SHAPES OF BIRDS' EGGS: EXTANT NORTH AMERICAN FAMILIES

F. W. PRESTON

ABSTRACT.—The shapes of birds' eggs, as distinct from their sizes, can be very closely specified by three parameters, elongation, asymmetry, and bicone, as used in the Handbook of North American birds (Palmer, 1962). The present paper shows that they cannot be specified by less than three because no significant correlation exists between any two of the three. The distribution of any one of the parameters is not normal or Gaussian, and strongly suggests that there must have been now-extinct families with intermediate properties. Existing reptiles considerably extend the range of some parameters beyond those of birds. Negative bicone, however, seems to be essentially an avian monopoly and its function is not clear. The properties of Monotremes' eggs are inadequately known.

FOR the Handbook of North American birds (Palmer, 1962) we made some 40,000 measurements of about 10,000 eggs, four measurements per egg, only one egg per clutch. The measurements were length (L), maximum breadth (B), and radius of curvature at the blunt end (R_B) and at the pointed end (R_P). These measurements all have the dimensions of length, and are therefore measures of size. By combining the figures into dimensionless arrangements we get three quantities which define shape independently of size. These quantities are elongation (E), which is defined as L/B; asymmetry (A), or extent to which one end is larger than the other, defined as $(R_B - R_P)L/B^2$; and bicone (C) defined as $(R_B + R_P)L/B^2 - 1$.

With these three parameters or shape-specifiers we may define the shape of any reasonable bird's egg with a very fair degree of accuracy, and photographing it "up" or "down" (enlarging or reducing the picture) will not change the shape or the values of E, A, or C. Some minor irregularities occur even with what we regard as normal eggs. Thus in the Peyton collection of 66 Murre eggs mentioned in a previous paper (Preston, 1968), 6 eggs had irregular puckers, creases, or ridges at the pointed end which made it impossible to get a good measure of R_P. These were presumably a natural product of the bird's oviduct and there is no reason to suppose they affected the viability of the egg. Eggs normally seem free from such irregularities, but they do occur at times in other species besides Murres.

The present paper is concerned with the range of values we actually encounter in E, A, and C, and with the fact that the characteristic range is different in different families. This has not escaped the notice of others, and I have mentioned it myself. Thus the tinamous lay eggs that are not only extremely glossy, but are very obviously biconical, and grebes' eggs

246 The Auk, 86: 246–264. April, 1969

are likewise pronouncedly "biconical," which means that they have what I call a "large negative bicone." Nearly all birds have some negative bicone, the exceptions being the hummingbirds, albatrosses, swifts, and cuckoos. The cuckoos are nearly neutral, but the other three families have unequivocal positive bicone, and the hummingbirds have it in an extreme degree. As a rule all species in a family are in rough agreement, and all individuals in a species; it is a genuine family resemblance.

The *Mimidae* are an exception. Mockingbirds, catbirds, and some thrashers lay normal eggs with negative bicone. Other thrashers, and notably the Brown Thrasher (*Toxostoma r. rufum*) of eastern North America, lay eggs with positive bicone. Occasionally an individual bird of a species that lays normal eggs will lay one with positive bicone, and it may be the only egg in the clutch of this type. This looks pathological, or suggests that it may be an adventitious egg from another parent. I remember seeing it only once, in a clutch of the Redwinged Blackbird (*Agelaius phoeniceus*).

Table 1 presents the average values by families of the egg shape-specifiers and the high and low values of North American birds. This table is constructed as follows: for each species or subspecies for which adequate material is available, we take one egg at random from each of 20 clutches, measure its parameters, and compute the shape-specifiers. This was done for some 500 taxa. The taxa were then grouped by families, and the average value of E, A, and C computed. The range given is the range of the species-averages, not the range of the individual eggs.

In Table 2 we condense this information to give, as it were, a picture of the shape of an average North American bird's egg. The averages are averages of the families, not of the species, and similarly the ranges are those of the families. This table considers passerines and nonpasserines separately and then in combination. From this it will be seen that the range, as might be expected, for any shape-specifier among passerines is only about one third that among the rest of the families, and that the range for nonpasserines overlaps the passerine range at both ends. This might mean that the eggs of passerines testify, as the birds themselves do, that they are a compact, more closely-related, group of families than the others.

VARIABILITY OF THE PARAMETERS

The breadth B of the eggs of any species tends to be the most constant parameter: the others follow in the order L, R_B, and R_P. Quite typically the coefficients of variation are of the order 3%, 4%, 7%, and 10% respectively.

