eye-rings examined	Modal no. of plates	Range of no. of plates	Segregation according to number of over- and underplates[1]				Typical position of over- and under-plates (ring pattern)	
					1	2	3	4	O	U
CUCULIFORMES										
Cuculidae	2	2	12			2			1–8	5–10
STRIGIFORMES										
Strigidae	7	31	15	14–17	30	1			1	6
CAPRIMULGIFORMES										
Caprimulgidae	2	4	15	15–16		3.5	0.5		1–9	5–11
MICROPODIFORMES										
Micropodii										
Micropodidae	3	22	15	14–16		17			1–9	6–11[4]
									1–8	6–11[5]
Trochili										
Trochilidae	1	3	12			3			1–6	4–8
CORACIIFORMES										
Alcedinidae	1	2	13			2			1–8	5–10
PICIFORMES										
Picidae	8	38	13	13–15		37.5	0.5		1–8	5–10
PASSERIFORMES										
Tyranni										
Tyrannidae	8	16	14	14–16		16			1–8	5–10
Passeres										
Alaudidae	1	11	14	13–15	1.5	9.5			1–8	5–9
Hirundinidae	6	19	14	13–15	1	18			1–8	5–10
Corvidae	9	60	14	13–15		59.5	0.5		1–8	5–10
Paridae	3	13	14	14–15		13			1–8	6–10

[4] Vaux's and White-throated Swift.

[5] Black Swift.

TABLE 1 (cont.)

A Systematic Survey of the Structure of the Sclerotic Ring

Order, Suborder and Family	No. of species examined	No. of pairs of eye-rings examined	Modal no. of plates	Range of no. of plates	Segregation according to number of over- and underplates[1]				Typical position of over- and under-plates (ring pattern	
					1	2	3	4	O	U
PASSERIFORMES										
Passeres (*cont.*)										
Sittidae	1	3	14			3			Not determined	
Certhiidae	1	2	14			2			Not determined	
Cinclidae	1	4	14	13–15		4			Not determined	
Troglodytidae	5	13	14	14–15	11	2			1	7
Mimidae	3	6	14			6			1–8	6–10
Turdidae	7	59	14	13–15		58.5	0.5		1–8	5–10
Sylviidae	2	5	14	14–16		5			1–8	5–10
Motacillidae	1	1	14			1			1–8	6–9
Bombycillidae	1	9	14	14–15		9			1–8	5–10
Ptilogonatidae	1	1	14			1			1–8	5–10
Laniidae	1	12	14	14–16	0.5	11.5			1–8	5–10
Sturnidae	1	1	14			1			1–8	7–10
Vireonidae	3	7	14			7			Not determined	
Compsothlypidae	10	22	14	13–15		22			1–8	5–10
Ploceidae	1	73	14	13–15	1	72			1–8	6–9
Icteridae	4	17	14	13–15		17			1–8	5–10
Thraupidae	1	4	14			4			1–8	6–10
Fringillidae	28	113	14	13–15	2.5	110	0.5	1	1–8	6–10

TABLE 2

Summary of Variation between Right and Left Eyes

Order	No. of pairs of eye-rings examined	Variation in no.	% of variation in no.	Variation in pattern	% of variation in pattern	Variation in no. or pattern or both	% of variation in no. or pattern or both
Gaviiformes	10	1	10	2	20	3	30
Colymbiformes	8	1	12.5	3	37.5	3	37.5
Procellariiformes	9	1	11.1	4	44.4	4	44.4
Pelecaniformes	10	0	0	4	40	4	40
Ciconiiformes	8	1	12.5	3	37.5	3	37.5
Anseriformes	331	44	13.2	54	16.3	71	21.4
Falconiformes	72	45	61.6	18	25	22	30.5
Galliformes	158	23	14.5	35	22.1	45	28.4
Gruiformes	26	4	15.7	3	11.5	4	15.7
Charadriiformes	166	30	18	27	16.3	35	21
Columbiformes	17	1	5.8	0	0	1	5.8
Psittaciformes	18	0	0	4	22.2	4	22.2
Cuculiformes	2	0	0	0	0	0	0
Strigiformes	31	10	32.1	6	19.3	12	38.7
Caprimulgiformes	4	1	25	1	25	1	25
Micropodiformes	25	3	12	1	4	3	16
Coraciiformes	2	0	0	0	0	0	0
Piciformes	38	3	7.9	15	42.1	15	42.1
Passeriformes	470	58	12.3	97	20.6	107	22.7
Total	1404	226	16	258	18.3	334	23.7

TABLE 2a

Variations between Right and Left Eyes in Selected Species

Mallard	111	11	10	9	8	17	15.5
White Leghorn Chicken	54	10	11.4	20	37	24	44.5
Glaucous-winged Gull	60	12	20	13	21.6	14	23.3
English Sparrow	65	16	25.4	18	28.5	21	33.3

TABLE 3

Comparison of Wild with Domestic Species

	No. of pairs of rings examined	No. of patterns occurring	Prevailing pattern	% of variation from prevailing pattern	Modal no. of plates	Range of no. of plates	% of variation from modal no. of plates
Domestic Duck	32	8	1–9 5–11	18.7	15	14–16	4.6
Mallard	111	8	1–9 5–11	10	15	14–17	10
Domestic Goose	19	12	1–9 5–11	47.3	15	14–16	15.7
Wild Goose	7	4	1–9 5–11	35.7	15	12–15	29.5
White Leghorn Chicken	59	7	1–9 6–10	53.3	14	13–16	14.4
Ring-necked Pheasant	25	9	1–9 7–10	30	14	13–15	12
Domestic Turkey	34	2	1–9 6–10	1.4	14	13–14	1.4
Domestic Pigeon	11	1	1–7 4–8	0	11	11–12	4.4
Wild Pigeon	6	1	1–7 4–8	0	11		0