No doubt there are physiological reasons for this. If a bird tries to

TABLE 1
SUMMARIZING EGG SHAPES BY FAMILIES

Family	Number of species or subspecies	Elongation average	High/low	Bicone average	High/low	Asymmetry	High/low
Gaviidae	4	1.60	1.63/1.58	—0.050	0.000/—0.092	0.193	0.214/0.155
Colymbidae	6	1.48	1.54/1.43	—0.141	—0.082/—0.173	0.117	0.144/0.058
Diomedeidae	2	1.58	1.59/1.58	+0.100	+0.120/+0.080	0.192	0.205/0.180
Procellariidae	8	1.48	1.56/1.44	—0.021	+0.022/—0.110	0.252	0.342/0.180
Hydrobatidae	9	1.34	1.40/1.29	—0.004	+0.026/—0.034	0.114	0.264/0.070
Phaethontidae	3	1.41	1.44/1.40	—0.052	0.000/—0.087	0.228	0.240/0.213
Pelecanidae	3	1.53	1.55/1.50	—0.114	—0.098/—0.136	0.170	0.203/0.116
Sulidae	5	1.50	1.62/1.44	—0.078	—0.010/—0.123	0.114	0.173/0.058
Phalacrocoracidae	9	1.60	1.64/1.57	—0.078	—0.042/—0.125	0.178	0.189/0.172
Anhingidae	1	1.51	1.51/1.51	—0.085	—0.085/—0.085	0.171	0.171/0.171
Fregatidae	1	1.48	1.48/1.48	—0.068	—0.068/—0.068	0.180	0.180/0.180
Ardeidae	19	1.37	1.43/1.30	—0.101	—0.027/—0.146	0.068	0.095/0.039
Ciconiidae	1	1.46	1.46/1.46	—0.012	—0.012/—0.012	0.122	0.122/0.122
Threskiornithidae	5	1.45	1.49/1.42	—0.037	—0.020/—0.054	0.143	0.166/0.125
Phoenicopteridae	1	1.64	1.64/1.64	—0.132	—0.132/—0.132	0.191	0.191/0.191
Anatidae	41	1.41	1.54/1.23	—0.046	+0.021/—0.100	0.137	0.216/0.082
Cathartidae	2	1.46	1.48/1.45	—0.082	—0.064/—0.100	0.149	0.157/0.141
Accipitridae	27	1.26	1.32/1.22	—0.067	—0.023/—0.110	0.127	0.190/0.100
Pandionidae	1	1.32	1.32/1.32	—0.090	—0.090/—0.090	0.130	0.130/0.130
Falconidae	11	1.26	1.32/1.21	—0.059	—0.039/—0.120	0.141	0.226/0.106
Cracidae	1	1.42	1.42/1.42	—0.146	—0.146/—0.146	0.162	0.162/0.162
Tetraonidae	6	1.38	1.44/1.32	—0.077	+0.020/—0.114	0.232	0.262/0.202
Phasianidae	6	1.26	1.28/1.24	—0.095	—0.082/—0.113	0.306	0.351/0.166
Meleagrididae	1	1.33	1.33/1.33	—0.120	—0.120/—0.120	0.218	0.218/0.218
Gruidae	2	1.57	1.58/1.56	—0.078	—0.077/—0.079	0.184	0.205/0.164
Aramidae	1	1.37	1.37/1.37	—0.120	—0.120/—0.120	0.082	0.082/0.082
Rallidae	11	1.39	1.47/1.30	—0.076	—0.037/—0.102	0.136	0.230/0.078
Haematopodidae	2	1.40	1.44/1.36	—0.133	—0.112/—0.154	0.209	0.214/0.204
Charadriidae	14	1.39	1.46/1.31	—0.117	—0.075/—0.171	0.333	0.425/0.244
Scolopacidae	22	1.40	1.44/1.31	—0.098	—0.068/—0.152	0.360	0.436/0.231
Recurvirostridae	2	1.44	1.47/1.42	—0.132	—0.150/—0.114	0.326	0.376/0.275

TABLE 1—*Continued*

Family	Number of species or subspecies	Elongation average	High/low	Bicone average	High/low	Asymmetry	High/low
Phalaropodidae	3	1.41	1.42/1.40	—0.077	—0.037/—0.100	0.351	0.364/0.332
Stercorariidae	3	1.41	1.42/1.40	—0.130	—0.110/—0.156	0.293	0.321/0.247
Lariidae	33	1.40	1.46/1.33	—0.088	—0.000/—0.150	0.264	0.322/0.204
Rynchopidae	1	1.34	1.34/1.34	—0.170	—0.170/—0.170	0.227	0.227/0.227
Alcidae	19	1.49	1.67/1.36	—0.020	+0.033/—0.075	0.264	0.381/0.140
Columbidae	4	1.35	1.36/1.33	—0.030	—0.010/—0.046	0.076	0.117/0.027
Cuculidae	4	1.30	1.33/1.29	+0.020	+0.035/—0.025	0.072	0.118/0.052
Tytonidae	1	1.30	1.30/1.30	—0.053	—0.053/—0.053	0.159	0.159/0.159
Strigidae	13	1.19	1.25/1.16	—0.060	—0.033/—0.104	0.068	0.102/0.044
Caprimulgidae	7	1.36	1.39/1.34	—0.006	+0.059/—0.065	0.087	0.105/0.068
Trochilidae	3	1.48	1.49/1.47	+0.250	+0.262/+0.240	0.019	0.028/0.012
Alcedinidae	1	1.26	1.26/1.26	—0.088	—0.088/—0.088	0.095	0.095/0.095
Picidae	9	1.31	1.36/1.27	—0.073	+0.018/—0.135	0.132	0.166/0.088
Tyrannidae	18	1.31	1.38/1.27	—0.085	—0.046/—0.115	0.166	0.199/0.128
Alaudidae	1	1.37	1.37/1.37	—0.035	—0.035/—0.035	0.171	0.171/0.171
Hirundinidae	7	1.41	1.45/1.38	—0.029	—0.010/—0.057	0.197	0.250/0.166
Corvidae	18	1.39	1.50/1.33	—0.089	—0.130/—0.058	0.184	0.232/0.136
Paridae	5	1.32	1.39/1.26	—0.029	+0.028/—0.089	0.118	0.166/0.070
Troglodytidae	8	1.30	1.40/1.24	—0.043	—0.010/—0.140	0.133	0.177/0.100
Mimidae	11	1.36	1.43/1.33	—0.010	+0.035/—0.046	0.138	0.156/0.102
Turdidae	8	1.33	1.38/1.28	—0.066	—0.030/—0.096	0.130	0.152/0.096
Sylviidae	2	1.28	1.30/1.26	—0.020	—0.008/—0.031	0.144	0.147/0.142
Motacillidae	1	1.34	1.34/1.34	—0.044	—0.044/—0.044	0.170	0.170/0.170
Bombycillidae	1	1.40	1.40/1.40	—0.008	—0.008/—0.008	0.213	0.213/0.213
Laniidae	1	1.33	1.33/1.33	—0.060	—0.060/—0.060	0.155	0.155/0.155
Sturnidae	1	1.41	1.41/1.41	—0.031	—0.031/—0.031	0.168	0.168/0.168
Vireonidae	4	1.36	1.38/1.35	—0.028	—0.005/—0.055	0.190	0.204/0.174
Parulidae	22	1.30	1.37/1.25	—0.038	—0.001/—0.075	0.154	0.213/0.115
Ploceidae	1	1.40	1.40/1.40	—0.005	—0.005/—0.005	0.157	0.157/0.157
Icteridae	19	1.38	1.48/1.29	—0.056	—0.020/—0.089	0.153	0.207/0.091
Thraupidae	2	1.38	1.39/1.38	—0.020	+0.008/—0.047	0.182	0.198/0.166
Fringillidae	43	1.32	1.41/1.26	—0.037	+0.025/—0.103	0.157	0.213/0.093

TABLE 2

SHAPE AVERAGES BY FAMILIES

	Families	Elongation	Range of family averages	Bicone	Range	Asymmetry	Range	Taxa	Taxa/Family
Nonpasserines	44	1.41	1.19–1.64	—0.066	—0.146–+0.250	0.176	0.068–0.360	328	7.5
Passerines	19	1.35	1.28–1.41	—0.038	—0.085–—0.008	0.162	0.118–0.213	172	9
All families	63	1.39	1.19–1.64	—0.058	—0.146–+0.250	0.172	0.068–0.360	500	8

develop too broad an egg, it may be unable to pass it, become egg-bound and die. But a domestic fowl can lay a double-yolked egg and survive, though the egg will perish. Such an egg is about normal in diameter but is much longer than normal. I once had the shell of a Laughing Gull (*Larus atricilla*) from Stone Harbor, New Jersey, that looked as if it might have been double-yolked, but unfortunately it had been blown before I received it. This is the only example of apparently double-yolked egg I have seen among wild birds. Abnormally small eggs are less uncommon in collections, and I have seen at least two eggs of the Ostrich (*Struthio cämelus*) and at least two of the Western Gull (*Larus occidentalis*) that were only about two thirds the size of normal eggs. They were, however, all of essentially normal shape.

CONSERVATION OF SHAPE OR VOLUME

This brings us to the question whether, when a bird lays eggs within the normal range of sizes, it conserves shape or volume more accurately. If the former, then length will increase with breadth; if the latter, length will decrease as breadth increases.

By an analysis of covariance on 286 eggs of 12 species, 1 egg per clutch, we find a positive correlation of about 0.27, which is significant at about the 0.001 level. The bird is trying, as it were, to conserve shape rather than volume, even among normal-appearing eggs. None of the 12 species were passerines.

In another test of 461 eggs of 8 species, using eggs from 211 clutches and generally all the eggs of each clutch, the average variation of the elongation E was 4.28%, varying from species to species from ±3.2% to ±6.5%. In the same test, the variation in B was ±3.15% and in L was ±3.58%, so that E was scarcely more variable than B or L. The most variable species was the Ring-billed Gull (*Larus delawarensis*). Of the 8 species, one was passerine, viz. the House Wren (*Troglodytes aëdon*), 62 eggs from 11 clutches.

STATISTICAL DISTRIBUTION OF THE SHAPE PARAMETERS: THE HISTOGRAMS

In 63 of the families of birds that are regarded as in some sense North American, though not all breed there, we have found that the ranges of the parameters are as follows:

Asymmetry	0.02	(hummingbirds) to 0.36 (snipe and sandpipers, *Scolopacidae*) with an average for all families of 0.17.
Bicone	–0.17	(skimmers: this is also the value of the extra-limital tinamous) to +0.25 or higher (hummingbirds). Average –0.06.
Elongation	1.19	(owls of the family *Strigidae*) to 1.64 (flamingos, *Phoenicopteridae*). Average 1.39.

Table 2 breaks this down into passerines and nonpasserines, since the 19 families among the passerines are, as judged by their eggs and by other criteria, less diverse than the 44 nonpasserine families.

In Figure 1 we plot the distributions of asymmetry, bicone, and elongation as histograms.

The asymmetry plots to a fair approximation to a normal or Gaussian distribution. It might be argued that the approximation would be even closer if the four families that comprise the last interval to the right (0.32 to 0.36) were omitted. These do hint at a trace of bimodality, as a purely mathematical matter, and the point is emphasized by the biological fact that the four families are all closely related, being the Charadriidae, Scolopacidae, Recurvirostridae, and Phalaropodidae, a compact group within the Charadriiformes. The other North American Charadriiformes do not show this phenomenon. Those that do show it have nidifugous young, nest solitarily, lay rather large eggs in proportion to the size of the bird, and with rare exceptions lay precisely four eggs to the clutch, which the parent arranges in the form of a cross, pointed ends inwards, so that they form a compact group. It is generally assumed that the bird can thus cover all eggs effectively in spite of their rather large size and large number, and that the sharp taper or asymmetry is necessary for this.

The other families of the Charadriiformes, the auks, gulls, terns, and skimmers, generally lay one, two, or three eggs, commonly nest colonially, and have nidicolous young.

Thus it seems likely that the slight bump on the tail of the histogram is not a mere curiosity or accident but corresponds to a biological phenomenon of some importance.

The histogram of the bicone shows a very different distribution. It might be regarded as a very skew distribution, but it is difficult to force

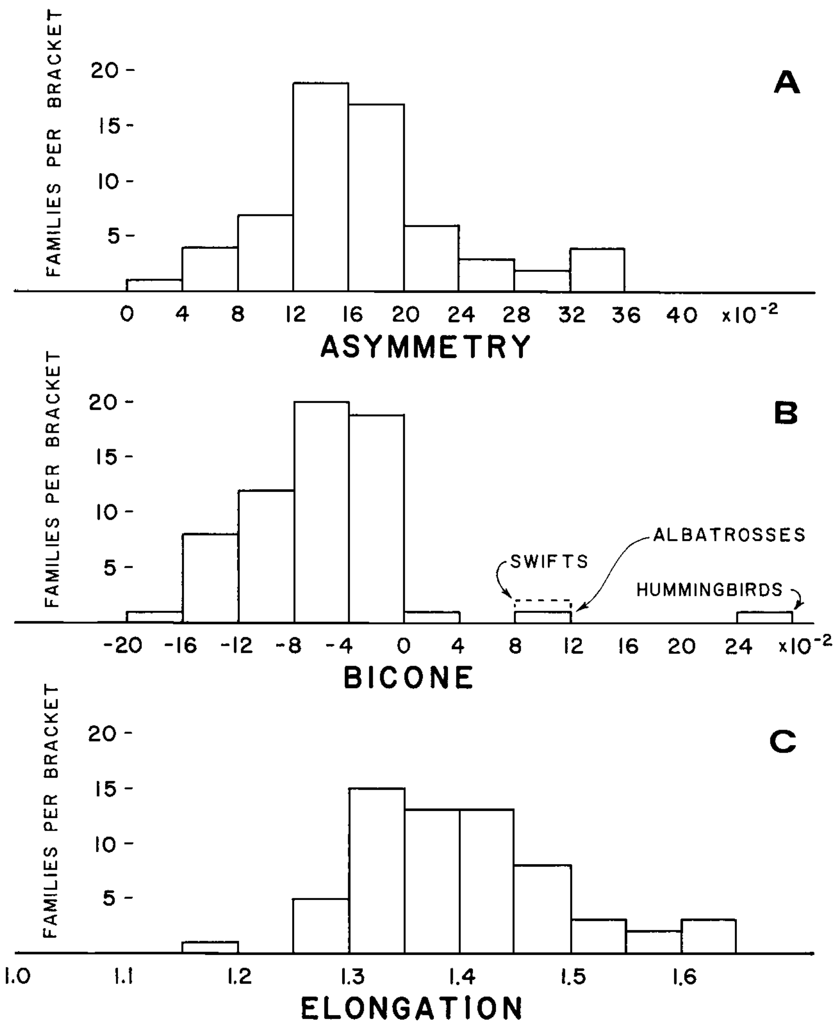

Figure 1. A. Distribution of asymmetry by families; 63 families are involved, mixed passerines (19) and nonpasserines (44). B. Distribution of bicone by families; this is clearly not a Gaussian distribution. C. Distribution of elongation by families; this is a skewed distribution and perhaps slightly bimodal.