TABLE 4

Constancy of Pattern and Number of Plates

	No. of pairs of rings examined	No. of patterns occurring	Type pattern	No. of rings showing type pattern	% of variation from type pattern	Modal no. of plates in ring	Range of no. of plates in ring	% of variation from modal no.
Lesser Loon	7	4	1, 8, 11, 5, 10, 12	5	28	14	14–15	7.1
Northwest Coast Heron	5	4	1, 8, 5, 10	3.5	30	14	14–15	24
Mallard	111	8	1, 9, 5, 11	99	10.8	15	14–17	10
Cooper's Hawk	9	3	1, 7	6.5	27	15	15–16	13.3
Ring-necked Pheasant	25	9	1, 9, 7, 10	13.5	30	14	13–15	16.6
California Quail	16	3	1, 9, 6, 10	11.5	29	14	13–15	21.8
Wilson's Snipe	5.5	7	1, 8, 5, 10	2	63.6	13	13–16	36.3
Glaucous-winged Gull	60	13	1, 9, 5, 11	48.5	19.2	15	13–17	17.4
California Murre	19	5	1, 8, 5, 10	14	26.3	13	13–14	18.4
Australian Paroquet	18	8	1, 7, 4, 9	8	55.5	12		0
Horned Owl	12	3	1, 6	8	33.3	15	15–16	12.5
Black Swift	12	1	1, 8, 6, 11	12	0	15	14–16	8.3
Flicker	21	8	1, 8, 5, 10	10	52.3	13	13–14	14.2
Steller's Jay	14	3	1, 8, 5, 10	12.5	10.7	14	13–14	3.5
Robin	27	8	1, 8, 5, 10	21	22.2	14	13–16	11.1
English Sparrow	65	9	1, 8, 6, 9	46.5	28.4	14	13–15	20.7

TABLE 4a

Constancy of Pattern and Number in Highest Group

FRINGILLIDAE								
Rusty Song Sparrow	17	6	1, 9, 7, 10	10	41.1	14	13–15	8.8
Fox Sparrow	12	5	1, 8, 6, 10	7.5	37.5	14	13–15	12.5
White-crowned Sparrow	11	3	1, 8, 6, 10	10	9	14	13–15	13.6
Golden-crowned Sparrow	5	2	1, 8, 6, 10	4	20	14	14–15	20
Pine Siskin	5	3	1, 8, 6, 10	3	40	14		0
Junco	10	3	1, 8, 6, 10	6.5	35	14	14–15	5
Towhee	7	4	1, 8, 6, 10	5	28.5	14	13–14	28.5

SUMMARY

1. A universal characteristic of the avian eye is the presence in the sclerotic coat of a number of small osseous plates, more or less overlapping to form a rather firm bony ring.

2. In the present study 1404 pairs of eyes have been examined, including those of 235 species belonging to nineteen orders. The study includes all orders of North American birds except Trogoniformes, of which no specimens have been obtained, and Psittaciformes of which the only representative studied was the Australian Paroquet.

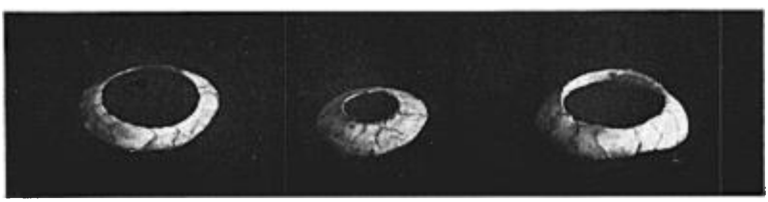
3. The ring pattern, as determined by number and position of overplates and underplates, is generally constant within a family.

4. The number of plates in the ring ranges from a minimum of eleven, which is characteristic of the entire order Columbiformes, to a maximum of eighteen, found in only two individuals (one Common Tern, one Baldpate)

1 2

3 4

5 6



7 8 9

SCLEROTIC RINGS

of all the specimens examined. The modal numbers of different orders ranged from eleven to fifteen, with fourteen or fifteen the most common.

5. No relation has been found between size of the ring and number of plates, nor with systematic position and number of plates.

6. The evidence does not indicate that domestication causes any unusual degree of variation in the number of plates, or in the ring pattern.

7. There is usually a close agreement in the number of plates in different genera within a family, but different families in one order may have different modal numbers.

8. The function of the ring is protection of the eyeball, and support during contraction of the ciliary muscles in the process of accommodation.

9. The ring is heavier and more steep-sided in diving birds than in their relatives which have not this habit. A steep-sided ring is also characteristic of swift-flying birds.

10. From the taxonomic standpoint, the structure of the eye-ring may be of value, considered in conjunction with other skeletal characteristics, in establishing degrees of relationship between neighboring groups.

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EXPLANATION OF PLATE

PLATE 9

Photographs of scleral rings: (1) Golden Eagle; (2) Dusky Horned Owl; (3) Domestic Turkey; (4) Tufted Puffin; (5) California Murre; (6) Saw-whet Owl; (7) Northwest Coast Heron; (8) Northern Pileated Woodpecker; (9) Lesser Loon.

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