it into such a mold. It shows that the vast majority of North American families have negative bicone, and that the distribution is cut off sharply at zero bicone. On the positive side of the cutoff are 3 out of 63 families, viz. cuckoos, albatrosses, and hummingbirds. The cuckoos, with bicone of +0.020, are only just on the positive side, and a more extensive collection of extra-limital cuckoos might move the family to the zero mark or beyond it to the negative side. This is surmise. It is unlikely that this would be the case with the albatrosses (bicone +0.100), and perhaps it would not with the swifts, as indicated by the broken line above the albatrosses in Figure 1B. (The swifts were not one of the 63 families; they make the 64th. Originally we were unwilling to measure many swift eggs, since they seemed so fragile. Our caution was really unnecessary, but we have fewer swift eggs than we should like.) The hummingbirds far out to the right appear completely anomalous, and a survey of more species might move the family much farther to the right.

The histogram creates the impression that negative bicone has, for some reason, substantial survival value—that there must have been families with positive bicone filling in the great gaps on the right, for it is difficult to believe that sudden mutations could have caused the isolation of the right-hand groups, but extinction has removed the intermediate families. It is possible, of course, that in the Old World, or in the Southern Hemisphere, there may be other families with positive bicone. Indeed the albatrosses and hummingbirds are themselves primarily birds of the Southern Hemisphere, or at least of lands and waters south of the Tropic of Cancer. However it seems more likely that birds with appreciable positive bicone are for the most part extinct. The significance of positive bicone in extant birds is not clear to me. Hummingbirds, swifts, and albatrosses are all marvelous fliers, but they use entirely different methods of flying. Indeed it is difficult to see what the three families have in common, and it might seem that they are merely successful relicts of a much larger unsuccesssful group.

One of my friends is dubious about this interpretation, perhaps rightly, because we know that an individual bird can, and often does, lay eggs of quite different shapes in the clutch-sequence. So it is conceivable that the switch from one shape to another could occur rather suddenly. In the clutch sequence it normally occurs somewhat gradually and is not primarily a matter of bicone but of asymmetry, so we must leave the matter open.

The distribution diagram of elongation, Figure 1C, is apparently skewed. It would appear even more so if the isolated family on the left, owls of the family Strigidae, which has no neighbors in the brackets to right or left, were missing. Once more however the gaps may conceivably be filled in by extant families outside North America, and must have been filled in the past. The figure 1.0 for elongation corresponds to a spherical egg, and the *Strix* owls' eggs may be described as subspherical. The barn owls' eggs are much less so.

In elongation, as in asymmetry, there is a hint of a small anomalous group of three families at the right hand end. Not too much emphasis should be placed on this. The families with elongations of 1.60 or more are loons, cormorants, and flamingos. They are not really isolated, as albatrosses and cranes occur in the next (lower) bracket. Moreover, on the basis of very scanty data on the eggs of the New Zealand kiwis, our three families do not lay the most elongated eggs on earth, for the kiwis fall in the next (higher) bracket. Loons and cormorants each rate 1.60, flamingos 1.64, kiwis 1.68. Buller (1888) reports one kiwi egg 4.3 inches by 2.4, with an elongation of 1.80.

It seems that most of these excessively long eggs belong to birds that lay only one or two eggs to a clutch, but this is not true of cormorants. Once more the reason for long eggs is not entirely clear, and it may be different in different families.

CORRELATIONS: THE SCATTERPLOTS

It may be advisable to ascertain whether any of our three shape-parameters are highly correlated with each other, either positively or negatively, in which case they would not be strictly independent variables.

The mathematical contamination.—In the previous paper (Preston, 1968) it was shown that by taking the square roots of R_B and R_P we could separate the factors that affected asymmetry from those that influenced bicone, and so in a purely mathematical or formal sense treat the two as separate matters. This of course would not prevent biological interactions or correlations. Then we proceeded, for sound practical reasons, to abandon the idea of taking square roots, and we used R_B and R_P to the first power. This results, theoretically, in a slight "contamination" of bicone with asymmetry, and vice versa. It is not strictly a matter of correlation, in the orthodox sense of the word, as what we have is a one-to-one correspondence, all points lying accurately on a line, which happens to be a nearly straight line over the range of properties encountered in birds' eggs. Thus we should have a correlation coefficient of ±1.00 if all that were involved were the mathematics. Because the "contamination" is so slight and we are interested only in eggs as we find them, we shall not discuss this matter further. We wish merely to point out that it does exist, though it is trifling.

Elongation and asymmetry.—There is no obvious reason why a very long egg should not be of about the same size at each end. Snake eggs give that impression, but as they do not hold their shape very well it is hard to say. Table 1 may give the impression that long eggs are usually highly unsymmetrical. We can run a correlation test on the 19 families of passerines, which cover a much shorter range of elongation, and we find a correlation of +0.537. This is significant at just about the 1% level.

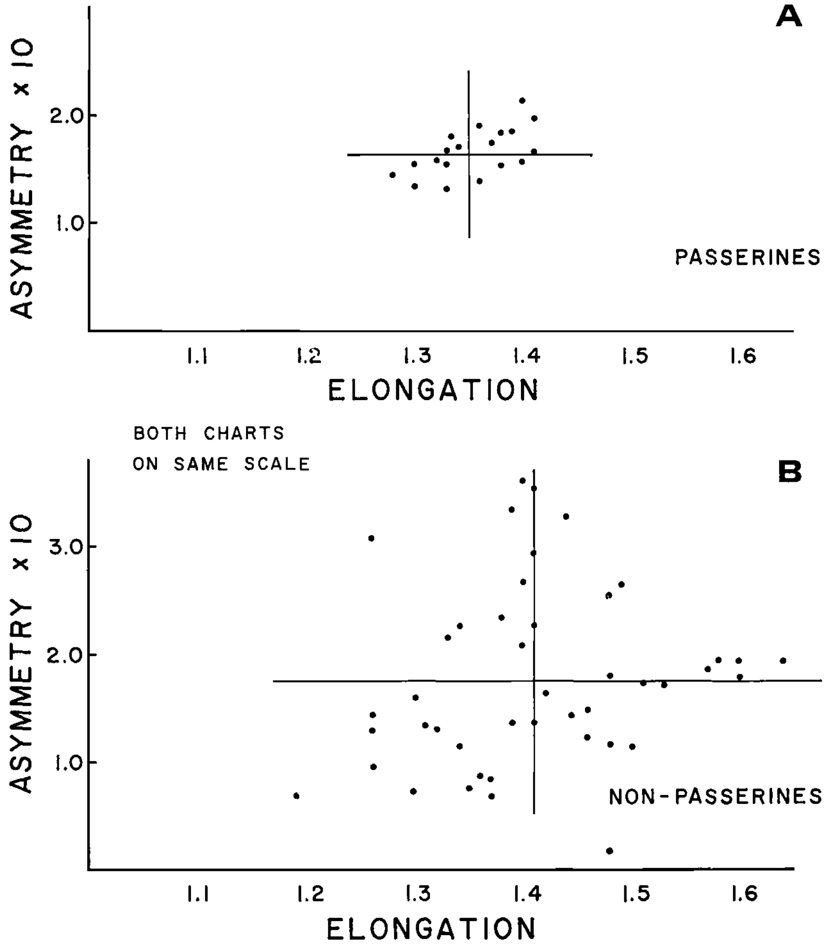

Figure 2. A. Correlation scatterplot, asymmetry vs. elongation for 19 families of passerines; there is clearly a significant positive correlation. B. Correlation scatterplot, asymmetry vs. elongation for 44 families of nonpasserines; no significant correlation.

That is, there is about 1 chance in 100 that a correlation as high as this could occur by accident: 99 times out of 100 it would happen only by some organic connection. When we test the 44 available families of non-passerines, we find a correlation of +0.165, which is not significant even at the 10% level. Thus except in a tightly-knit group of families such as those of the passerines, we must conclude that elongation and asymmetry are completely independent variables. Figure 2A shows the scatterplot for the passerines, from which it is easy to see that a positive correlation

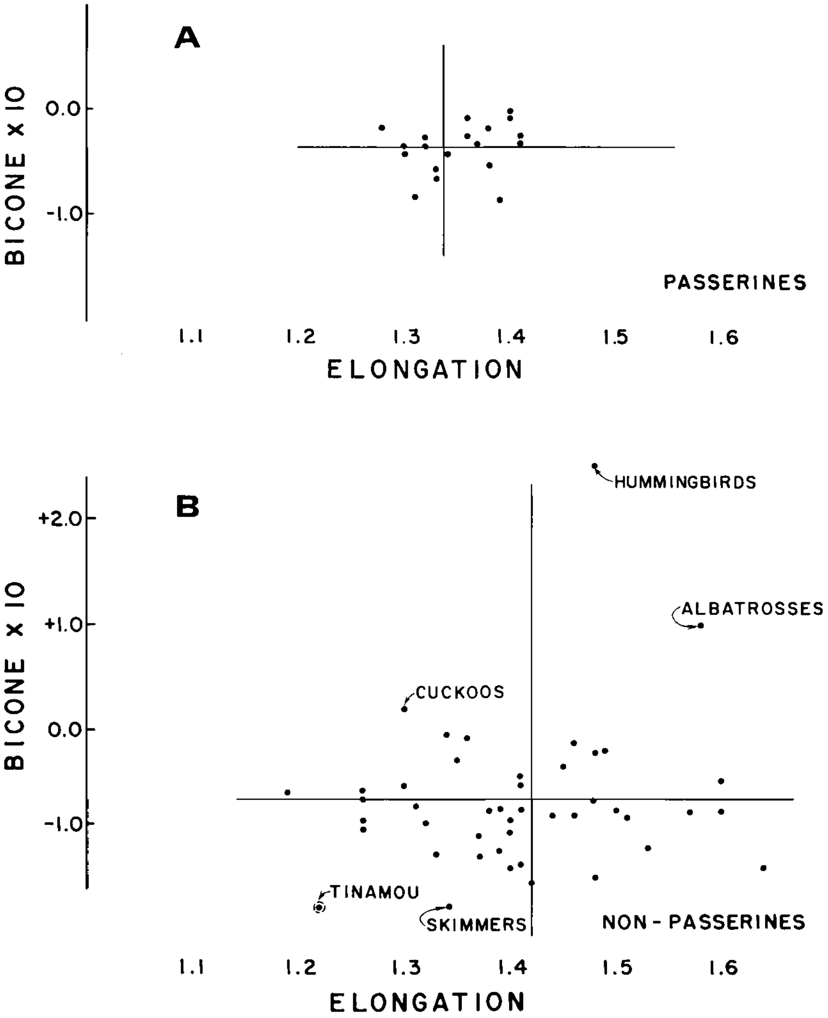

Figure 3. A. Correlation scatterplot, bicone vs. elongation for 19 families of passerines; no significant correlation. B. Correlation scatterplot, bicone vs. elongation for 44 families of nonpasserines. This, like the histogram (Figure 1B) emphasizes the outlying position of the hummingbirds; in their absence there is no significant correlation. The position of the tinamous is indicated, though it is not one of the 44 families.

does exist. Figure 2B does the same for nonpasserines and the correlation is obviously slight or absent.

Elongation and bicone.—The correlation between these two quantities for 19 families of passerines comes out as –0.329, which is not significant

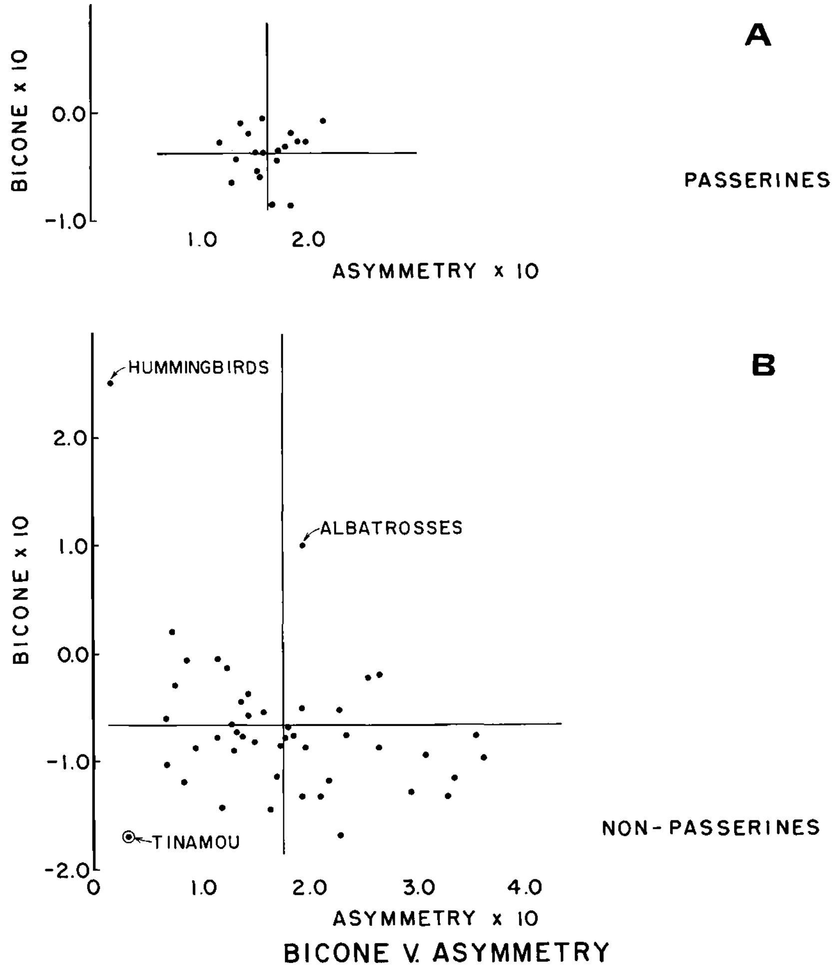

Figure 4. A. Correlation scatterplot, bicone vs. asymmetry for 19 families of passerines; no significant correlation and very little scatter. B. Correlation scatterplot, bicone vs. asymmetry for 44 families of nonpasserines; this again stresses the outlying position of the hummingbirds. The position of the tinamous is indicated.

even at the 10% level (see also Figure 3A). Similarly the correlation for 44 families of nonpasserines is +0.122 which is far below significance at the 10% level (see Figure 3B). It looks as though bicone is not well correlated with elongation.

Bicone and asymmetry.—For passerines the correlation comes out at -0.031. This is virtually zero and quite insignificant (Figure 4A). For nonpasserines it is -0.391, which is theoretically significant at the 1%

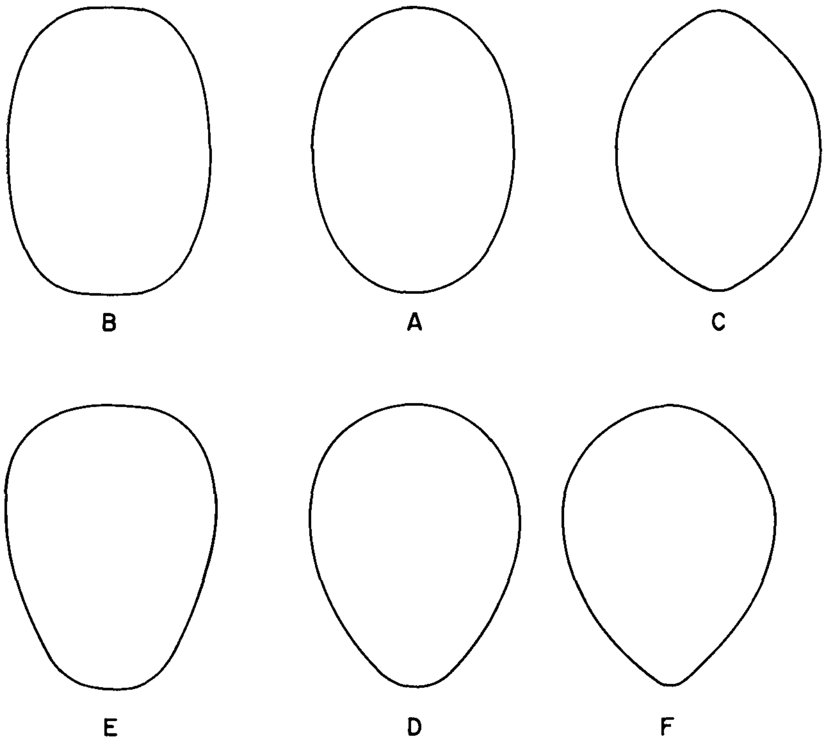

Figure 5. All outlines have an elongation of 1.4. A. Basic ellipse; no asymmetry, no bicone. $y = 1.4 \sin \theta$: $x = \cos \theta$. B. Positive bicone; no asymmetry. $y = 1.4 \sin \theta$: $x = \cos \theta \ (1 + \frac{1}{2} \sin^4 \theta)$. C. Negative bicone; no asymmetry. $y = 1.4 \sin \theta$: $x = \cos \theta \ (1 - \frac{1}{2} \sin^4 \theta)$. D. Asymmetry only; no bicone. $y = 1.4 \sin \theta$: $x = \cos \theta \ (1 - \frac{1}{4} \sin \theta)$. E. Asymmetry and positive bicone. $y = 1.4 \sin \theta$: $x = \cos \theta \ (1 + \frac{1}{4} \sin \theta + \frac{1}{2} \sin^4 \theta)$. F. Asymmetry and negative bicone. $y = 1.4 \sin \theta$: $x = \cos \theta \ (1 + \frac{1}{4} \sin \theta - \frac{1}{2} \sin^4 \theta)$. In most cases the phenomena are exaggerated beyond what we find in normal bird eggs to make them immediately conspicuous.

level. However when we examine the scatterplot, Figure 4B, we see the extreme isolation of the hummingbirds, and readily suspect that this one family has a quite disproportionate influence on the correlation coefficient. If we omit this family and retain the other 43, the correlation falls to -0.271, which is significant at the 10% level, but not much more. This confirms our suspicions. We can carry the argument a little further. The hummingbirds and the tinamous are both Neotropical families. A few species of hummingbirds reach the United States; no tinamous do. The hummingbirds have an extreme positive bicone; the tinamous have a very high negative bicone, though by no means so extreme as the hummingbirds'

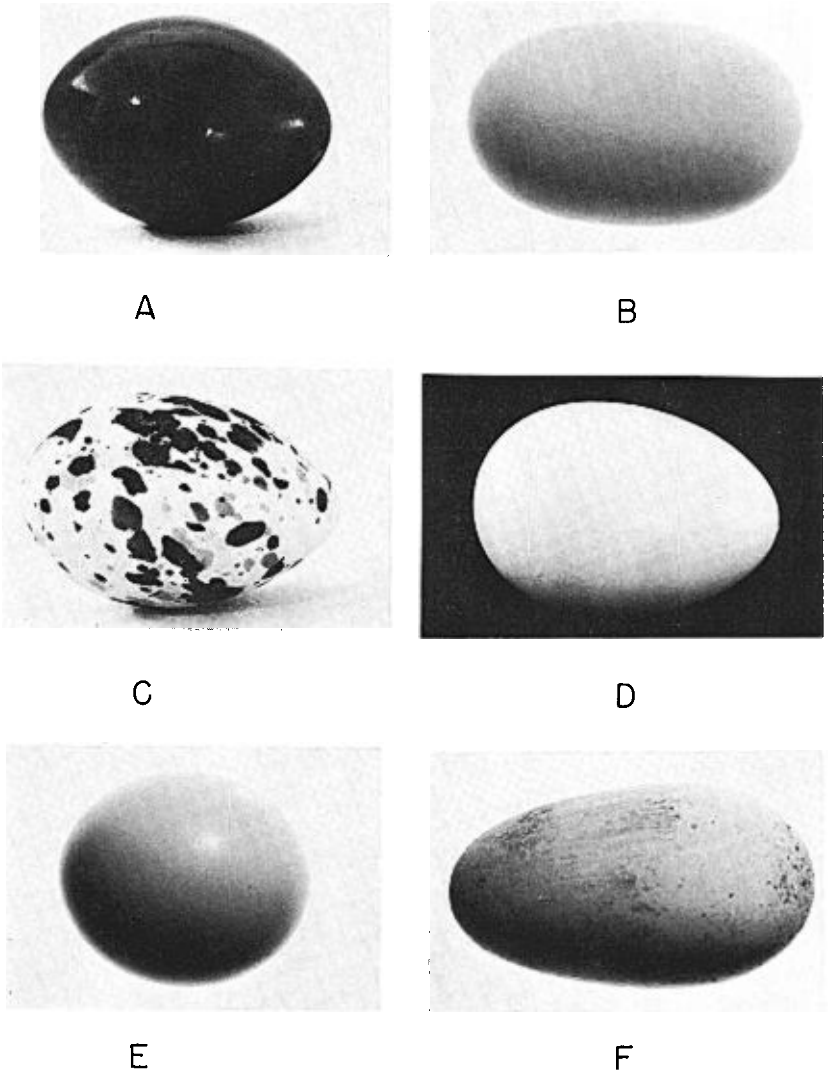

Figure 6. A. Tinamu *Nothocercus* sp.; very pronounced negative bicone, very little asymmetry. B. Hummingbird, *Stellula calliope*; very pronounced positive bicone, very little asymmetry. C. Skimmer, *Rhynchops nigra*; negative bicone, noticeable asymmetry. D. Swift, *Chaetura pelagica*; positive bicone, noticeable asymmetry, elongation much as in C. E. Owl, *Bubo virginianus*; an egg of minimum elongation, subspherical. F. Albatross, *Diomedea immutabilis*; an egg of near maximum elongation, distinct asymmetry, and pronounced positive bicone. The photographs are enlarged or reduced so that all eggs have very nearly the same maximum breadth (photography by Leo T. Sarnaki; courtesy of Carnegie Museum).

positive one. If it had happened that the tinamous had reached the United States and the hummingbirds had not, the correlation coefficient we should have found would be about –0.224, which is not significant even at the 10% level.

Thus our considered conclusion must be that, so far as their eggs are concerned, hummingbirds do not belong in the general comity of bird families. In more mathematical language, they are not part of the same Gaussian distribution of bicone, but are a separate subpopulation, a sort of island universe on their own. The albatrosses are perhaps another island universe in respect of bicone, but are very average in respect to asymmetry. The hummingbirds are peripheral in respect to asymmetry, while the tinamous, though they do not constitute an island universe, are peripheral in respect to both asymmetry and bicone.

The broadest conclusion is that all three shape-specifiers are completely independent variables, and that birds use them in all possible combinations. Thus the shape of an egg cannot be given with less than the three specifiers.

Figure 5 shows diagrammatically the shapes that eggs might take with rather extreme values of bicone, while elongation is kept constant. Figure 6 (plate) shows six examples from "life," the breadth being adjusted to be the same in all cases. In one pair we show positive and negative bicone, in the absence of appreciable asymmetry; another pair shows it in the presence of asymmetry; the third pair shows near minimum and maximum elongation.

THE EGGS OF OTHER VERTEBRATES

Most vertebrates lay eggs, most fishes, all amphibians, most reptiles, all birds, and a few mammals. We are concerned only with those whose eggs are encapsulated or shelled to the extent of being rigid or substantially permanent in shape. This restricts us to some of the reptiles, the birds, and the Monotremata.

Just as the nonpasserine families expand the range of elongation of the passerines, so the reptiles greatly extend the range beyond that of birds. Indeed the Chelonia, the turtles and tortoises, do this without any assistance from other reptiles.

Examination of 22 species of hard-shelled eggs in Carnegie Museum, Pittsburgh, plus a larger number of soft-shelled ones, shows that no species of snake, crocodilian, or chelonian in the collection lays asymmetrical eggs; there is no large or small end. (One small lizard (*Anolis carolinensis*) seems sometimes to lay slightly asymmetric eggs.) Moreover all eggs seemed to have positive bicone; the ends were blunter than those of a true ellipse. This is the opposite of the normal condition of birds' eggs. This at any rate was true of the elongated eggs; with the nearly spherical eggs that some chelonians lay, it was not possible for me to judge.

I measured only one egg of each species (in many cases this was all that was available) and measured only length and breadth and calculated the elongation, with these results:

Snakes:	Indian Python (Ceylon) *Python molurus*	E = 1.48
	Keeled Green Snake (Florida) *Opheodrys aestivus*	2.42
	Rainbow Snake (Florida) *Farancia erythrogramma*	1.47
Chelonians:	Black Galapagos Tortoise (S. Albemarle Island) *Geochelone e. elephantopus*	1.04
	Gopher Turtle (Florida) *Gopherus polyphemus*	1.42
	Elegant Tortoise (India) *Geochelone elegans*	1.42
	Radiated Tortoise (Madagascar) *Geochelone radiata*	1.06
	Leopard Tortoise (Africa S. of Equator) *Geochelone pardalis*	1.06
	Indian Saw-back Turtle *Kachuga kachuga*	1.57
	European Land Tortoise *Testudo graeca*	1.19
	Muhlenberg's Turtle (Eastern U.S.) *Clemmys muhlenbergi*	2.17
Crocodilians:	American Alligator (Florida) *Alligator mississipiensis*	1.78
	American Crocodile (Jamaica) *Crocodylus acutus*	1.48

From this it appears that a number of species have elongations comparable with those of passerine birds, roughly 1.4–1.5. Others have elongations within the range of birds generally, 1.2 to 1.7, but some overstep these limits at both ends 1.04 to 2.42. The chelonians are remarkable for ranging from nearly spherical (1.04) to very elongated 2.17, extending far beyond the limits of birds' eggs at both ends of the range.

Birds' eggs are apparently unique among those of vertebrates in having, typically, pronounced asymmetry and, also typically, pronounced negative, not positive, bicone. The reasons for this are not at present clear, nor how it arose.

The Australian monotremes lay eggs that are not strictly rigid. *Platypus* lays two twin eggs seriatim, then glues them together side by side. Burrell (1927) describes the eggs as ellipsoidal in shape and his pictures indicate that they are subspherical. His measurements (p. 180) indicate an elongation of about 1.13 to 1.20, somewhat stubbier than birds'. There is no clear evidence of asymmetry or bicone. Another description, sent me by K. Doutt of Carnegie Museum, agrees with this.

On *Echidna* I have no satisfactory information. In a somewhat popular work I have seen pictures that would indicate a measure of asymmetry, and the embryo is shown with its head in the small end of the egg. I am not sure how authentic either feature may be.

COMPUTER ANALYSIS OF EGG SILHOUETTES

In this paper numerical results are those obtained by measuring and curvatures. This is vastly less time consuming than the method of intercepts (Preston, 1953), but nonetheless it is extremely tedious and slow. With the development of modern computers and their accessories it is entirely possible that automated intercept-sensing and reduction of observations by computer to give all the shape parameters would eliminate all the tedium and most of the chances for error. The time involved would be simply that of placing the egg, once only, in the proper position, and the apparatus would do all the rest almost instantly. Thus vastly more eggs could be measured, if they were available, and the statistics would be more complete and trustworthy. Clearly a number of methods and devices could be used. I mention the matter because it is just possible that some day it may seem worthwhile to understand egg shapes more completely, and the deterrent may be the immense amount of manual work at present needed.

It may, of course, be said with some justice that the immense number of measurements we have already collected could be treated better by more elaborate statistical methods. We could for instance partition the total variance of each shape parameter into certain logical fractions, for instance the intraspecific variance, the interspecific intrafamily varance, and the interfamily variance, and the unaccounted for residue. Part of the last item is likely to be the intraclutch variance, as we have seen earlier (Preston and Preston, 1953; Gemperle and Preston, 1953) that all eggs of a clutch are not alike in shape. But having established in this earlier work that this variation is not random but proceeds in a predictable way from first to last egg of a clutch, we are already farther ahead than we should be by treating it as a random variable.

Similarly I think we do well in the present paper to discuss the properties of individual families by name, and not just treat them as a random collection of families. This pinpoints the families whose properties most need explaining in terms of anatomy, physiology, or behavior. We are more interested in locating biological problems and in answering them than in mathematical elegance, and I have felt it best to employ only simple correlations and not multiple ones. Clearly the full mathematical treatment would require a high-speed electronic computer. It does not follow that nothing useful would come of more ambitious treatments, or indeed of equally simple, but different, treatments. I think the present paper says enough to indicate that many unsolved problems exist. Species and families not represented in North America may be one of the more promising sources of information.

Literature Cited

Buller, W. L. 1888. A history of the birds of New Zealand. London, published by the author.

Burrell, H. 1927. The platypus. Sidney, New South Wales, Angus and Robertson Ltd.

Gemperle, M. E., and F. W. Preston. 1955. Variation of shape in the eggs of the Common Tern in the clutch-sequence. Auk, 72: 184–198.

Palmer, R. S. 1962. Handbook of North American birds, vol. 1. New Haven, Connecticut, Yale Univ. Press.

Preston, F. W. 1953. The shapes of birds' eggs. Auk, 70: 160–182.

Preston, F. W. 1968. The shapes of birds' eggs: mathematical aspects. Auk, 85: 454-463.

Preston, F. W., and E. J. Preston. 1953. Variation of birds' eggs within the clutch. Ann. Carnegie Mus., 33: 129–139.

A Note on Kiwi and Megapode Eggs

Since this paper was written and accepted for publication, I was able to visit the British Natural Hitory Museum in London, which has a significant collection of Kiwi (Apteryx) eggs. Some of these were laid in captivity and some are incomplete as to data. Some date back to the 1860s and are therefore more than 100 years old. They are comparable in size with Emu (*Dromaeus novae-hollandiae*) eggs, the product of a much larger bird, but the shells are white, rather smooth, and distinctly thin. They are more elongated than most ratite eggs, but very variable both in elongation and in the other aspects of shape, asymmetry, and bicone, generally pronouncedly positive in the latter. Three species are recognized, *A. oweni*, *A. haasti*, and *A. australis*, the last in three subspecies, *A. a. australis*, *A. a. mantelli*, and *A. a. lawryi*. C. J. O. Harrison has kindly measured for me the length and breadth of all measurable specimens, and from these measurements I obtain the following estimates of elongation:

A. oweni.	Av. of 15 eggs, 1.62 (max. 1.80, min. 1.49)
A. haasti.	Av. of 2 eggs, 1.64
A. a. australis.	1 egg, 1.49
A. a. mantelli.	Av. of 14 eggs laid in the wild, 1.62 (max. 1.84, min. 1.43)
	Av. of 7 eggs laid in captivity, 1.62 (max. 1.84, min. 1.49)
A. a. lawryi.	Av. of 3 eggs, 1.69 (max. 1.75, min. 1.64)

For comparison note that our present data on flamingos gives 1.64, and of loons and cormorants each 1.60.

Mr. Harrison, on his own initiative, also measured 10 eggs of another southern hemisphere bird, *Megapodius pritchardi* from Polynesia. The average elongation was 1.73, maximum 1.87, minimum 1.65, so these are more elongated than even Kiwi eggs. The megapode eggs, Mr. Harrison comments, are generally strikingly lacking in asymmetry, "there being little immediate indication of the 'larger end'." The eggs in fact look distinctly reptilian.

I am indebted also to Mr. Harrison for a few measurements of swift and hummingbird eggs: one egg of *Apus melba,* elongation 1.71, two of *A. murinus* averaging 1.67, and one of *Patagona gigas* 1.75. These are not statistically valid samples, but suggest that there may be other species, and possibly genera or families, that lay exceptionally elongated eggs.

Box 49, Meridian Station, Butler, Pennsylvania 16001.